



# Fish and crab coprolites from the latest Triassic of the UK: From Buckland to the Mesozoic Marine Revolution

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## ABSTRACT

Coprolites from the Rhaetian bone beds in south-west England can be assigned to crustaceans and fishes. Here, we report crustacean microcoprolites, including *Canalispalliatum* and *Favreina*, the first records from the British Rhaetian, from Hampstead Farm Quarry near Bristol, evidence for diverse lobsters and their relatives not otherwise represented by body fossils. Further, we identify five fish coprolite morphotypes that differ in shape (cylindrical, flattened) and in presence or absence of a spiral internal structure. Many coprolites show bony inclusions on the surface, often relatively large in proportion to the coprolite; these show little or no evidence for acid damage, suggesting that the predators did not have the physiological adaptations of many modern predatory fishes and reptiles to dissolve bones. CT scanning has revealed the nature, packing and identity of inclusions within the coprolites, mainly fish scales, and some coprolites can contain more than twenty. An extraordinary discovery in one coprolite comprises a single sculptured skull element of the large bony fish *Severnichthys* together with two caudal vertebrae of the marine reptile *Pachystropheus*: did the coprolite producer, likely a fish, scavenge some flesh from the head of *Severnichthys* and then bite off the tail of the reptile? Assigning coprolites to producers is difficult, but it seems that *Gyrolepis* was preyed on by nearly every predator. The faunas and trophic relations revealed by the coprolites show that this was a modern-style marine ecosystem, with abundant crustaceans and several species of durophagous fishes, evidence for an early stage in the Mesozoic Marine Revolution.

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## 1. Introduction

Coprolites, fossilized faeces, have been reported for over 200 years, and indeed those from the marine reptiles and fishes of the British Mesozoic featured in classic early researches by luminaries such as William Buckland (Buckland, 1829a; Duffin, 2009, 2012b). Although Buckland coined the term 'coprolite' in that 1829 paper, the first report of a vertebrate coprolite had been written much earlier, by Edward Lhwyd in 1570 (Duffin, 2012a).

Coprolites are fossilized faeces, and they are regarded as trace fossils (ichnofossils), together with tracks, trails and burrows, because they record behaviour. Most coprolites have their original organic matter replaced by minerals, but elements of digested food may remain. Coprolites can provide unique insights into otherwise

largely inaccessible aspects of the palaeoecology of ancient ecosystems, and provide direct evidence of trophic relationships. Their morphologies may preserve information concerning the structure of the gut of their producers. Further, inclusions within the faecal groundmass of the coprolite represent either partially digested or undigested food components which, in turn, reflect aspects of feeding and diet including prey-selection behaviour, the means of food ingestion and processing, mechanical and chemical digestion techniques and their associated physiology. While inferences can be made concerning the assignment of coprolites to their producers, unequivocal association is only possible when the faecal material is still within the body cavity of its host (termed a consumulite by Hunt et al., 2012). Indeed, coprolites themselves represent unique taphonomic microenvironments with the potential to act as conservation Lagerstätten in their own right (Qvarnström et al., 2016).

Although relatively rare in the fossil record, when found, vertebrate coprolites can sometimes be remarkably abundant and

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well preserved because of their commonly high phosphatic content (Hunt et al., 2007), and this is especially true in marine bone beds. Here we focus on coprolites from the classic Rhaetian bone beds of SW England, a theme that combines insights into the early work of Buckland, but also our understanding of that time of turmoil, and the general use of coprolites in reconstructing ancient palaeoecology.

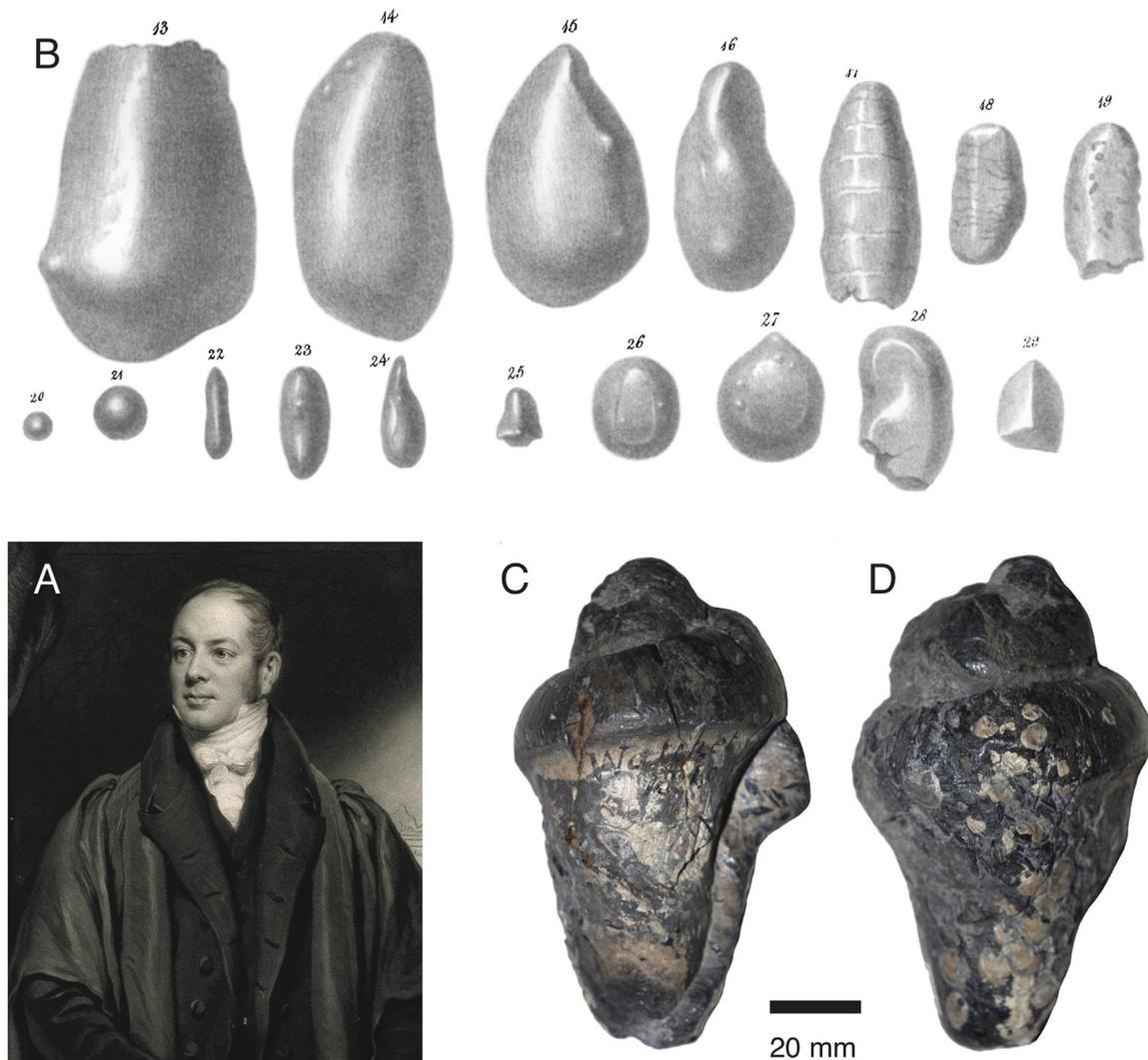
The Rhaetian was the short (4.1 Myr; 205.5–201.4 Ma; Kent et al., 2017) final stratigraphic stage of the Triassic, and famed in Europe for evidence of a major marine transgression that terminated the underlying continental red bed successions and frequently commenced with a bone bed. In the Bristol area, there can be as many as five or six bone beds throughout the Rhaetian, classified as the Penarth Group, and predominantly in the basal Westbury Formation, but sometimes in the lower parts of the overlying Cotham Member of the Lillstock Formation (Swift and Martill, 1999; Allard et al., 2015).

Sepkoski (1984) identified a major changeover in marine faunas from Permian to Triassic, in which 'Paleozoic' ecosystems comprising brachiopods, crinoids, trilobites and graptolites were replaced by 'Modern' ecosystems comprising bivalves,

gastropods, echinoids, malacostracans, and neopterygian fishes. Sepkoski tied this changeover to the devastating effects of the Permian–Triassic mass extinction, and the 'Modern' fauna emerged during the recovery of life in the Triassic (Chen and Benton, 2012). In recent years (e.g. Harper, 2003; Hautmann, 2004; Baumiller et al., 2012), this restructuring of marine ecosystems in the Triassic has been posited as a first step in the Mesozoic marine revolution (Vermeij, 1977), associated with escalations in predator–prey interactions.

The aims of this paper are to explore the diversity of coprolites from the British Rhaetian and to use these to reconstruct a likely food web for the Rhaetian seas and to consider how this reflects novel trophic relations as part of the establishment of the 'Modern' marine ecosystem during the Triassic. We develop the theme of the historical investigation of Rhaetian coprolites first, as this takes us back nearly 200 years to the origin of the discipline, and we reflect on the fact that Buckland and contemporaries were examining the same Rhaetian coprolite specimens we study today.

*Repository abbreviations:* **BRSMG**, Bristol City Museum, Geology Collection; **BRSUG**, University of Bristol Geology Museum; **OXFUM**, Oxford University Museum of Natural History.



**Fig. 1.** William Buckland and his Rhaetian coprolites. (A) 'The Reverend William Buckland D.D., F.R.S., Canon of Christ Church and Professor of Geology and Mineralogy in the University of Oxford, 1833. Painted by Thomas Phillips Esq. R.A. Engraved by Samuel Cousins.' This mezzotint engraving was produced by Molteno & Graves (London), May 20th 1833. Wellcome Collection, London (CC BY 4.0). (B) Rhaetian coprolites as figured by Buckland (1835, pl. 30, figs. 13–29). (C, D) OXFUM J23743, holotype of *Strabelocprospollardi* Hunt, Lucas and Spielmann, 2012 from the Rhaetian of Watchet, Somerset.

## 2. Rhaetian coprolites: history of research

William Buckland (1784–1856; Fig. 1A) read a paper to the Fellows of the Geological Society of London on 6th February 1829 that spanned several topics – the first pterosaur, ‘fossil sepia’ in cephalopods and fossil faeces in ichthyosaurs, all from the Liassic rocks outcropping at Lyme Regis (Buckland, 1829a). Four months later, at the meeting of the Society on May 1st, he revisited the idea of the existence of fossil faeces and recorded that :

“He has also ascertained, by the assistance of Mr. Miller and Dr. Prout, that the small black rounded bodies of various shapes, and having a polished surface, which occur mixt with bones in the lowest strata of the lias on the banks of the Severn, near Bristol, are also of faecal origin:- they appear to be co-extensive with this bone bed, and occur at many and distant localities.” (Buckland, 1829b, p. 142)

Later in the same paper, concerning these and other specimens, he proposed ‘to include them all under the generic name of Coprolite’ (Buckland, 1829b, p. 143). The Rhaetian Stage was not recognised in Britain until the 1850s (Duffin, 2019), so Buckland’s remarks concerning the ‘Lias bone bed’ actually refer to the Rhaetian Bone Bed. The fuller account of his paper was eventually published in the *Transactions of the Geological Society*, dated 1829 but not actually published until 1835. The first word in this account was his newly coined term ‘coprolites’ and he added further detail to the remarks given in the preliminary accounts of his lectures which had appeared in the *Proceedings*. Firstly, he records the presence of these structures, which he termed ‘faecal balls of digested bone,’ in the Rhaetian bone beds at Westbury Garden Cliff, Aust and Watchet, remarking that:

“Mr. Conybeare and myself have described these Coprolites as irregular bodies of various form, usually cylindrical, with rounded ends, some having a black and glossy surface and fracture, others being of a dull brown colour; and have conjectured them to be rolled palates, or rolled fragments of very solid bone: at that time no one suspected that they were bone reduced to the state of faeces.” (Buckland, 1835, p. 227)

Buckland also noted that ‘Mr. Dillwyn has applied to them the name of nigrum graecum, from their resemblance in form to the album graecum of the cave of Kirkdale’ (Buckland 1835, p. 227). The Mr Dillwyn here is Lewis Weston Dillwyn (1778–1855), a porcelain manufacturer who, at various times, served as High Sheriff of Glamorgan, MP for Glamorganshire and Mayor of Swansea. He was also a renowned and published naturalist, and one of his sons married Henry de la Beche’s daughter in 1838.

Buckland described Rhaetian coprolite specimens from the collection of J.S. Miller in typically economical and clear style, stating that, in comparison to the Lyme Regis material, they were:

“much smaller, and differ in the absence of spiral structure, and the rare occurrence of scales or bones in them. Externally they are of a bright glossy black, internally of a dark brown colour; their substance is compact, their fracture splintery, and sometimes conchoidal; their surface often smooth as if they had been polished. They vary in size from that of a small potatoe to a hemp seed: in shape, many of them resemble the subangular concretions found in the human gall-bladder, and in the cavities of a diseased kidney; others are spherical, like sheep’s dung, or cylindrical, like that of rats and mice, with various intermediate varieties of size and form; some are flat like a bean, others polygonal.” (Buckland, 1835, p. 228)

He even speculated about the producers of these Rhaetian coprolites, although his account pre-dates the work of Louis Agassiz who later named many of the Rhaetian fish species (see Cross et al., 2018):

“There is no direct evidence to show from what animals the smaller varieties of these Coprolites have been derived. Many may probably be referred to the small reptiles, and others to the fishes, whose broken and scattered bones, teeth, palates, and spines, are so frequent in the same breccia with themselves: others may possibly be derived from the inhabitants of the Nautili, Ammonites, Belemnites, and other Cephalopodes which abounded at the period of the lias formation.” (Buckland 1835, p. 228)

Briefly referring to records of coprolites from numerous other Rhaetian localities, and figuring 17 specimens (reproduced here in Fig. 1B), Buckland marvels at the geographical extent of the Rhaetian bone bed, sometimes comprising 25 % by volume of coprolites, and accounting for the richness of the deposit by long periods of slow or non-deposition in an area “which must for a long time have been the bottom of an ancient sea, and the receptacle of the faeces and bones of its inhabitants, the cloaca maxima, as it were, of primaeval Gloucestershire” (Buckland, 1835, p. 229). The comment regarding the ‘cloaca maxima’ is an allusion to the main sewer in ancient Rome, constructed around 600 BCE, and used to carry the citizen’s effluent to the River Tiber.

Coprolites were mentioned in numerous papers listing the faunal components of the Rhaetian bone bed and Penarth Group sediments in general from a wide range of localities in subsequent literature. No serious attempt was made to characterise the Rhaetian coprofauna in any way until Duffin (1979), who focused on specimens from the conglomeratic bone bed at Aust Cliff. Duffin recognised four broad morphotypes and discussed the identities of potential producers. In brief, he identified:

Type 1: Large (up to 80 mm long), brown, often tapered, amphipolar spiral coprolites with well-defined internal structure and visible inclusions of fish remains. Producers probably included hybodontiform and neoselachian sharks, and perhaps palaeoniscid chondrosteans.

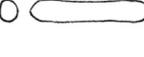
Type 2: Light brown to black, elongate amphipolar and occasional heteropolar spiral coprolites with relatively poorly defined internal structure, measuring up to 30 mm in length and lacking inclusions. Producers may have included the dipnoan *Ceratodus*.

Type 3: Capsule-shaped, non-spiral coprolites lacking inclusions and measuring up to 30 mm long.

Type 4: Flattened non-spiral coprolites lacking inclusions and measuring up to 30 mm across.

The only British Rhaetian coprolite to be designated by a formal taxonomic ichnological binomen is *Strabelocopros pollardi* Hunt, Lucas and Spielmann, 2012. The holotype (OXFUM J23743; Hunt et al., 2012, Fig. 4A–D; Fig. 1C, D) comes from an unrecorded level in the Watchet succession, which also preserves Lower Jurassic rocks. These authors also figure an isolated, un-named coprolite from the Buckland Collection at the OXFUM (Hunt et al., 2012, Fig. 1D). Further information on Buckland’s studies of Rhaetian-age coprolites, and illustrations of more OXFUM specimens are provided by Hunt et al. (2013, Fig. 12).

Recent studies by members of the Palaeobiology Research Group at Bristol University have concentrated on the Rhaetian microvertebrate faunas from a wide range of localities in the West of England, and the coprolite components of the various faunas have been noted (e.g. Korneisel et al., 2015; Nordén et al., 2015; Allard et al., 2015; Lakin et al., 2016; Slater et al., 2016; Mears et al., 2016; Landon et al., 2017; Cavicchini et al., 2018; Cross et al., 2018; Ronan et al., 2020). One locality, Hampstead Farm Quarry, near Chipping Sodbury in Gloucestershire, has yielded a numerically abundant coprofauna. The specimens have the advantage over coprolites from the Aust Cliff bone bed in that they have all been

Morphotype	Morphology	Number of specimens	Length	Inclusions	Scheme
Morphotype A	Cylindrical to sub-cylindrical	249 (A + A1 + A2 + A3 = 383)	2 to 52 mm	Fish scales, fish bones (rare)	
Sub-morphotype A1	Cylindrical with constant diameter and rounded ends	36	5 to 21 mm	Fish scales	
Sub-morphotype A2	Ellipsoidal – Ovoid – anisopolar	62	5 to 30 mm	Fish scales	
Sub-morphotype A3	Cylindrical slightly flattened	36	4 to 23 mm	Fish scales (rare)	
Sub-morphotype A4	Sub-rounded to rounded	49	3 to 18 mm	Fish scales	
Morphotype B	Spiral	132 (B + B1 + B2 = 213)	3 to 37 mm	Reptile vertebrae, fish bones, fish scales (very common)	
Sub-morphotype B1	Spiral Scroll type	61	5 to 22 mm	Fish scales (abundant in specimens)	
Sub-morphotype B2	Spiral amphipolar	20	7 to 34 mm	Fish scales	
Morphotype C	Thin sub-ovoid	110	3 to 31 mm	Fish scales (rare)	
Morphotype D	Irregular in shape	164	3 to 44 mm	Fish scales, fish bones	
Morphotype E	Cylindrical elongate (length > 5 times diameter)	1	31 mm	No	
Morphotype Crustacean	Cylindrical with furrow down one side	19	1 to 2 mm	No	

**Fig. 2.** Summary scheme of the 12 coprolite morphotypes from the Rhaetian bone beds at Hampstead Farm Quarry, Gloucestershire. There are five fish coprolite morphotypes (A–E), some of these subdivided into sub-morphotypes (A1–A4, B1, B2), and a broad category of crustacean coprolites. Summary of morphological characters, size, inclusions, numbers, and sketch outlines in transverse and lateral views.

isolated from the surrounding sediment. This coprofauna can be used to update the classification and discussion given by Duffin (1979) and Swift and Duffin (1999), be subject to modern non-destructive imaging techniques and form the basis for simple statistical analysis with a view to elucidating more of the palaeoecological factors at play during the Late Triassic.

### 3. Materials and methods

The studied coprolites come from two Rhaetian bone bed localities near Bristol, Hampstead Farm Quarry (HFQ) and Aust Cliff. The specimens from Hampstead Farm (National Grid Reference: ST 726840) were collected and donated by Mike Curtis (1950–2008), who was in charge of the Chipping Sodbury quarries for around 20 years (Mears et al., 2016). Coprolites were prepared out of the sediment by Curtis himself, using acid digestion with dilute acetic acid, and sieving the residue to 425  $\mu\text{m}$  (Cross et al., 2018). That huge collection is now maintained between the BRSUG and BRSMG. A few specimens from Aust Cliff (ST 566 898) were added to complete and compare the two localities and to help identify some of the inclusions noted in the Hampstead Farm quarry coprolites. This second collection is also stored in BRSUG and was collected in the 1950s and 1960s (Cross et al., 2018).

In total, 1062 coprolites were studied from HFQ. The Aust Cliff specimens were not included in the quantitative data. All measurements were taken with a ruler to the nearest millimetre by eye: maximum length and width were recorded for all specimens. The length is the distance between the two ends of the coprolite, and the width is the maximum diameter. Other characteristics were recorded: colour, surface sculpture, morphology, breakage and general condition for each coprolite from this locality. Special attention was paid to inclusions within the coprolites, whether identifiable or not.

An example of each morphotype was photographed, and the digital images were then processed using GIMP software to remove backgrounds and adjust colour balance to be as realistic as possible.

We observed inclusions in many of the coprolites, and these were identified by external examination of the specimens. In addition, we CT-scanned three macrocoprolites (BRSMG Cf15467, BRSMG Cf10155 and BRSMG Cf10162) and a few microcoprolites (BRSUG MF60–6i-38) to enable production of a 3D model, showing hidden parts of the inclusions using a non-destructive method. We scanned the coprolite specimens on the Nikon XT H, 225 ST CT scanner in the Palaeobiology Research Group laboratories at the University of Bristol. Scan parameters were set at 170 kV, 76  $\mu\text{A}$ , reflection 225, detector pixel size 0.2 mm, and 3141 projections with one frame per projection. The data files were then imported into Avizo (version 8.0, Visualization Science Group), running on HP Workstations with 72 GB of RAM, using Windows 10.

The study of vertebrate coprolites received an enormous stimulus with the publication of a dedicated volume in 2012, which we follow (Hunt and Lucas, 2012a, 2012b). Hunt and Lucas (2012b) developed a terminology for vertebrate coprolites and related trace fossils, termed collectively as bromalites, 'food items that have entered the oral cavity or gastrointestinal tract of an animal and have been expelled (either orally or rectally and either pre- or post-mortem) from or retained within them' (Hunt and Lucas 2012b, p. 140). Several sub-types were recognised by Hunt and Lucas (2012b) and are relevant to discussion here. Consumulites embrace all trace fossils comprising ingested food and found within the body cavity. Classified according to their position in the body, these include gastrolites (preserved in the stomach), cololites (parts of the gut posterior to the stomach, enterospirae being found in a spiral valvular intestine), intestinulites (preserved in the body cavity) and eviscerulites (in-filled intestinal material

found separate from and outside the body cavity). In its strictest sense, the term coprolite is reserved for faecal material that has been ejected from the posterior end of the gastro-intestinal tract, although the word is generally used informally for any faecal mass found in the fossil record.

### 4. Fish coprolites

#### 4.1. Classification

Coprolites can be classified by the use of informal terms (e.g., 'cylindrical coprolite A') or by the application of a Linnaean parataxonomy, because they are trace fossils. Numerous fish coprolite ichnotaxa have been noted in the Rhaetian-aged sediments of Europe and North America (Hunt and Lucas, 2012a), and yet it was difficult to assign coprolites in our collections to these named morphotypes. Therefore, we establish our own scheme, but do not apply formal ichnotaxon names.

We identify four main categories of coprolite forms involving at least seven morphotypes (some of them with different varieties) in the HFQ collection (Fig. 2), whereas in the Hunt and Lucas (2012a) scheme, there are 27 morphotypes of coprolites in 11 main categories. We divide some morphotypes into varieties or sub-morphotypes because of the great diversity of shapes: morphotype A comprises four sub-morphotypes and morphotype B comprises two sub-morphotypes. The average size of HFQ coprolites is 6.8 mm wide and 11.4 mm long (complete and incomplete specimens).

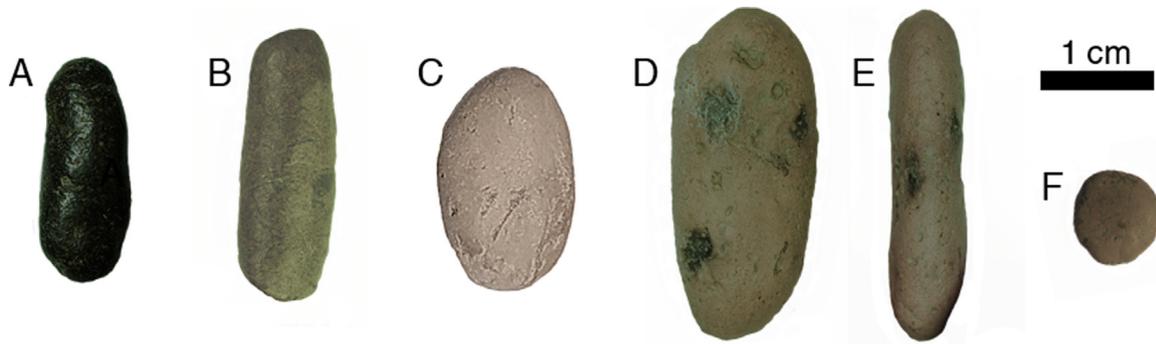
Most vertebrate coprolites are sub-cylindrical (Hunt and Lucas, 2012a), and we find this at HFQ, where around 70 % of coprolites are cylindrical or ellipsoidal. The most represented morphotype at HFQ is A, with almost 41 % of the sample. In spiral coprolites, morphotype B, they may be slightly cone-shaped or lens-shaped. The rest are irregular in shape or too incomplete to be sure, and they are listed as "unknown morphotype". 44 % of the coprolites are incomplete, and 20 % of the complete specimens are irregular in shape.

Because of their nature and preservation, it is difficult to link coprolite ichnotaxa with their producers (Luo et al., 2017; see Discussion). There are many larger coprolites from Aust, but they are almost all incomplete and any inclusions are very rare, making it impossible to use them to help reconstruct a food web.

#### 4.1.1. Morphotype A

Cylindrical to sub-cylindrical in shape and straight to slightly curved, and complete specimens are 2–52 mm long (average 8–12 mm) and 2–26 mm wide (average 5 mm). The external surface of the coprolite possesses occasional longitudinal and transverse striae, but no spiral structure is visible. Some specimens have a "phosphatised skin", presumed to be a consequence of diagenesis (Duffin, 1979), and only visible in transverse sections of incomplete coprolites. Relatively homogenous overall, the coprolitic matrix varies from coarse-grained, resulting in an irregular external surface, to fine grained, giving rise to a smooth surface.

The majority of morphotype A specimens (89 %) are cylindrical (Fig. 3A) while the remaining 11 % are more rounded and sub-cylindrical in shape. A wide range of forms is present, but all are cylindrical in cross-section, which is the basis for assignment to this category. 60 % of the cylindrical coprolites have fewer than five inclusions visible at the surface, almost all of which are scales (unidentifiable inclusions are very few in number). Only 16 % have more than ten inclusions breaking the surface of the coprolite. The nature of the surface is not indicative for this morphotype, with 51 % of the surfaces being irregular and 49 % smooth. Most morphotype A coprolites are light in colour; many are white, but light brown and light grey specimens are also present. Only 7 % are dark coloured. There is apparently no correlation between the



**Fig. 3.** The smooth-surfaced coprolite morphs. (A) Coprolite morph A, BRSMG Cf9630, lateral view, (B) Coprolite morph A1, BRSMG Cf10055, lateral view, (C) Coprolite morph A2, BRSMG Cf10158, lateral view, (D and E) Coprolite morph A3, BRSMG Cf9819, in lateral (D) and longitudinal (E) views, (F) Coprolite morph A4, BRSMG Cf15516, transverse view.

nature of the surface and the colour of the coprolite. The first cylindrical form, here designated sub-morphotype A1 (Fig. 3B), is a classic cylinder with both terminations rounded and convex (isopolar), and a constant diameter along the full length of the specimen. These specimens are quite rare in the collection because only fairly complete, well preserved specimens can be assigned with confidence to this category. Many specimens are incomplete being preserved as short segments of coprolite with an ovoid cross-section; that shape allows them to be classified as sub-morphotype A, but there is the danger that some might be misidentified.

The second type, A2 (Fig. 3C), is more ellipsoidal in lateral view, but still thick, with ends which are less rounded than in A1, or slightly tapered. Most of the specimens are almost cone-shaped with one tapered end (sometimes strongly tapered), while the other end is always rounded and convex (anisopolar).

The third type, A3 (Fig. 3D–E), embraces flattened coprolites, but specimens which are not flat enough to qualify as Morphotype C. Both ends are usually rounded with an ellipsoidal cross-section. These coprolites might have been flattened after extrusion, by compaction during the burial processes. Most of their diameters are around half the size of specimens belonging to morphotypes A1 and A2, and they can be isopolar or anisopolar.

The remainder (11 %) of Morphotype A coprolites (type A4) are round to ovoid forms (Fig. 3F). Complete specimens have lengths from 3 to 18 mm and widths from 3 to 18 mm. The general shape is ovoid, and they have no ends. Some of the specimens are slightly flattened. Many of them are pellet-shaped to spherical in form.

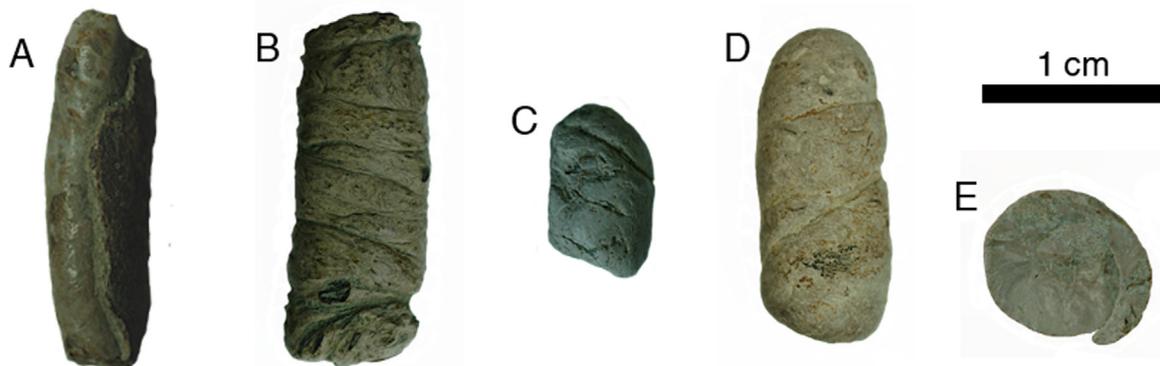
**Discussion.** The absence of spiral structures in Morphotype A coprolites could reflect their true structure, or such structures might have been lost (see Discussion of Morphotype B). Inclusions are quite rare in these coprolites; where absent, the coprolites

could have been produced by durophagous fishes such as *Lepidotes* or more probably *Sargodon tomicus*. This is because durophagous fishes generally ate only invertebrates. Many small fishes could also be potential producers, such as the prey of *Gyrolepis albertii* (Cross et al., 2018). Morphotype A coprolites with included scales usually have just one (95 %), and 62 % of those with scales show fewer than five. This contrasts with the spiral, morphotype B, coprolites, where inclusions are much more abundant, suggesting probably differences in diets rather than taphonomic losses (all coprolites are preserved together in the same conditions).

#### 4.1.2. Morphotype B

These coprolites all show spiral structure, attesting to passage through a spiral valve in the intestine. Most of the spiral coprolites in this study have fewer than ten longitudinal striations (and many have fewer than five) on the outer surface of the coprolite. Some 25 % of all specimens possess more than ten scales breaking the coprolite surface, the highest percentage for all coprolite morphotypes. There are two predominant colours, grey and brown, with a few white specimens and one black (BRSMG Cf9993). There are two sub-morphotypes of Morphotype B.

The most common is variety B1 (Fig. 4 A, E), the “scroll type” which has a paper-roll shape, and makes up 28 % of Morphotype B specimens. These coprolites have lengths ranging from 5 to 22 mm and widths from 2 to 9 mm (based on complete specimens only). Most of these coprolites are anisopolar, with one end very tapered and the other slightly rounded. Two-thirds of the specimens have an irregular surface with a rough texture, and the rest have a smooth surface. These scroll specimens are distinctive, with a visible last whorl which is a large fold of the coprolite along the length of the entire specimen, even if no characteristic spiral



**Fig. 4.** The spiral coprolite morphs. (A) Coprolite morph B1, BRSMG Cf15557, lateral view, (B–D) Coprolite morph B2, BRSMG Cf9823 (B); BRSMG Cf15621 (C); BRSMG Cf9848 (D), all lateral views, (E) Coprolite morph B1, BRSMG Cf9833, transverse view of a cross section.

striations are visible. Two specimens have a visible spiral structure in cross-section (BRSMG Cf9833 and BRSMG Cf10326; Fig. 4E). The overall shape is cylindrical, and slightly ovoid for the smaller ones. Some have both ends tapered, giving a lensoid shape overall. Inclusions consist of scales only and 30 % lack visible inclusions altogether. 61 % of B1 coprolites have more than five scales and 70 % have at least one inclusion, the highest proportions in all the coprolite morphotypes in the collection.

Variety B2 is the second morphotype in order of importance, making up 10 % of Morphotype B specimens (Fig. 4B–D). These coprolites are amphipolar, with both ends of similar shape (isopolar) and spiral striations are visible from one end to the other of the specimen. This is quite similar to specimens of *Hyronocopros amphipolar* described by Hunt et al. (2007). The spiral form is well defined, but never perfectly concentric (Duffin, 1979). Some coprolites are incomplete, but broken surfaces reveal the entire spiral, which is useful when the exterior spiral striations are not clearly visible.

Some spiral coprolites cannot be classified as either B1 or B2 because of poor preservation. They may have only one to three visible spiral turns, and the spiral configuration cannot be defined precisely. These are the most common spiral specimens in the HFQ collection, comprising 61 % of morphotype B specimens.

**Discussion.** The HFQ specimens of morphotype B1 are similar to those described as Morphotype F1 by Hunt and Lucas (2012a), and HFQ Morphotype B2 specimens are similar to their Morphotype F2. Our examples show the highest numbers of inclusions of all the HFQ coprolite morphotypes, and especially the Scroll coprolites show more than five or ten scales as inclusions, which suggests they should be assigned to a larger predator such as large bony fishes or sharks.

Fossilised faecal masses showing spiral form are cololites (enterospirae) when found in the body cavity. These are fairly rare in the fossil record and tend to be found in faunas where special conditions of fossilisation occur, such as various Conservation Lagerstätten, as in specimens of *Cladoselache clarki* from the Devonian Cleveland Shale of Ohio and a number of xenacanth sharks from the Permian of the Czech Republic (Woodward, 1917; Williams, 1972). Isolated specimens, such as those here, could be either coprolites *sensu stricto* (ejected from the posterior part of the gut), or evisceralites, intestinal spiral valve fills never ejected as coprolites but separated and removed from their original site of residence in the body cavity, perhaps following scavenging or decomposition of the host carcass (Duffin and Ward, 2020). The holotype of *Strabelocopros pollardi* from the Rhaetian of Watchet, Somerset (Fig. 1C, D) is most likely an example of an evisceralite.

Spiral coprolites were first designated by Buckland and their origins (coprolite versus enterospirae, and the nature of the source animal) have been actively debated (e.g. Buckland, 1835, 1836; Ammon, 1889; Neumayer, 1904; Woodward, 1917; Williams, 1972; Duffin, 1979; McAllister, 1985, 1988, 1996, 2003; Hunt et al., 2015). Much of what we know about the morphology and variation in intestinal spiral valves relies on the original work of Thomas Jeffrey Parker (1850–1897) who recognised four types of spiral valve or *valvula spiralis* in which coiling takes place around a longitudinal axis, and the internal structure comprises a series of stacked, spiralling cones whose apices may be directed either anteriorly or posteriorly (Parker, 1885; Jain, 1983; McAllister, 1985, 1996; Hunt and Lucas, 2012b). In addition, the *valvula voluta* or scroll valve is wound a little like a roll of paper.

Valvular intestines are indicated for some or all agnathans, placoderms, possibly some acanthodians and all chondrichthyans (McAllister, 1996; Hunt and Lucas, 2012b; Bajdek et al., 2019). Among bony fishes, spiral valves are known in sarcopterygians (lobe-finned fishes) and have been described for extant coelacanths and lungfish (Millot et al., 1978; Hassanpour and Joss, 2009). They are also reported in non-teleostean primitive

actinopterygians, in particular polypterids (bichirs and reedfish), acipenseriforms (sturgeons and paddlefishes), holosteans (including gars, bowfins and caturids) and pachycormids (Arratia and Schultze, 2013; Cataldi et al., 2002). There is circumstantial evidence also for a spiral valve in palaeoniscid chondrosteans (Price, 1927; Duffin, 1979); direct evidence of a spiral valve is known from certain fossil sturgeons (*Peipiaosteus pani* from the Early Cretaceous of Liaoning, China; Capasso, 2019) and pachycormids (Arratia and Schultze, 2013). However, spiral coprolites are not seen in teleost fishes or tetrapods (Bajdek et al., 2019).

The spiral valve is explained as an adaptation to life in 'variable and hostile environments' (Capasso, 2019, p. 23). It is a means to increase the surface area of the intestinal wall without increasing its length, thereby optimising nutrient absorption and conserving total gut volume. It is also associated with slow transit of food through the gut, another adaptation to maximise nutrient uptake. The number of turns of the spiral valve may relate to diet.

From the above discussion, it is clear that many groups of marine vertebrates could have contributed spiral coprolites in the Rhaetian bone beds, including selachians, palaeoniscid chondrosteans and dipnoans. Among the chondrichthyans, there are several hybodont sharks (*Lissodus minimus*, *Hybodus cloacinus*, *Palaeobates reticulatus*) and numerous neoselachian taxa (*Synechodus rhaeticus*, *Rhomphaiodon minor*, *Pseudodalatia barnstonensis*, *Parascylloides turnerae*, *Vallisia coppi*, *Duffinseleche holwellensis*, *Pseudocetorhinus pickfordi*) that must have had spiral valves. The rather rare myriacanthid holocephalians *Myriacanthus paradoxus* and *Agkistracanthus mitgelensis* had spiral valves, probably with only a small number (five or fewer) turns, based on spiral valves of Tithonian holocephalians from the Solnhofen Plattenkalk. Among sarcopterygians, lungfish are represented in the British Rhaetian by tooth plates of *Ceratodus latissimus*, and rare coelacanth elements have been reported (Duffin, 1999; Hauser and Martill, 2013; Allard et al., 2015). Among primitive actinopterygians, it is likely that *Sargodon tomicus*, *Severnichthys acuminatus* and perhaps *Gyrolepis albertii* all possessed spiral valves (Argyriou et al., 2016). The same might also be true of rarer components of the osteichthyan fauna, such as '*Lepidotes*', *Colobodus* and *Dapedium* (Nordén et al., 2015; Slater et al., 2016; Cross et al., 2018).

It seems reasonable to suggest that elasmobranchs produced most of the spiral coprolites. Rakshit et al. (2019) concluded that scroll coprolites described as *Tikicopros triassicus* from the Carnian Tiki Formation of India, laden with inclusions, were probably produced by lonchidiid hybodont sharks. Bajdek et al. (2019) applied this conclusion to coprolites from the middle or late Norian Grabowa Formation of Pořeba in Poland, and considered that they too might have been produced by *Lissodus*. Hybodontiforms are the most common sharks, and *Lissodus* in particular, at HFQ (Mears et al., 2016), and indeed in most other Rhaetian bone beds in the district, including Aust Cliff (Cross et al., 2018). Therefore, *Lissodus minimus* might have been the producer of many scroll coprolites classified here in sub-morphotype B1. However, the cylindrical morphotype (A) is the major morphotype in the HFQ collection: it is possible that many scroll coprolites could have been incomplete or damaged to such an extent that, their internal structure having degenerated, they might have been mis-classified in Morphotype A instead of B. *Rhomphaiodon minor* is the second most common species at HFQ (Mears et al., 2016), and other sharks there and in neighbouring bone beds include *Duffinseleche* and *Pseudocetorhinus* (Korneisel et al., 2015; Cross et al., 2018), all of which might have produced these spiral coprolites.

Sharks are also most likely to have produced heteropolar spiral coprolites, and bony fishes amphipolar spiral coprolites (Northwood, 2005). The osteichthyan *Severnichthys*, often seen as the top predator in UK Rhaetian food webs, could also have been a main producer of spiral coprolites.

There could also be dipnoan coprolites in our sample. The lungfish *Ceratodus* is recorded as abundant at Aust Cliff (Agassiz, 1833–1843; Agassiz, 1833–1843; Cross et al., 2018), and has also been found in other basal Rhaetian bone beds at other localities. Coprolites previously assigned to *Ceratodus* are characterised by having the spiral at one end of the specimen (Duffin, 1979), but the coprolites tend to lose this spiral form during excretion (Hansen et al., 2016), so it might be barely visible or absent. Extant lungfish are fairly opportunistic omnivores, feeding upon a range of materials including algae, plant remains, soft and shelled invertebrates and even small fish. *Ceratodus* has tooth plates suited to durophagous feeding on invertebrates or plants and is therefore unlikely to be the producer of coprolites with inclusions of fish remains (Duffin, 1979) and plants (Günther, 1871). *Ceratodus* might be a candidate producer of spiral coprolites (B2) containing no inclusions. This hypothesis was also suggested by Northwood (2005), who attributed amphipolar spiral coprolites with no inclusions and a smooth surface to *Ptychoceratodus* for coprolites from the Lower Triassic of Australia.

#### 4.1.3. Morphotype C

Morphotype C coprolites are 3–31 mm long and 2–16 mm wide, based on measurements of complete specimens. The shape is flattened, with the overall outline varying from triangular, rectangular to rounded, but most of them are ovoid (Fig. 5A–B). The oval form always has rounded ends. The surface is smooth in 60 % of specimens, greater than in other morphotypes which have rather irregular surfaces. The main colour shown by coprolites in this group is different shades of brown (53 %), and 11 % are white, which is unusual. The quantity of inclusions is low, with almost 69 % of coprolites containing no inclusions at all, and only 9 % possessing more than five inclusions.

*Discussion:* 110 specimens of the HFQ collection correspond to Morphotype C, which is similar to those ascribed to Morphotype “H” by Hunt and Lucas (2012a). Proportionally to the number of specimens, this morphotype is the one presenting the lowest

number of inclusions, with generally fewer than five inclusions or none. This morphotype could have been produced by osteichthyans, and producers could have been durophagous fishes, based on the rarity or absence of phosphatic inclusions. The flattened shape might not reflect the exit form of the coprolite but might reflect also some collapse before preservation.

#### 4.1.4. Morphotype D

Morphotype D comprises coprolites with irregular shapes and textures, with a large variety of general shapes: 164 specimens were classified in this type, all of which are amorphous or massive coprolites (Fig. 5C–E). These coprolites range from 3 to 44 mm in length and 3–27 mm in width. There is an important diversity of colours, with uncommon ones like orange or greenish brown, but most are brown (35 %) and grey (26 %). As with morphotypes A and B, the surface is irregular in most (70 %). Despite being relatively large (average of 12.21 mm width and 18.37 mm length), inclusions are few, with only 17 % of specimens having more than five inclusions. Numerous dimples and irregularities are present on the coprolite surface, together with special striations and traces which are discussed below.

*Discussion:* Many coprolites irregular in shape could have been distorted when initially striking the substrate, any impact marks making coprolite morphotype unidentifiable. These kinds of contact marks could also have been produced if the coprolite were to rest against sand grains, larger clasts, shells, or other hard substrates during transport. This morphotype matches morphotype “K” of Hunt and Lucas (2012a), who suggest this type of coprolite might have been produced by different sorts of fishes.

#### 4.1.5. Other morphotypes

Morphotype E: This is represented by a single complete specimen (BRSMG Cf10400) which has a long cylindrical shape and is 31 mm long and 5 mm wide (Fig. 5F). This type is characterised in Hunt and Lucas (2012a) as morphotype A4 which is cylindrical and has a length at least five times greater than the



**Fig. 5.** Variety of coprolite morphs. (A and B) Coprolite morph C, BRSMG Cf10422, in lateral (A) and longitudinal (B) views, (C–E) Coprolites morph D, BRSMG Cf15545 (C); BRSMG Cf10060 (D); BRSMG Cf9660 (E), all lateral views, (F) Coprolite morph E, BRSMG Cf10400, lateral view, (G–I) Massive coprolites, BRSMG Cf9841 (G); BRSMG Cf10184 (H); BRSMG Cf10182 (I), all lateral views.

width. The shape is perfectly cylindrical, with a constant diameter and rounded ends, and its length is about six times its width.

**Massive coprolites:** some specimens are bigger than the high average, and they have a typical texture and a dark colour (most of the time), with a variety of shapes (Fig. 5G–I). They are 20–52 mm long and 9–27 mm wide. They have some inclusions, but not as densely packed and as numerous as in morphotypes A and B, despite their larger size. Marine reptiles and large fishes could be the producers of massive coprolites with an irregular shape.

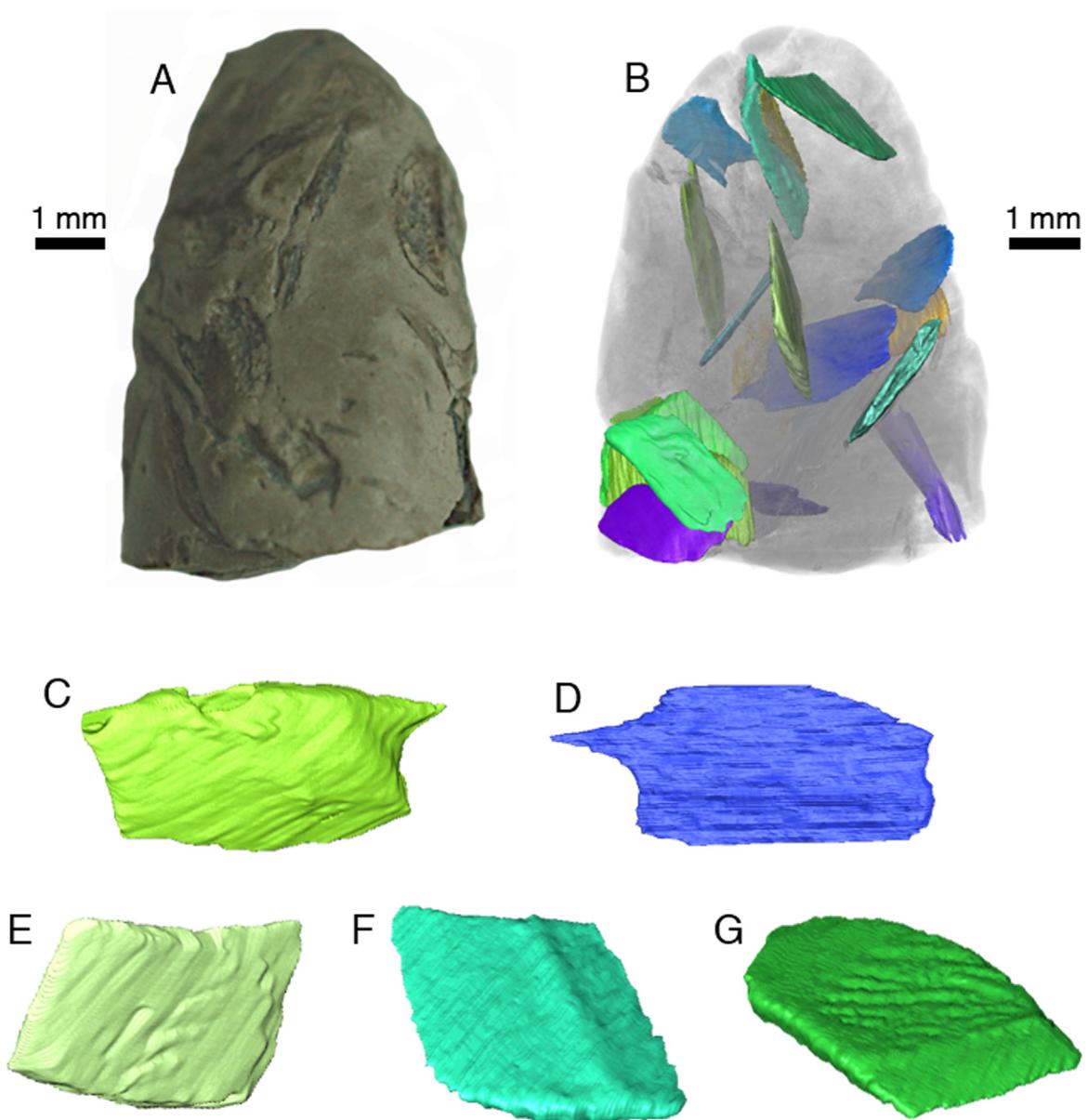
**Unknown morphotypes:** many coprolites are too small, too incomplete or both to be assigned to a morphotype. A few specimens have a shiny black colour, which might be the result of complete phosphatisation (Duffin, 1979). We note that 17 % are white; Krause and Piña (2012) note that calcium minerals acquired during the digestion of bones could give whitish colours to coprolites. However, here the colours probably indicate a different diagenetic pathway.

#### 4.2. Inclusions

The coprolites from HFQ contain a wide range of inclusion types embedded in the coprolitic ground mass, with a high predominance of fish scales. Most inclusions are restricted to the surface of the specimens; many coprolites are incomplete and are broken revealing a cross-section, but few inclusions are completely enclosed in the faecal matrix of the coprolite.

A total of 50.8 % of specimens have at least one inclusion ( $n = 546$ ), and 48.1 % possess inclusions of scales only ( $n = 517$ ). However, there is no correlation between the number of inclusions and the size of the coprolite (taking only width into account so as to be able to include data from incomplete coprolites). This same phenomenon has been noticed by Northwood (2005) in her study of Early Triassic coprolites from Australia.

Furthermore, there is also no correlation between coprolite size and the nature of inclusions, except in the case of the vertebrae of *Pachystropheus*, which were found in a relatively large specimen



**Fig. 6.** Coprolite morph B1, BRSMG Cf10155, CT scan, in lateral view (A), and in lateral view with transparent matrix and coloured scales in 3D (B). (C–G) Different morphotypes of scales found as inclusions.

(14 mm width; see discussion below). Most of the scales were found in brown/light brown and grey/light grey specimens, with fewer inclusions in darker coprolites. The white coprolites are quite rare, but they often contain many incompletely digested food remains. In general, the quality of preservation of inclusions is better in light-coloured coprolites.

CT scans show the numbers and distribution of inclusions in three spiral coprolites (BRSMG Cf10155, Cf10162 and Cf15546), described below.

In one specimen, representing perhaps half a coprolite (BRSMG Cf10155, Fig. 6), there are 16 scales, seemingly randomly arranged; the contrast between external and internal appearance (Fig. 6A, B) shows how many are concealed inside. These all appear to be scales of similar size, some (Fig. 6C, D) with posterior pegs, and some (Fig. 6E–G) apparently lacking such pegs. The scales are all rhomboid in shape, about 2 mm long, and generally lacking sculpture, except for some markings on the outer surface of one (Fig. 6G).

A second partial coprolite (BRSMG Cf10162, Fig. 7) shows even denser packing of scales, with at least 20 packed irregularly into the structure. These elements include some similar scales to those in the previous coprolite, as well as scales and bone fragments of different shapes. Here, it seems some of the scales (Fig. 7D, E) might have been rounded, or lost their edges, perhaps through the action of stomach acids.

The third scanned coprolite (BRSMG Cf15546, Fig. 8A) shows a remarkable association of bony remains – a tuberculated element (Fig. 8B) and two vertebrae (Fig. 8C–D). The tuberculated element is curved, with a narrower and a broader end, and there appears to

be a slight bifurcation at the broader end. The tuberculation is on one surface only, presumably the outer surface. It is not clear whether this tuberculation represents the external sculpturing on the surface of a bone, or possibly part of a tooth-bearing bone. The specimen shows some resemblance to the surface ornament of a saurichthyiform lower jaw from the Middle Triassic of China (Wu et al., 2013, Fig. 9), the 'actinopterygian jaw fragment' figured by Slater et al. (2016, Fig. 5Q), and to the palatal area of *Colobodus* sp. figured from the Rhaetian of Italy by Boni (1937, pl. 4, Fig. 3). Unfortunately, no complete or partial fish skulls have so far been described from the Westbury Formation of the UK.

The two vertebrae are similar in shape, showing a low and slender-sided centrum 12 mm long and 4.5 mm wide and high. The centrum is topped by a narrow neural arch enclosing the tubular neural canal. In lateral view (Fig. 8C), the neural arch shows a low anterior portion and small prezygapophyses, and the dorsal margin sweeps gently up to a narrow slightly posteriorly oriented neural spine, at the base of which are the small postzygapophyses. These are caudal vertebrae of the small marine reptile *Pachystrophia*, by comparison with published examples; the middle to distal caudal vertebra figured by Storrs et al. (1996, Fig. 6E) is identical to our specimens, except that the neural spine in their example extends to twice the height. The height of the neural spine probably diminishes posteriorly along the length of the tail, as the musculature responsible for lateral tail movements reduces. One of the vertebrae (Fig. 9D–F) shows some pitting on one side, probably the result of the action of stomach acids.

These three coprolites reveal several things about the predators that produced them. First, the pH milieu of the gut and/or the

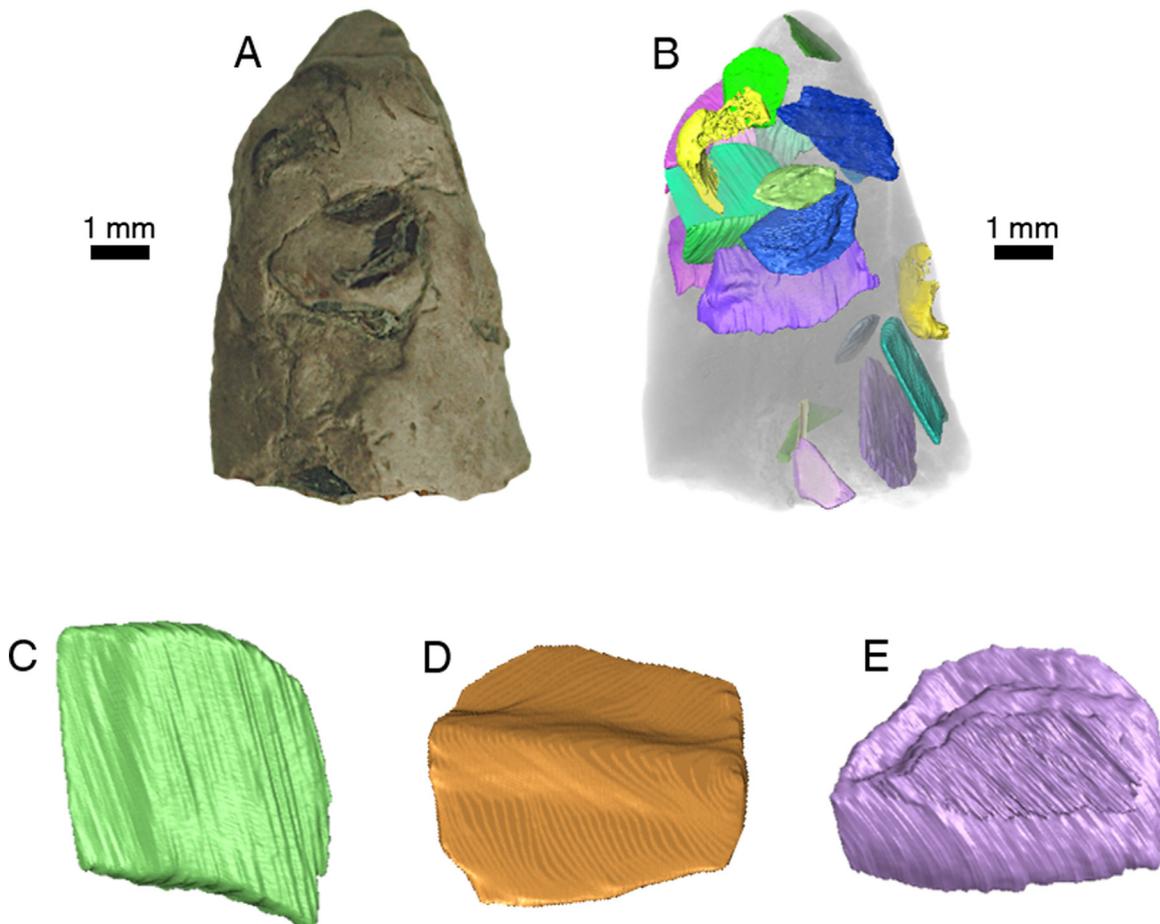
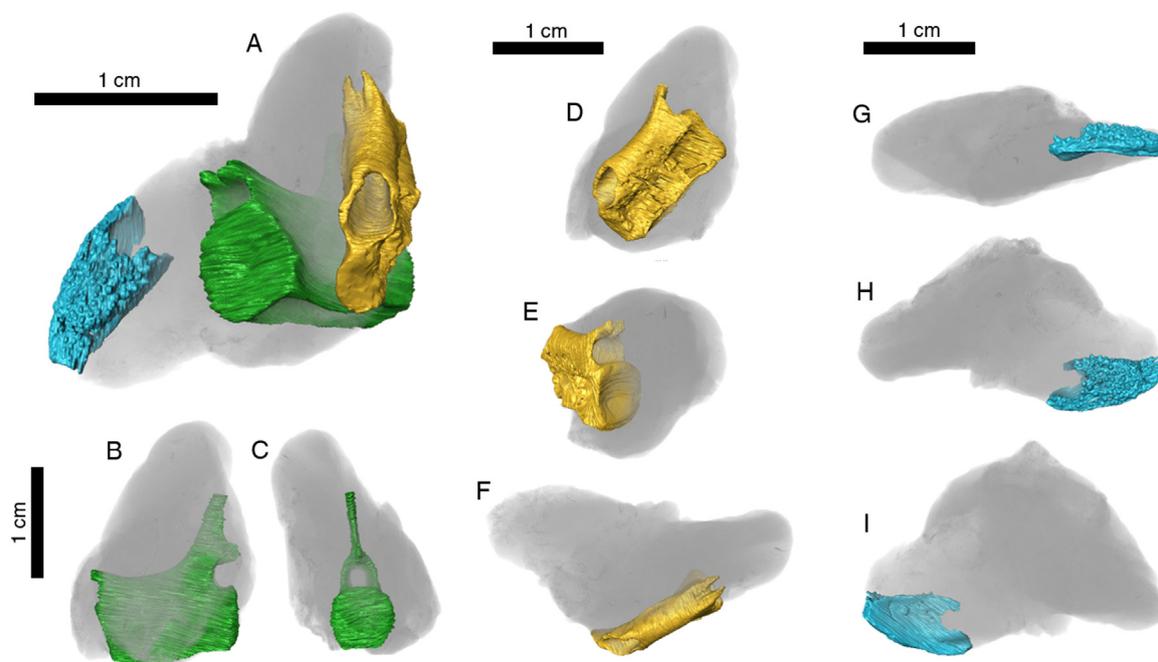


Fig. 7. Coprolite morph B1, BRSMG Cf10162, in lateral view (A), and in lateral view with transparent matrix and coloured scales in 3D (B). (C–E) Different morphotypes of scales found as inclusions.



**Fig. 8.** Coprolite morph B1, BRSMG Cf15546, in lateral view with transparent matrix and coloured scales in 3D (A). (B) Tuberculated bone inclusion, three different views, (C) First vertebra inclusion, lateral and frontal view, (D) Second vertebra inclusion, three different views.

residence time of the bones within it were insufficient to achieve complete digestion of the bones and scales, contrary to the condition in many modern predators such as sharks and crocodiles. Second, the coprolites presumably represent the partial ejecta of a single meal; in other words, the predator snatches its prey, such as a specimen of *Gyrolepis*, bites off pieces and swallows them, or perhaps swallows the whole prey animal. Then, after digesting the flesh, the bones and scales are ejected in one or more coprolites. The fact that we find 15–20 scales in a single coprolite suggests that a whole *Gyrolepis* might be represented in numerous coprolites if all scales had to be ejected. The third coprolite (Fig. 8) is most unusual because it contains mixed remains, part of a fish skull and part of a reptile tail; was this producer scavenging bits and pieces of dead animals, or did it snatch a bit of the head of a fish and then nip off the end of the tail of a passing *Pachystropeus*? Mixing bony remains of two kinds of prey animals in one coprolite is both unexpected and unusual.

#### 4.2.1. Scales

Fish scales are by far the most common inclusion type (in both BRSUG and BRSMG collections; Fig. 9A–F) and they can be attributed to osteichthyans. The scales are commonly rhomboid to subquadrate in shape, always with a smooth and shiny surface of the preserved ganoine and frequently black in colour (Fig. 9A–C). Many scales have ridges across the external ganoine-covered free face of the scale (see Schultze, 2016 for nomenclature), with a straight or slightly wavy pattern running in a cranial-caudal direction (Fig. 9A–C). Most scales on the coprolite surfaces have lost all or part of the ganoine around margins of the free face of the scale, as shown by Jain (1984) in scales of *Lepidotus maximus*, presumably due to the corrosive effects of digestive acids. Many scales also show concentric striae especially on the inner, non-ganoine-covered, surface; these are growth rings, as described by Goodrich (1907).

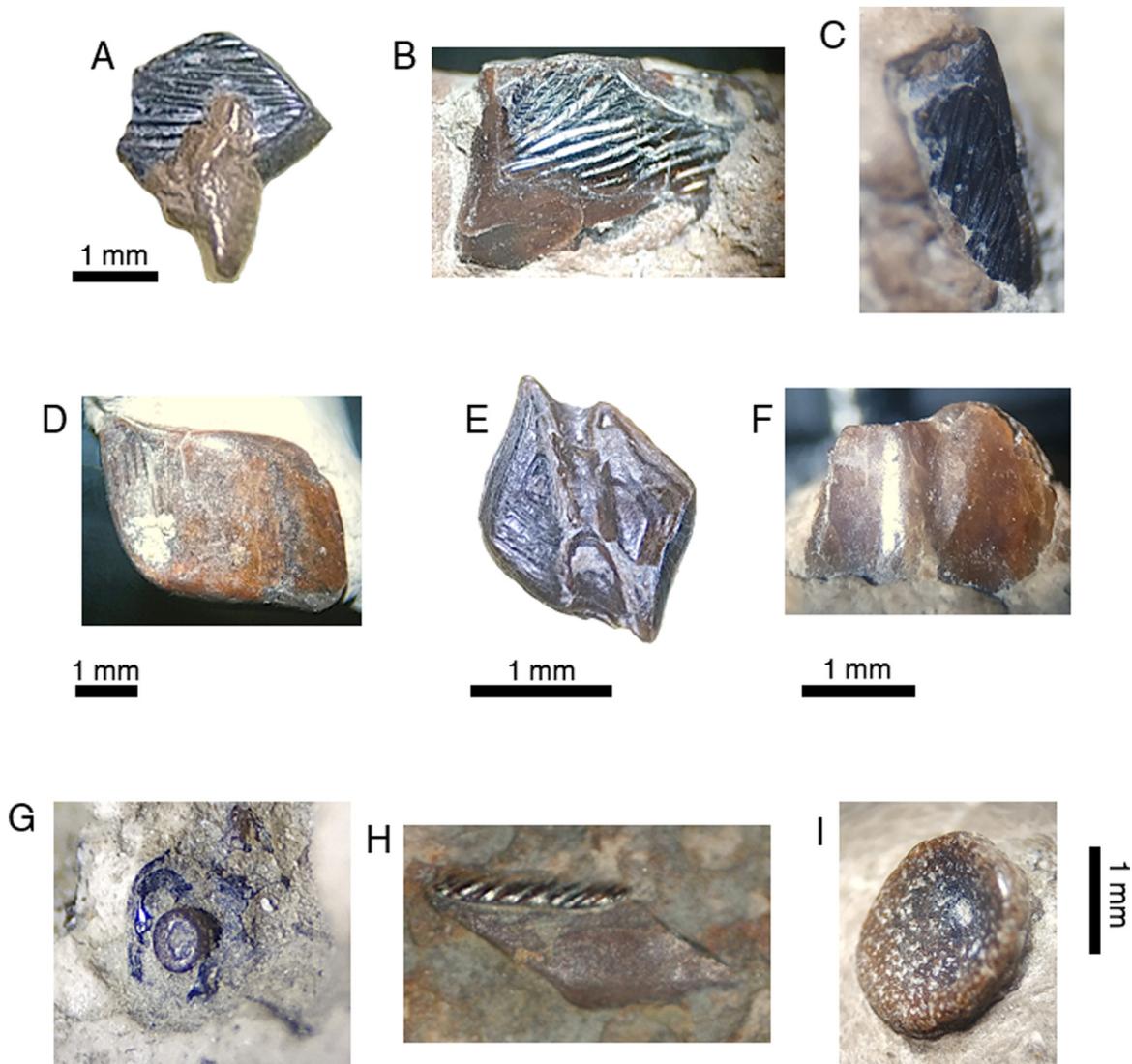
The scales with regular rhomboidal shape, black and thin ganoine, and a diagonal pattern of undulating ridges (Fig. 9A–C) are typical of Palaeonisciformes (Storrs, 1994), and commonly attributed to the genus *Gyrolepis*, which was abundant in Rhaetian

bone bed collections, including at HFQ (Mears et al., 2016). Some coprolites show the moulds of scale surfaces that confirm the former presence of *Gyrolepis* scales that have become detached from the coprolite surface, presumably during or shortly after the process of extrusion. These *Gyrolepis* scales are by far the most common inclusions in the coprolites from HFQ. This high abundance is corroborated by the coprolite data from Aust (BRSMG collections), which includes many similar scales. Other included scales (Fig. 9D–F) are more irregular with a general rhomboidal shape but thinner ganoine layer, and sometimes one or two furrows on the surface, representing the position of the lateral sensory canals.

CT data confirms there are two scale patterns. The first comprises thin, subquadrate scales with a marked keel running longitudinally, and one corner among the four being very prominent (Figs. 6F, 7C). The second category comprises subquadrate scales that are more elongated and have a spike projecting from the upper margin, the original peg structure that served to anchor the scale to an adjacent one by fitting into a corresponding socket in its lower margin (Fig. 6C–D). The scales are up to 5 mm long (BRSMG Cf15609). These two varieties could represent remains of two species, but they need not as scales of the same species can vary considerably across the flanks and around the fins in a single individual.

The distribution of scales inside the coprolite also varies and is most prominent in the spiral coprolites of Morphotype B where most are oriented according to the turn of the spiral. Indeed, there are as many oriented inclusions in Morphotype B as in Morphotype A, but we know that type A contains twice as many inclusions as type B. This orientation is mostly seen in coprolites having more than five scales, which leads to a bias because of the number of inclusions: the orientation cannot easily be discerned if there are fewer than five. Inclusion orientation is best in spiral specimens containing more than ten scales.

Rhomboid scales belong to actinopterygians (Schultze, 2016), and the ganoid type to all except modern Teleostei (Goodrich, 1907). Some sharp-pointed, rhomboid scales might be attributed to *Lepidotes*, which belongs to a group of neopterygian fishes



**Fig. 9.** Inclusions within Hampstead Farm coprolites, mainly fish remains. (A–C) Osteichthyan scales, probably *Gyrolepis albertii*, external view, BRSUG 29,371-1-974 (A); BRSMG Cf9786 (B), BRSMG Cf15618 (C). (D–F) Osteichthyan scales, other morphotypes, different views, BRSMG Cf9907 (D); BRSUG 29,371-1-974 (E); BRSMG Cf15528 (F). (G) Miscellaneous inclusion, BRSMG Cf10390. (H) Osteichthyan fin ray, BRSMG Cf9601, lateral view. (I) Fish inclusion, probably a fish vertebra, BRSMG Cf9988.

recorded throughout most of the Mesozoic (Jain, 1984; Cavin et al., 2015), although their scales are not known in the British Rhaetian.

#### 4.2.2. Bones

Few bones have been found in the HFQ coprolites, and almost all are difficult to identify confidently (Fig. 9G–I). Some small boss-like structures (Fig. 9G) might be scales or denticles. One vertebra, circular and with a shallow conical depression on the centrum face (Fig. 9I) belongs to a neoselachian shark and is similar to those figured by Mears et al. (2016) Fig. 8).

#### 4.2.3. Fin ray

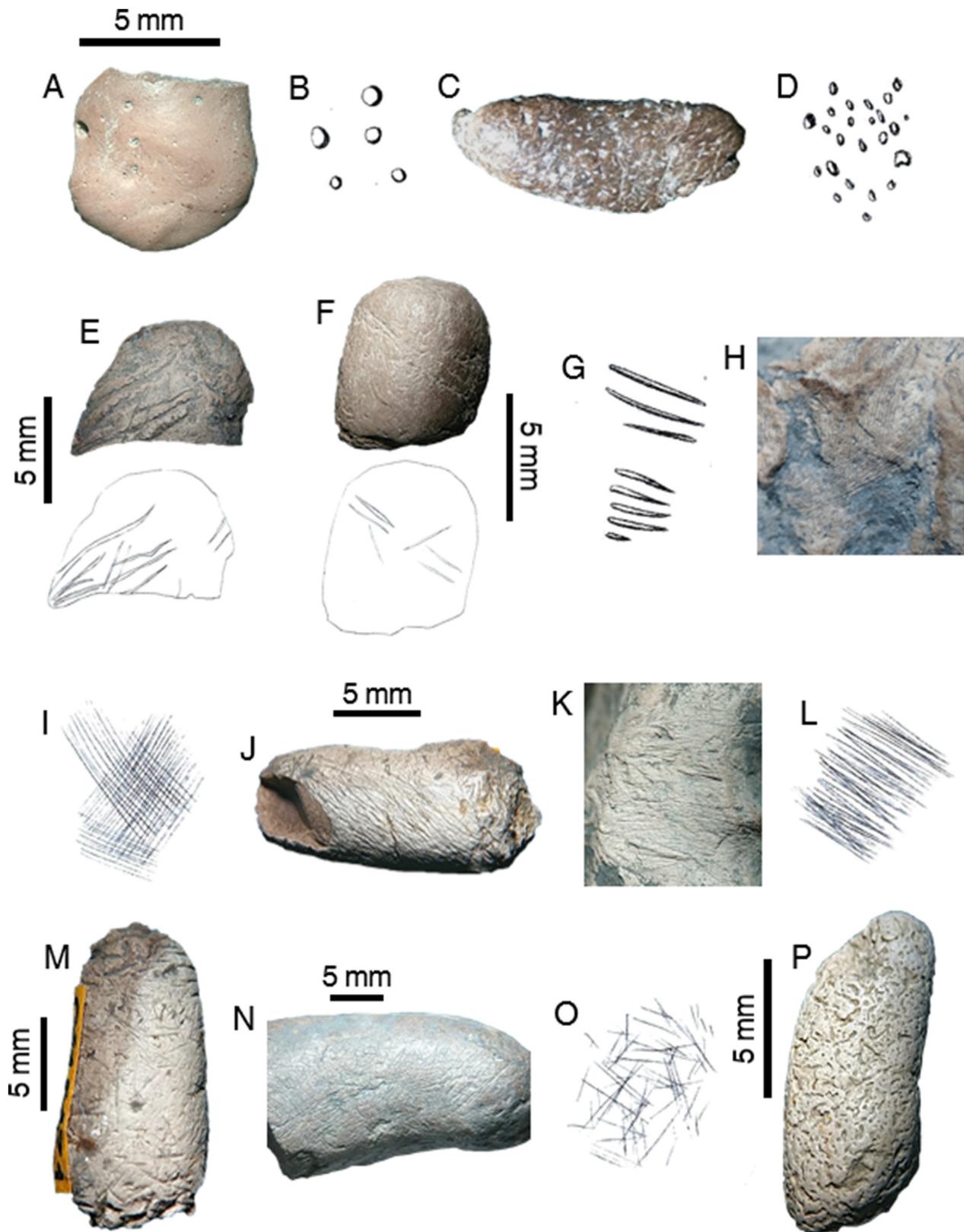
Four fin structures were found in three different coprolites. All the fin rays are associated with several other inclusions in the coprolite, with at least five other inclusions; two of the coprolites have more than ten inclusions in total. All these inclusions are osteichthyan scales; this association was already noticed by Mears et al. (2016, p. 15). The three morphotypes of coprolites are different, but most of them are complete with light colours. The fin rays (e.g., Fig. 9H) are similar to those of morphotype F1 described by Mears et al. (2016).

### 4.3. Surface markings on the coprolites

Features on the surface of coprolites may provide information about the context of excretion, such as the environment, diagenetic features and the physiology of the producer. They can also record the time of preburial exposure (Northwood, 2005). The nature and state of preservation of these features can indicate in which environment the fossil faeces were produced and the impact of taphonomic processes (Oliveira and Santucci, 2017). For example, good preservation of such traces could involve a marine environment with rapid sedimentation rates, rather than a depositional environment with high sedimentary influx (Northwood, 2005). In our study, details of the surface features on coprolites from the HFQ collection have been classified into seven morphotypes. It should be noted that several types of surface features can be seen on a single coprolite, including massive examples.

#### 4.3.1. Holes

35 specimens show a few visible regular rounded holes with a diameter varying from around 300–500  $\mu\text{m}$  to 1–2 mm (Fig. 10A, B), many of which are still filled with sediment. 40 % of the



**Fig. 10.** Surface markings on Hampstead Farm coprolites. (A, B) BRSMG Cf9807, lateral view (A), diagram of holes on coprolite surface (B). (C, D) BRSMG Cf9649, lateral view (C), diagram of pits on coprolite surface (D). (E–G) BRSMG Cf10071, lateral view (E), BRSMG Cf?, lateral view (F), diagram of straight lines on coprolite surface (G). (H, I) BRSMG Cf10326, enlarged view (H), diagram of grid on coprolite surface (I). (J) BRSMG Cf15468, lateral view. (K, L) BRSMG Cf10326, enlarged view (K), diagram of holes on scratched surface (L). (M–O) BRSMG Cf15468, lateral view (M), BRSMG Cf10144, slightly enlarged lateral view (N), diagram of irregular scratches on coprolite surface (O). (P) BRSMG Cf15571, lateral view.

specimens having holes are flat coprolites, and only 25 % are cylindrical (the others are morphotype D or unknown). Flat coprolites are significantly burrowed and perforated with holes; most of them have more holes than representatives of other coprolite morphotypes. These features could have been caused by early bacterial decomposition because of their “bubble” shape but are probably too large, the size range relevant to bacteria being 0.5–2  $\mu\text{m}$  (Hollocher et al., 2005). Alternatively, the holes might be invertebrate traces such as boring or burrow marks (Dentzien-Dias et al., 2012). The possibly coprophagous decapod species *Tropifer laevis*, whose remains have been found in the Rhaetian of Aust Cliff (Cross et al., 2018), could be the producer of such marks. However, Harper et al. (1998), in describing Liassic bivalves from the United Kingdom, consider that a single hole per specimen is the key indicator that a boring originated from the action of a predatory gastropod. None of our specimens has fewer than two holes on the surface, but it is hard to imagine why a predatory gastropod would wish to penetrate a coprolite with its radula.

#### 4.3.2. Dotted

Eleven specimens show multiple tiny ovoid holes, randomly scattered over and most of the coprolite surface (Fig. 10C, D). As with specimens with holes, five dotted examples are flat, which could indicate a tendency for flat coprolites to have holes as a surface feature. The holes seem far too big to have originated from bacterial action (Hollocher et al., 2005).

#### 4.3.3. Straight lines

17 specimens possess parallel or semi-parallel furrows on their surface, often in groups of two or more furrows lying side by side, each clearly separated from the other (Fig. 10E–H). The shape of each striation with one end tapered could indicate a biogenic origin, such as fish bite traces. Similar bite marks (dentalites) suggested as having been made by coprophagous fishes have been noted from the Late Miocene of Venezuela (Dentzien-Dias et al., 2018, Fig. 7B), the Eocene of Virginia (Dentzien-Dias et al., 2020 Fig. 8E–F) and the Miocene of Italy (Collareta et al., 2019). Another hypothesis for the furrows is that they were formed during extrusion of the coprolite through the terminal twist of the cloacal or other sphincter. However, if that were the case, the striae ought to be oblique, not parallel, as in some specimens of this type. These types of striae are likely not pre-diagenesis features, such as abrasion marks produced during entrainment and transport within the sediment which would be expected to lie parallel or sub-parallel to the long axis of the coprolite; the HFQ specimens show no such orientation of the striations.

#### 4.3.4. Grid

Three specimens (BRSMG Cf9736, Cf15545, Cf10144) possess thin parallel striations which intersect to form a grid-like pattern on the surface of the coprolite (Fig. 10I, J). These are all massive coprolites. It is not clear what this grid-like pattern represents.

#### 4.3.5. Scratched

Thirteen specimens have numerous shallow scratches, often along a single side and sometimes passing fully from one end to the other (Fig. 10K, L). Each scratch cannot be clearly separated from the others, and they are not all parallel with each other. The scratches are about the same length, about 4 mm, and lie next to each other in the same general direction. According to Cross et al. (2018), these marks might have been made during passage through the gut, knowing that peristaltic muscular movements can produce longitudinal striations (Northwood, 2005). The striations which are oblique to the long axis of the coprolite might reflect the twisting trajectory of the faecal mass as it passed down the gut.

*Irregularly scratched:* 23 specimens have several visible shallow striations of different sizes and shapes (Fig. 10M–O). The relevant part of the surface also varies in size, from a few millimetres to one whole side of the specimen. Nevertheless, this feature has not been found covering the whole surface of a coprolite. The furrows intersect with each other. Nine coprolites with this feature are massive, and it may be that their size enables preservation.

#### 4.3.6. Others

A few other specimens show further features. Massive coprolites display several different types of striation, including those detailed above. Six specimens show some wavy and curved furrows on their surface, but the similarities are not distinctive. One coprolite has a series of odd surface features resembling shallow borings parallel to the outer surface; these form little networks, with criss-crossing curved and V-shaped lengths (Fig. 10P). They are likely borings (fungal mycelial traces?) made in the surface of a semi-solidified coprolite.

#### 4.3.7. Discussion

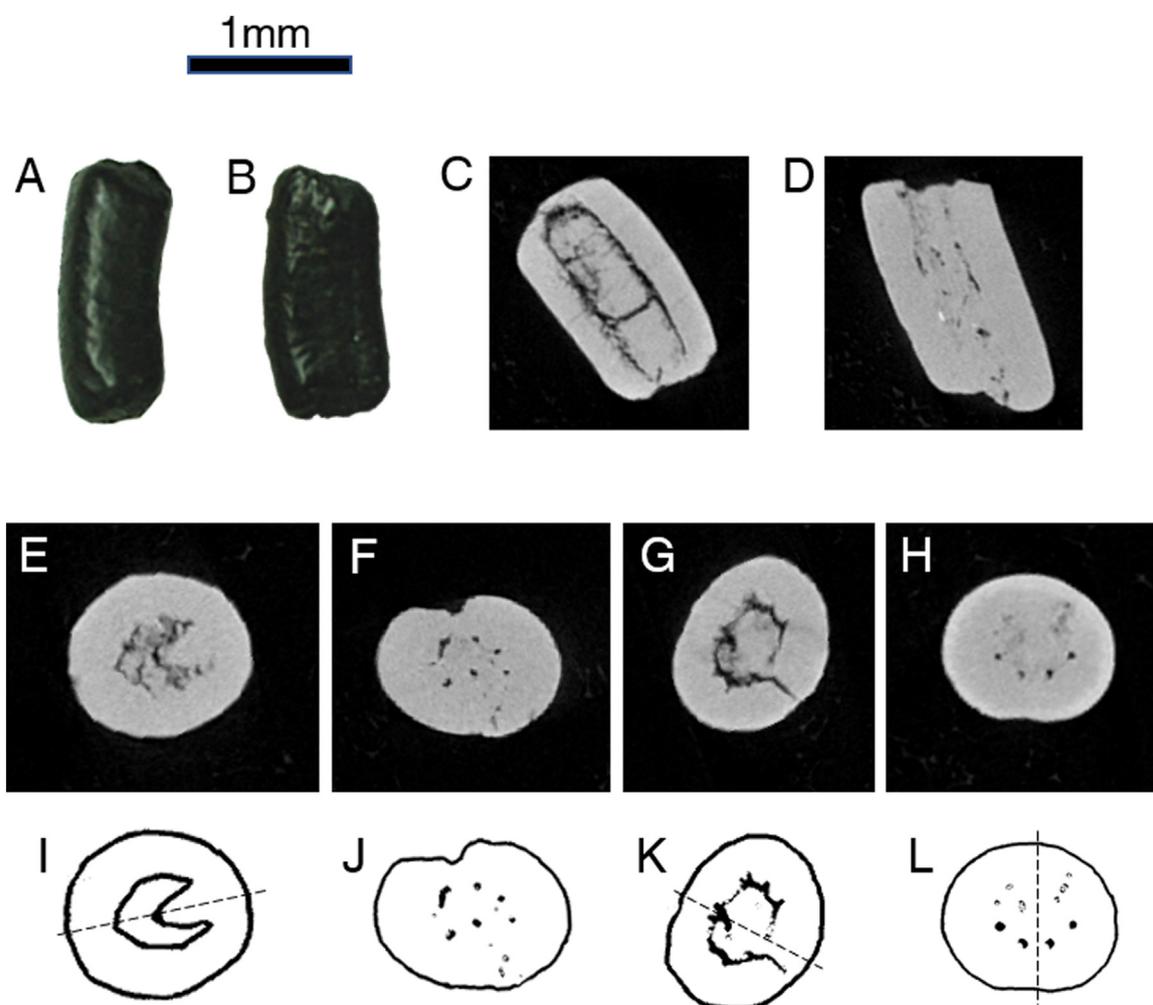
Are these pits and scratches biological or geological in origin? Some coprolites might have been little transported, whereas others may have been transported or washed back and forth in the storm beds associated with the Rhaetian marine transgression. As they were transported, we might expect them to acquire impact marks and abrasion. Transport marks in the form of fine striations might be expected parallel or sub-parallel to the long axis, or orthogonal if the coprolites were rolled along. Few coprolites from our collection show such striations, with most of them having oblique or transverse striations across the surface. Abrasion and contact marks produced when the soft coprolite rested against sand grains, shells, or hard substrates could be expressed as roughness of the coprolite surface, with a different transport context for smooth or irregular surfaces, the latter having many dimples and bumps over the whole coprolite. Desiccation features (such as cracking on the surface, as noted by Dentzien-Dias et al. [2012] for coprolites dropped on land) have not been observed in any HFQ specimens, confirming that our Rhaetian coprolites remained immersed in water.

One massive coprolite (BRSMG Cf10298) has an unusual hole, with a long ovoid curved shape, decorated with concentric striae like those on the shell of a bivalve. Some coprolites were colonized by epifaunal taxa such as *Atreta intusstriata*, an oyster-like adherent bivalve (Radley, 2002) already noted on Late Triassic coprolites from UK bone beds (Hunt et al., 2012), as well as on the holotype of *Strabelocopros pollardi* (Fig. 1C, D). But the shell shape of that species (Rigo et al., 2013, Fig. 6.4) does not correspond to the shape of the hole in BRSMG Cf10298. No other biogenic marks, such as impressions of plant or bryozoans, seem to be present in the sample.

Some coprolites have a black surface probably representing a phosphatised diagenetic crust, with the inside of the coprolite being of a significantly lighter colour. This crust could indicate prior burial and pre-fossilisation of the coprolite, which was later exhumed by storm action. Phosphatisation of coprolites is very common (Qvarnström et al., 2016).

## 5. Crustacean microcoprolites

It has recently been suggested that the term ‘microcoprolite’ should be restricted to coprolitic structures measuring up to 1 mm long (Knaust, 2020, p. 2). The smaller coprolites from HFQ range from 300  $\mu\text{m}$  to 2.4 mm in length, so for simplicity all coprolites in this size range are referred to here as microcoprolites. Furthermore, the descriptive terminology used here follows that recommended by Knaust (2020).



**Fig. 11.** Crustacean microcoprolites. (A, B) Two different coprolites morph “crustacean”, BRSUG MF06-6i-38, lateral views. (C, D) Two different coprolites morph “crustacean” CT-scanned, BRSUG MF06-6i-38, lateral view in cross section, not to scale. (E–H) Four different coprolites CT-scanned, BRSUG MF06-6i-38, transverse views in cross section, not to scale. (I–L) Four corresponding schemes of coprolites E–H.

Nineteen of the microcoprolites from HFQ are identified here as having been produced by decapod crustaceans, the first record of coprolites belonging to this group from the British Rhaetian. This identification was accomplished by means of CT scans (Fig. 11A–B). So far as we are aware, this is the first use of CT scanning to study microcoprolites in general and decapod coprolites in particular. Decapod coprolites are usually identified from petrological thin sections, but we show here that CT scanning is useful for the non-destructive characterisation of microcoprolites and their internal structure. The only problem is that CT scans do not provide the same degree of detail as thin section, for example, in determining the cross-sectional shapes of the longitudinal canals.

The small, cylindrical specimens from HFQ have a uniform dark grey colouration, and measure on average 1–2 mm long and 0.05–0.1 mm wide. Both ends of the microcoprolite are identical (i.e., isopolar), being rounded and slightly flattened, resulting in a pellet-like, cylindrical overall shape. The long axis is straight, or occasionally slightly curved (Figs. 11A–D). Each coprolite has a longitudinal furrow running down one side from one end to the other, but otherwise the microcoprolite surface is smooth. Internally, there is a complex of tiny longitudinal canals (Figs. 11E–L) with a bilaterally symmetrical arrangement, which correspond to similar structures in thin sections of decapod coprolites (e.g., Gaździcki et al., 2000; Senowbari-Daryan et al., 2010; Knaust,

2020). Four different internal canal arrangements can be identified in our sample, corresponding to three morphotypes.

Decapod microcoprolite morphotype 1 (Figs. 11E, I): defined by the presence of a relatively large (occupying up to 25 % of the cross-sectional area) central longitudinal canal, which is roughly U-shaped in cross section (BRSUG MF06–6i-38). The microcoprolite cross-section is round to sub-rounded.

Decapod microcoprolite morphotype 2 (Figs. 11F, J): defined by the presence of a series of small longitudinal internal canals, each seemingly circular in cross-section. The canals are relatively small in number (fewer than ten) and are arranged in a simple arc. The microcoprolite cross-section is ellipsoidal.

Decapod microcoprolite morphotype 3 (Figs. 11G, K): defined by the presence of a strong radial canal leading to a series of relatively large canals arranged in a circular fashion about a central core of faecal material and interconnected by a series of tangential canals. The microcoprolite cross-section is ellipsoidal.

Decapod microcoprolite morphotype 4 (Figs. 11H, L): defined by an arcuate series of around seven longitudinal canals, interconnected by a series of faint tangential canals. Two solitary canals lie within the arc, in an off-centre position. The microcoprolite cross-section is ellipsoidal. This morphotype is similar to morphotype 2, and any differences are likely a result of poor preservation and other particles.

The shape and arrangement of the internal canals is an important taxonomic feature of crustacean coprolites (Schweigert et al., 1997). These structures are related to their passage down the digestive tract, where longitudinal ridges on its internal walls increase the surface area available for nutrient absorption. In posterior parts of the stomach, these ridges give way to a system of finger-like fleshy processes sometimes referred to as pyloric fingerlets (Powell, 1974; Kietzmann et al., 2010, p. 277). As the faecal material is squeezed past these projections, which act a little like a gastric sieve, they initiate the action of the longitudinal canals on the faecal matter. The overall arrangement and morphology of the canals is retained as the faecal material enters the hindgut and is eventually expelled (Elliott, 1962, p. 30; Senowbari-Daryan and Stanley, 1986).

There have been no comparative studies of the microcoprolites produced by extant decapod taxa, which means that allocation of distinctive crustacean microcoprolite morphotypes to any group of lower taxonomic rank is currently impossible. As a consequence, a utilitarian ichnological classification scheme has emerged which has recently been revised by Knaust (2020). According to this revised ichnotaxonomy, the HFQ microcoprolites all belong in the Ichnofamily Favreinae as originally defined by Vialov (1978). The Favreinae embraces 12 ichnogenera. We identify morphotype 1 as the favreineid ichnogenus *Canalispalliatum* (Blau et al., 1997), morphotypes 2 and 4 as *Favreina* sp. and possibly *Favreina martellensis* Brönnimann and Zaninetti (1972, cf. Fig. 3), and morphotype 3 as likely *Helicerina keuperina* (Schweigert et al. 1997, cf. fig.4).

Microcoprolites provide the only evidence for the presence of crustaceans in most Triassic rocks. Indeed, the coprolites are relatively common components of reef and inter-reef limestones of the Tethyan Triassic, including sediments of Rhaetian age (e.g., Brönnimann et al., 1972a, 1972b; Kristan-Tollman, 1988), some of which are transgressive sequences with subordinate limestones only (Brönnimann et al., 1972a).

As infaunal burrowers, many crustaceans are important agents of sediment bioturbation, helping to mix sediments and alter their textures for a significant depth below the sediment-water interface. As they produce the burrows and galleries for which they are well known, they help to aerate the sediment, redistributing nutrients and altering rates of organic matter decomposition. The only crustaceans known from the British Rhaetian are ostracods, cirripedes, an isopod, the dendrobranchiate *Aeger gracilis*, and the polychelidan lobster *Tropifer laevis* (Gould, 1857; Duffin, 1978; Förster and Crane, 1984; Boomer et al., 1999; Audo et al., 2017). Other evidence for crustaceans in British Rhaetian sequences includes *Thalassinoides*-type and *Spongeliomorpha* burrows at various localities and levels (Swift and Duffin, 1999; Korneisel et al., 2015). These burrows are mostly produced by glypheid lobsters, which are indeed known to be producers of microcoprolites of the *Favreina* type, as found here (e.g., Förster and Hillebrandt, 1984).

*Tropifer* has a close association with coprolites, as previously noted by Duffin (1978), being recorded in coprolites from the Rhaetian Bone Bed of Aust Cliff. There are considerable similarities between the Rhaetian faunas at Aust and HFQ (Mears et al., 2016; Cross et al., 2018). It is not clear whether *Tropifer* was a food item in the coprolites in which it has been found, or whether it was feeding as a coprophage. If the latter were the case, there is the possibility that its faeces might possess enhanced levels of phosphate which would have increased the preservation potential of its microcoprolites.

Invertebrate coprolites might be more common components of the Rhaetian bone bed fauna than is currently appreciated; since they are composed mainly of calcium carbonate and often only lightly phosphatised, normal acid processing techniques would

likely reduce them to dust. Perhaps the phosphatisation rate observed in the HFQ bone beds (Mears et al., 2016) has permitted their preferential preservation. Unlike the macrocoprolites, the homogenous material of the microcoprolites shows significantly less remineralisation in the CT images, which might suggest an alternative origin for their contained phosphate.

## 6. Palaeoecology

### 6.1. The Hampstead Farm vertebrate fauna

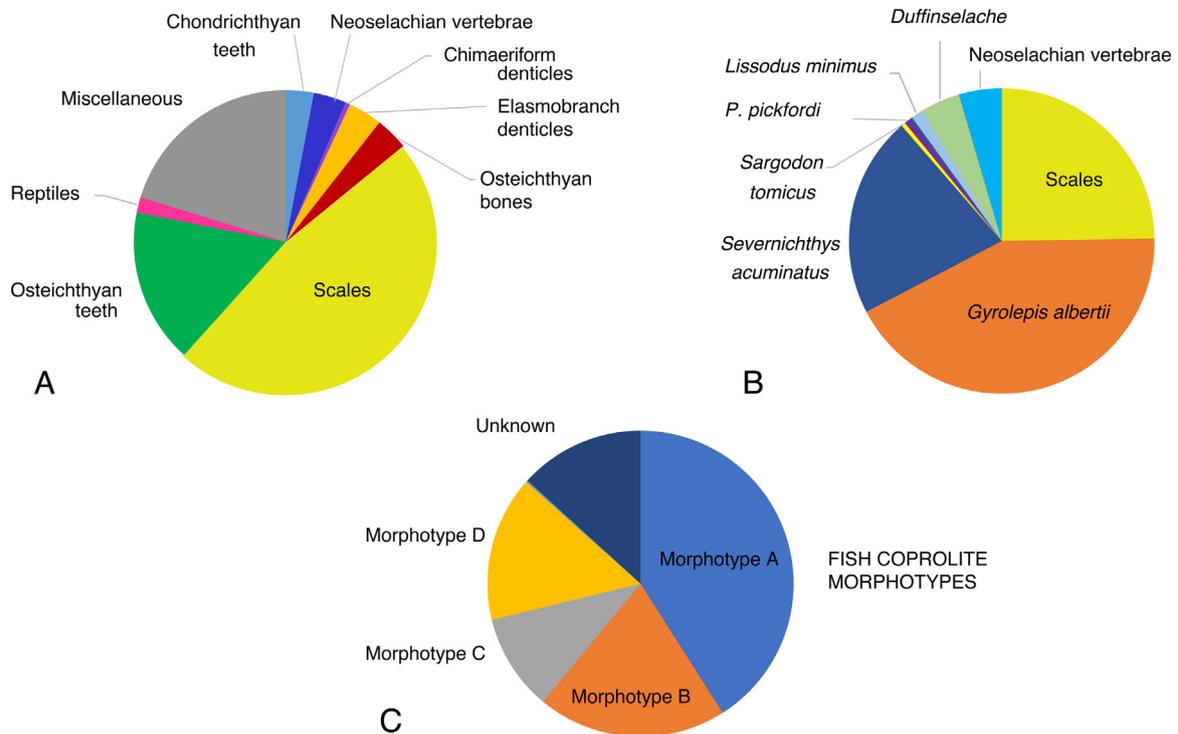
Hybodont sharks were the dominant predators in Late Triassic marine vertebrate communities (Rakshit et al., 2019). According to Cross et al. (2018), the faunas of the quarries around Bristol were similar in terms of species diversity, and there are four main taxa: *Lissodus minimus*, *Rhomphaiodon minor*, *Gyrolepis albertii* and *Severnichthys acuminatus*, namely two sharks and two bony fishes. Of these, the most common species in five quarries (Aust Cliff, Manor Farm, Hampstead Farm, M4 Junction and Charton Bay) is *Lissodus minimus*, and this is the second most common species in Stowey Quarry (Cavicchini et al., 2018). Nevertheless, the relative abundance of species is quite different among the quarries, even if the taxa are approximately the same.

In censuses of the large collections of teeth, scales and other bones from HFQ, Mears et al. (2016) noted that osteichthyan remains made up 66 % of the collection of over 26,000 specimens, chondrichthyan remains made up 12 %, marine reptile remains 2%, and indeterminate remains 20 % (Fig. 12A). These figures combine information derived from sampling of two productive bone beds, the basal Rhaetian bone bed, and the so-called 'bed 9', some 4 m higher, at the top of the Westbury Formation, as well as several intermediate beds. This sampling showed (Mears et al., 2016, fig. 20) changing proportions of different taxa through time. The durophagous shark *Lissodus minimus* comprises nearly 50 % of identifiable teeth in the basal bone bed, and the predatory *Rhomphaiodon minor* is also present. These two disappear in higher beds, and the shark *Pseudocetorhinus pickfordi* appears, comprising 20–45 % of the sample, as well as rare examples of *Duffinselache* and *Sargodon*. The osteichthyans *Gyrolepis* and *Severnichthys* are present throughout, comprising respectively 15–55 % and 20–50 % of the fauna, varying in importance between the different horizons. The collection from bed 9, near the top of the Westbury Formation (Fig. 12B), lacks the larger elements, and comprises 40 % *Gyrolepis albertii* teeth, 25 % *Severnichthys acuminatus* teeth, 25 % osteichthyan scales, and 10 % chondrichthyan teeth and scales.

### 6.2. Assigning fish coprolites to producers

The sample of 1062 vertebrate coprolites from HFQ show that Morphotype A was dominant (41 %), followed by Morphotype B (20 %), Morphotype D (16 %), Morphotype C (10 %), and Morphotype E (0.2 %). Coprolites of 'unknown' morphotype comprise 13 % of the collection (Fig. 12C). These proportions might suggest that, for example, the most common coprolite, morphotype A, was produced by the most common fish at HFQ, perhaps *Gyrolepis albertii* (Fig. 12B). However, *Gyrolepis* was not the most abundant fish at every level through the Westbury Formation: *Lissodus minimus* was most common in the basal bone bed, and at times *Severnichthys* or *Pseudocetorhinus* were most abundant (Mears et al., 2016, fig. 20).

In fact, identifying producer and coprolite by referring to relative proportions is fraught with difficulty. First, estimating percentages of different fishes based on their isolated teeth, scales and bones (Fig. 12A, B) is difficult because most microremains are unidentifiable, and of those that are identifiable, there is no way of knowing whether teeth were shed at an equivalent rate in all



**Fig. 12.** Comparison of relative proportions of the main faunal elements from Hampstead Farm Quarry (A, B) and coprolites (C): pie charts of (A) the entire Curtis collection (n = 26,237); (B) specimens from bed 9 (n = 2862); and (C) coprolite morphotype proportions (n = 1066). (A, B) Modified from Mears et al. (2016, fig. 18); (C) data from this paper.

species. Second, we suffer similar, or greater, problems in estimating proportions of coprolite types – do all fishes produce as many coprolites as each other over a fixed time span, and do they all survive fossilisation equally well? Hunt et al. (2015) gave a specific case, where the Chalk fish faunas contain far higher diversities of taxa than the corresponding collections of spiral coprolites, an anomaly they termed the “shark surplus.”

There are also taphonomic considerations. We simply cannot be sure that all coprolites are preserved or if some were chemically different and lost through diagenesis (Hansen et al., 2016). Further, coprolites of carnivores contain higher amounts of phosphate than those from herbivores because of the bones and scales they pass through their guts, and the amount of phosphate determines how well the coprolites survive in the fossil record (Schiffbauer et al., 2014). This is probably why there are many more carnivorous coprolites in our sample than those of durophagous or herbivorous producers, whereas durophages such as *Lissodus*, *Sargodon* and *Lepidotes* are relatively abundant at some levels.

This idea of comparing proportions of skeletal taxa and proportions of coprolites was applied by Woodward (1917) when he was trying to assign Early Jurassic coprolites to marine reptiles or large sharks. Such allocations might be possible where, as in Woodward’s case, the decision is between two major taxa, especially where one species is very common and the other is quite rare. In our Rhaetian example, it is much harder because numerous species of fishes were apparently present in similar proportions, and they are all of similar size, so we cannot even use coprolite size as a possible indicator of species provenance.

What about relative sizes? On the whole, large animals might be expected to produce large coprolites (Qvarnström et al., 2019), but this is only a very general rule and there is no exact relationship between coprolite length or width and body length or mass of the producer. Further, it might be argued that the size of coprolite inclusions would indicate the size of the producer, because for almost all marine animals, a predator is bigger than its prey. However, some coprolites in the BRSUG collection contain

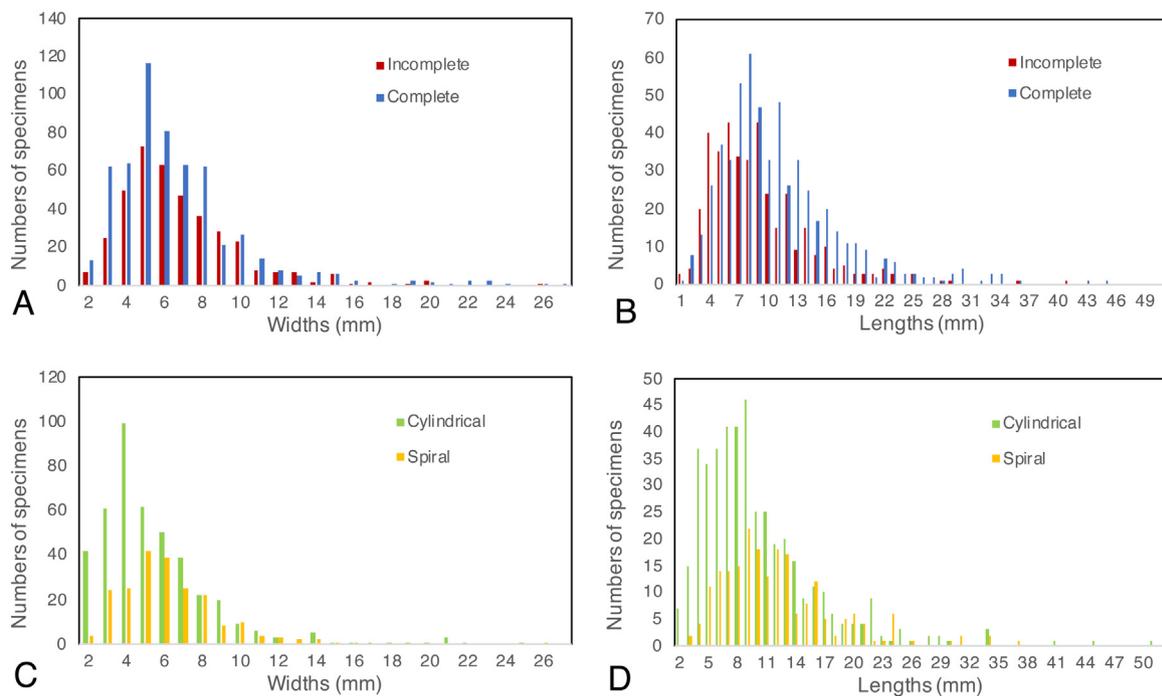
inclusions (scales) that are larger than their own size, and this shows that during Rhaetian times at least, predators were grabbing prey of all sizes and presumably did not yet have the stomach acids to reduce the bones and so would have to pass often relatively huge skeletal debris.

In terms of predator and coprolite relative sizes, there is a special case for spiral coprolites: maximum body size is proportional to the maximum number of valves, although with some exceptions (Argyriou et al., 2016). In the case of a coprolite with < 10 valves, the producer is at most 2–3 m long, and for < 5 valves the maximum length is 1–2 m (Argyriou et al., 2016). Most of our spiral coprolites show fewer than five valves, which suggests that the average length of the HFQ fauna was not above 1 m, because the largest predatory sharks are the producers of the spiral coprolites. Most of the prey was smaller than these predators, so overall mean fish size was < 1 m.

In our coprolite sample, the size ranges show some variations. First, when considering complete and incomplete coprolites (Fig. 13A, B), there is little difference in the distributions of widths and lengths. Further, the mean widths are very similar, at 6.79 mm for incomplete specimens and 6.64 mm for complete specimens. However, the lengths differ, as expected, because incomplete specimens (mean length, 9.83 mm) are shorter on average than complete specimens (mean length, 11.87 mm).

The size distributions of cylindrical (morphotype A) and spiral (morphotype B) types of coprolites appear to differ, with seemingly many more small-sized examples of the cylindrical coprolite type (Fig. 13C, D). However, the mean sizes do not bear this out, showing rather similar mean sizes for cylindrical coprolites (width 6.40 mm, length 11.11 mm) and spiral coprolites (width 6.28 mm, length 12.16 mm). The concentration of smaller cylindrical coprolites reflects the larger size of the sample (440 specimens of cylindrical coprolites; 211 specimens of spiral coprolites measured), and the fact these sizes are offset by only 1–2 mm smaller.

In all cases, the distributions of size tallies (Fig. 13) are right skewed, meaning there is a preponderance of smaller specimens



**Fig. 13.** Size ranges of 900 coprolites from Hampstead Farm Quarry (A, B) Widths (A) and lengths (B) of incomplete and complete coprolites in the complete sample. (C, D) Widths (C) and lengths (D) of large samples of coprolites of morphotype A (cylindrical) and B (spiral).

and a long tail to the right. This size distribution could emerge from a sedimentological process whereby smaller specimens are favoured by current energy which perhaps leaves larger specimens upstream. On the other hand, the skewed distribution could be biological, indicating a dominance by smaller fishes, with smaller numbers of larger forms producing larger coprolites to the right-hand end of the distribution.

Coprolite inclusions can identify the prey. In the HFQ collection, the most common are actinopterygian fishes, with characteristic shapes and structures of scales. Scale size need not indicate prey size as a single fish might have relatively large or relatively small scales in proportion to body size, or a mix of scales of multiple sizes.

There is, as noted, a mismatch in the presence of durophagous fishes, which are common at Aust (Cross et al., 2018), and the coprolite contents. Further, although fossil invertebrates such as bivalves, gastropods, brachiopods and echinoids have been reported commonly from the British Rhaetian (Storrs, 1994; Swift and Martill, 1999), no remains of any of these were visible in the coprolites of our sample (although durophagous predators might have spat the shells out before swallowing). *Lepidotes* might also have fed on small gastropods and bivalves (Thies et al., 2019), forming a partially durophagous diet, although we have no evidence of that from the British Rhaetian.

Crustaceans have been found in Rhaetian coprolites, such as remains of the decapod *Tropifer laevis* in coprolites from Aust (Cross et al., 2018). Duffin (1978) suggested *Severnichthys* was a potential predator of *Tropifer laevis*, as well as *Gyrolepis albertii*. Many remains of crustacean shells have been found in the stomachs of the genus *Lepidotes* sp. from the Early Jurassic (Thies et al., 2019), so Rhaetian representatives of the genus might too have had a similar diet.

### 6.3. The Hampstead Farm food web

We present an estimated food web (Fig. 14) based on a food web reconstructed for Aust (Cross et al., 2018), and modified

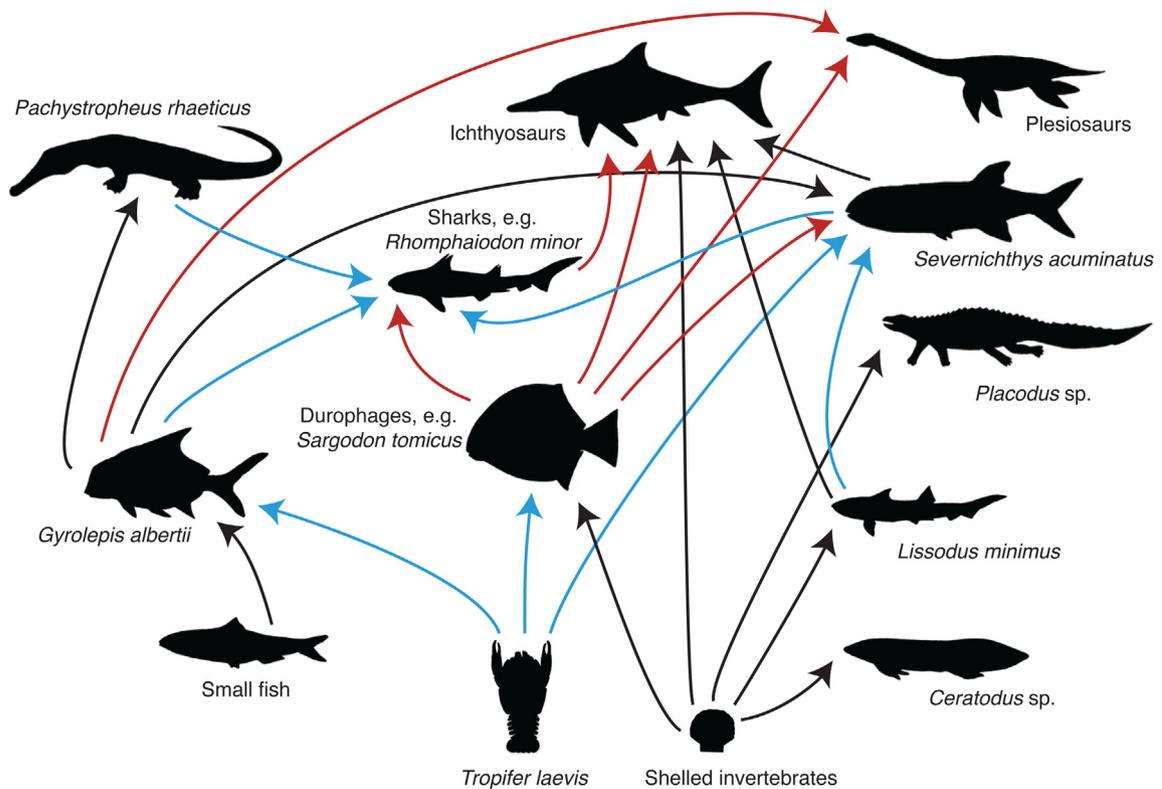
based on data from HFQ, and especially from the coprolites. The base of the food chain comprises shelled invertebrates (bivalves, gastropods, brachiopods, echinoderms), all with calcium carbonate skeletons, the crustacean *Tropifer laevis*, as well as plankton (not shown).

The shelled invertebrates likely formed the diet of durophagous fishes such as *Sargodon tomicus*, *Lepidotes* and the small shark *Lissodus minimus*. The osteichthyan *Sargodon tomicus* could reach 1 m long (Tintori, 1998; Latimer and Giles, 2018), but was probably a common prey item for predatory fishes and marine reptiles because of its durophagous diet and the deep-bellied shape of its body, which is peculiar to slow-moving swimmers (Tintori, 1998). The osteichthyan *Lepidotes* was also a durophage (Cavin et al., 2015), and could be a part of the prey in our sample, as shown by scale inclusions (e.g., Fig. 6E). Finally, the shark *Lissodus minimus* also had teeth that indicate that it crushed hard-shelled benthic prey (Fischer, 2008; Korneisel et al., 2015; Lakin et al., 2016; Cross et al., 2018), with a body size range from 15 to 50 cm. Its abundance and small size suggest that it was prey for bigger predators such as *Severnichthys* or marine reptiles.

These durophagous fishes were relatively abundant in the HFQ fauna (Fig. 12A, B), and so might be expected to have produced abundant coprolites, but these would not have contained inclusions such as scales or bones, and the coprolite shape might be cylindrical or flattened. More than 55 % of the cylindrical coprolites from HFQ have no inclusions visible on the surface, and many of them could have been produced by durophagous fishes, such as *Lepidotes* or *Sargodon*.

The lungfish *Ceratodus*, which have a plant and soft-bodied invertebrates diet, is a durophagous fish with a small size (Cavin et al., 2015), and could be at the same trophic level as other durophages fishes which are eaten by larger predators. However, it is unlikely that it was a prey item, unless its carcass was scavenged or there was a shortage of other prey.

The predatory *Rhomphaiodon minor* is the second most important shark found in the Rhaetian bone beds of the Bristol area, feeding on smaller fishes like *Gyrolepis* or *Sargodon*. It was



**Fig. 14.** Reconstructed food web for the Hampstead Farm bone bed, showing all the taxa mentioned in the paper. Arrows indicate the line from prey to predator. The blue arrows indicate predator-prey relationships inferred in this study from coprolites, the red arrows inferred by Cross et al. (2018), and the black arrows other likely relationships. Modified from Cross et al. (2018).

probably be the producer of many spiral coprolites with included scales of osteichthyans.

Only 17 % of cylindrical coprolites have more than five visible inclusions: potential producers of these specimens might not have been top predators and should probably be attributed to the osteichthyan *Gyrolepis albertii*. *Gyrolepis* was some 20 cm in length (Tintori, 1998) and it was a predator, presumably feeding on young fishes, plankton and possibly crustaceans such as *Tropifer*. According to scales in coprolites, *Gyrolepis albertii* was by far the most common prey species, and it must have been abundant and easy to catch by many larger predators at HFQ as it occurs in coprolites of all sizes.

*Severnichthys*, like other saurichthyiform bony fishes was a fast moving piscivorous predator about 1 m long (Wu et al., 2013; Cross et al., 2018; Tintori, 2019). *Severnichthys* was probably an opportunist, feeding as scavenger or predator depending on what was available, likely including *Gyrolepis albertii* and *Sargodon tomicus* (Cross et al., 2018). In studies of its relative *Saurichthys*, Northwood (2005) noted that some coprolites contain only one type of scales of similar size and shape, suggesting predatory behaviour, whereas Tintori (2019) presented some gut contents from the Italian Middle Triassic attesting to scavenging behaviour. At HFQ, *Severnichthys* may be associated with large coprolites: the largest from HFQ is 52 mm long and 23 mm wide (BSRMG Cf10182, Fig. 51), and the largest coprolite with inclusions from Aust is 31 mm long and 21 mm wide, but it is incomplete and so was probably at least 50 mm long. These coprolites may have come from a marine reptile or a large predatory fish such as *Severnichthys*. *Severnichthys* in turn could have been the prey of conspecific cannibals as well as ichthyosaurs (Tintori, 2019).

One of the most unexpected fossils is the coprolite BSRMG Cf15467 containing caudal vertebrae of the slender marine reptile *Pachystropeus rhaeticus* (Fig. 8). This specimen also contains a

possible *Severnichthys* skull bone, so the predator appears to have nipped off the tail of a *Pachystropeus* at about the same time as it swallowed at least a chunk of a *Severnichthys* head. Generally, the inclusions within a coprolite tend to belong to a single species, and presumably a single individual. Where the predator was not enormously larger than the prey, this would be expected – each prey item would be processed, digested and excreted before the next prey was tackled.

Most *Pachystropeus rhaeticus* fossils from the Rhaetian of England suggest they are from an animal measuring about 1 m long (Storrs, 1994), and would have been eaten by predators such as large sharks and marine reptiles; sharks are indicated in cases where the bones are in spiral coprolites (Cross et al., 2018). BSRMG Cf15467 is apparently only part of a coprolite, and possibly a spiral coprolite, so it was probably produced by a shark.

#### 6.4. Breakdown of prey in coprolites

According to Rakshit et al. (2019), hybodont sharks retained their food for a long time in digestive transit, as indicated by the large surface for nutrient absorption in the scroll intestines. The longer the period the food is held in the gut, the more effective the action of gastric juices and the less intact the ganoine layer remains on the scales in the swallowed prey (Barrios-de-Pedro et al., 2018). We suggest then that the food may have passed rather rapidly through the guts of our predators because many *Gyrolepis* scales included in coprolites, such as those of *Gyrolepis* (Fig. 9A–C), bear most or all of the black, sculpted outer ganoine layer. The edges of the scales may be blunted or rounded, possibly by some acid digestion in the predator gut, as seen in the CT-scanned coprolites (Figs. 6–8). Short retention time in the gut may be characteristic of an environment with abundant prey (Barrios-de-Pedro et al., 2018).

The breakage rate of coprolites can be affected by the diet of the producer (Northwood, 2005), but this is probably masked by the fact that most of the HFQ fossils were transported a considerable distance (Mears et al., 2016).

## 7. Discussion

### 7.1. Early start of the Mesozoic Marine Revolution

The Triassic was a key period for the development of the “Modern” marine fauna. The Mesozoic Marine Revolution (MMR) marked an important turning point in the evolution of marine ecosystems, and more precisely their trophic chains, predator–prey interactions being a central part of ecosystem shifts. The Permo-Triassic mass extinction (PTME) triggered an overhaul of ecosystems, and then the setting up of the “Modern fauna” in place of the previous “Palaeozoic fauna” (Sepkoski, 1984), clearly apparent in the marine environment notably in the marine primary producers (Knoll and Follows, 2016) and the invertebrates. This was paralleled on land by the emergence of a similarly ‘modern’ fauna, characterised by dinosaurs, but also the first frogs, turtles, lizards, crocodylians and mammals (Benton, 2016).

For a long time, events in the Triassic, as the Modern marine fauna became established were treated as separate phenomena from Vermeij’s (1977) Mesozoic Marine Revolution (MMR). He noted that typical Mesozoic and modern marine predators, such as malacostracan arthropods (crabs and lobsters), gastropods, echinoids, and vertebrates (including neoselachian sharks, teleost bony fishes, and marine reptiles) were all faster and nastier than their Palaeozoic precursors. As predators became faster in order to catch their prey, the prey evolved means of escape, including a thicker shell or the ability to burrow deep. Predatory modes also became more deadly, with many fishes and reptiles becoming durophages, capable of crushing thick-shelled oysters, and with gastropods perfecting their hole-piercing equipment to penetrate through shell to flesh, and sharks and teleosts with mobile mouth parts to enlarge their gapes. Vermeij pointed to the origins of many of these adaptations in the Cretaceous and suggested the MMR began in the Jurassic.

New evidence, however, contradicts this earlier view, and suggests that there was a first phase of the MMR in the Triassic. New finds from Europe and especially from China provide evidence for an explosion of malacostracans, fast-swimming, and durophagous neopterygian fishes, and marine predatory reptiles in the Early and Middle Triassic (Hu et al., 2011; Benton et al., 2013; Brayard et al., 2017), more than 100 Myr earlier than Vermeij (1977) had suggested, and if this is true, it links the initial driver of the MMR to the recovery of life following the PTME.

There is direct evidence for a faster pace of the arms race in Middle Triassic seas when compared to the Palaeozoic. For example, the major bivalve clade Pteriomorpha, which diversified through the Triassic and Jurassic, and includes mussels, scallops, and oysters, shows a particular ligament that substantially strengthened the hinge line (Hautmann, 2004). It enabled pteriomorphs to adopt one of two new defence strategies, in oysters and mussels to clamp down and keep the shell shut against attempts to prise it open by starfishes, and in scallops and other swimmers to close the shell fast under attack and to escape by snapping shut and squirting water out.

In addition, Baumiller et al. (2010) reported evidence for active predation by cidaroid echinoids on stalked crinoids from the Middle Triassic of Poland, with the suggestion that this element of the MMR arms race promoted the evolution of motile crinoids as a means of escape from predation. Also, from the Middle Triassic of Poland, regurgitates of bivalve shell debris and crinoid remains (‘bromalites’) have been interpreted as produced by the new

durophagous predators (sharks, colobodontid fish, placodonts, and some pachypleurosaurs), and explicitly posited as evidence for an early start of the MMR (Salamon et al., 2012). Moreover, the increasingly effective adaptations for avoidance (infaunalization), escape (facultative mobility), and resistance (cementation) of level-bottom benthos during the Norian Stage reflected the elevated frequency of demersal or epifaunal durophagous predation in Late Triassic oceans (Tackett, 2016; Tackett and Bottjer, 2016).

A Triassic start for the MMR was already suggested by Harper et al. (1998) when they reported high levels of boring predation marks on bivalve shells from the Lower Jurassic. Such boreholes, evidence of the new gastropod predation modes, were reported also from the Triassic (Fürsich and Jablonski, 1984). Strong external shell sculptures, interpreted as an antipredatory feature, and typical of the MMR (Vermeij, 1977), are reported in Triassic gastropods and bivalves (Nützel, 2002). This all suggests that the MMR began in the Triassic, and the likelihood is that this early start is associated with two consequences of the PTME. First is that the extinction cleared ecospace and allowed new taxa to dominate Triassic ecosystems, and these new taxa established new, faster life modes and arms races than seen in the Palaeozoic. Second are the more immediate aspects of the turmoil of post-PTME seas, when harsh environmental conditions interfered with the recovery and forced some strong ecological interactions. During the Early and Middle Triassic, new clades with their new adaptations emerged, both new antipredatory strategies such as thickened shells and cementation in oysters and mussels, snap escape swimming by scallops, motile crinoids, prominent sculpture by gastropods and bivalves, and deep burrowing by many taxa, as well as the new hunting modes, including shell snipping by malacostracans, hole boring using chemical and mechanical means by gastropods, and durophagy by diverse fishes and reptiles.

This first phase of the MMR was boosted by the plankton revolution of the Late Triassic (Falkowski et al., 2004) when all modern marine plankton (calcareous nannoplankton, planktonic foraminifera, dinoflagellates, radiolaria, marine diatoms) originated or diversified. These provided the basis for new trophic structures in the oceans and could have triggered the explosive diversification of consumers at all levels during the Norian and Rhaetian.

### 7.2. Rhaetian marine communities and the MMR

The high proportion of durophagous fishes in Rhaetian bone beds, including the sharks *Lissodus* and the bony fishes *Sargodon* and *Lepidotes* already noted in previous studies (Korneisel et al., 2015; Cross et al., 2018), marks a change between the Palaeozoic and Modern marine faunas and evidence of the arms race between this kind of predator and the shelled invertebrates (Signor and Brett, 1984; Walker and Brett, 2002; Barhdan and Chattopadhyay, 2003; Knoll and Follows, 2016). These durophagous fishes diversified in the latest Triassic and Early Jurassic, perhaps partly ecologically replacing the placodonts, which were durophagous, shell-crushing marine reptiles. Some, such as *Dapedium* specialised in crushing shells of molluscs (Smithwick, 2015), whereas other such as *Lepidotes* may have specialised in more elusive, softer-shelled prey such as crustaceans (Thies et al., 2019).

The Rhaetian documents an extensive fauna of marine invertebrates that were key constituents of the ‘Modern’ fauna, including bivalves, gastropods, and crustaceans (Swift and Martill, 1999). Unfortunately, no clear evidence of mollusc or crustacean remains has been noted in the coprolites here. However, the crustacean coprolites we report from HFQ provide evidence to match reports of *Tropifer laevis* in association with the Rhaetian bone beds (Duffin, 1978). An important shift in crustacean

populations occurs during Mesozoic Marine Revolution, with notably a diversification of decapod crustaceans during the Jurassic (Buatois et al., 2016).

The Rhaetian bone bed fauna shows some transitions between old and new. The Late Triassic and Early Jurassic interval saw replacements of hybodont sharks by neoselachian sharks and 'holostean' fishes by teleosts (Cuny and Benton, 1999; Underwood, 2006; Friedman and Sallan, 2012; Smithwick and Stubbs, 2018). The Rhaetian bone beds around Bristol, including Hampstead Farm and Aust, show dominance by the hybodontiform shark *Lissodus*, but the neoselachian *Rhomphaiodon* is also an important part of the fauna. The bony fishes, such as *Gyrolepis*, *Sargodon*, and *Lepidotes* are all at the 'holostean' level, and we see no teleosts in the Rhaetian bone beds.

### 7.3. Buckland and the nomenclature of Rhaetian coprofaunas

Most of the coprolites figured by Buckland appear to fit well with those designated as Morphotype A here (Buckland, 1835, pl. 30 figs 13–16, 18–28), with one specimen matching sub-morphotype A3 (Buckland, 1835, pl. 30, fig. 19). One of the coprolites figured by Buckland may belong to Morphotype D (Buckland, 1835, pl. 30 fig. 29). Neither Buckland (1835) nor Duffin (1979) described or figured any specimens of submorphotype B1 (scroll spiral coprolite), although both authors included coprolites of submorphotype B2 (Buckland, 1835, pl. 30 fig. 17; Duffin, 1979, pl. 21 Figs. 7–9). Duffin's (1979) Type 1 and Type 2 coprolites show spiral morphology and are therefore generally similar to Morphotype B coprolites in the present paper, although note that details of the coiling and presence or absence of inclusions preclude an exact match. The Type 3 coprolites of Duffin (1979) correspond to those of Morphotype A here, and Type 4 coprolites of Duffin (1979) may correspond in part to Morphotype C of this paper.

Duffin (1979, p. 196) remarked on the difficulty of assessing the relative abundances of different coprolite morphotypes from the British Rhaetian, and the bone beds in particular. The HFQ collection has provided an opportunity to address this difficulty, at least for the upper parts of the Westbury Formation (probably Late Rhaetian). But is the HFQ fauna similar to those described by Buckland (1835) from Aust, Westbury Garden Cliff and Watchet, and by Duffin (1979) from the basal bone bed at Aust and Lavernock?

It is interesting to note that, while there are similarities, there is no exact equivalence between the coprofauna of HFQ and those of the basal bone beds elsewhere, suggesting that further work on the coprolites of the British Rhaetian is warranted to refine both the classification of its contained coprolites, and to investigate more fully the reasons for coprofaunal differences at different levels in the succession and at different localities. To what extent, for example, are these variations due to differences in community structure, to sedimentary regime or to other factors?

### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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