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Multi-proxy analyses of Late Cretaceous coprolites from Germany

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Abstract: A total of 462 coprolites from three localities exposing Upper Cretaceous deposits from the Münster Basin, northwestern Germany, have been subjected to an array of analytical techniques, with the aim of elucidating ancient trophic structures and predator–prey interactions. The phosphatic composition, bone inclusions, size and morphology suggest that most, if not all, coprolites were produced by carnivorous (predatory or scavenging) vertebrates. The bone inclusions further indicate that the coprolite producers preyed principally upon fish. Putative host animals include bony fish, sharks and marine reptiles – all of which have been previously recorded from the Münster Basin. The presence of borings and other traces on several coprolites implies handling by coprophagous organisms. Remains of epibionts are also common, most of which have been identified as the encrusting bivalve *Atreta*. Palynological analyses of the coprolites and host rocks reveal a sparse assemblage dominated by typical Late Cretaceous dinoflagellates, and with sub-ordinate fern spores, conifer- and angiosperm pollen grains. The dinoflagellate key taxon *Exochosphaeridium cenomaniense* corroborates a Cenomanian age for the Plenus Marl. The findings of this study highlight the potential of a multiproxy approach when it comes to unravelling the origin, composition and importance of coprolites in palaeoecosystem analyses.

Keywords: Coprolites, Münster Basin, Late Cretaceous, Palaeoecology, Cenomanian

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The behavioural repertoire of long extinct organisms is difficult to assess and usually relies on inferences from circumstantial evidence. The palaeobiological “tool box” for such studies commonly includes statistical analyses of associated and/or co-occurring fossils (such as potential predators and prey animals), theoretical models, trace fossil analyses, and inferred functional morphology and phylogeny. Although infrequently preserved, the fossil record can also yield extraordinary material that documents behaviour and organismal interactions more directly, with illustrious examples including fish putatively choking on large prey, dinosaurs that died while fighting, or organisms caught in the act of reproduction (e.g., Kowalewski 2002; Joyce *et al.* 2012, and references therein). Such unusual fossils typically derive from Konservat Lagerstätten, and amber deposits in particular (Poinar & Poinar 1994).

Occasionally, however, seemingly unremarkable fossils can provide quite remarkable insights. Coprolites, or fossil faeces, represent one such group. Despite their rather unappealing origin (and sometimes morphology), they can provide extraordinary palaeobiological and palaeoecological information, obviously with a focus on diet, feeding, predation, and parasitism of long extinct animals (e.g., Bertrand 1903; Prasad *et al.* 2005; Poinar & Boucot 2016; Eriksson & Terfelt 2007; Eriksson *et al.* 2011; Dentzien-Dias *et al.* 2013; Shen *et al.* 2014; Zatoń *et al.* 2015; Peel 2015; Vajda *et al.* 2016; Bajdek *et al.* 2016; Qvarnström *et al.* 2017). Moreover, coprolites can reveal novel aspects of the digestive system of the producer (e.g., Chin *et al.* 1998; 2003; Bajdek *et al.* 2016). Furthermore, they can form “micro-Lagerstätten” that preserve labile structures, organisms or parts thereof, and biomarkers that typically are rare or otherwise lacking in the fossil record (e.g., Chin *et al.* 2003; Northwood 2005; Zatoń *et al.* 2015; Qvarnström *et al.* 2016, 2017). Another significant advantage – which is counter-intuitive given their origin and primary characteristics – is that these fossils are quite common in the Phanerozoic fossil record (e.g. Hunt *et al.* 2012).

Despite problems of linking coprolites to specific producers, their potential as sources for palaeobiological information has been much appreciated. In the published literature there is, however, a bias towards coprolites produced by vertebrates and particularly those from carnivores, partly because they are often less complicated to identify but also because they seem to be more commonly preserved than are those of herbivorous animals (Chin 2002; Hunt *et al.* 2012).

In this study, we have analysed a large number of coprolites from the Upper Cretaceous strata of the Münster Basin, north-western Germany. By subjecting these ancient faeces to a wide range of analytical techniques we aimed at categorising and describing them, thereby elucidating the nature and composition of coprolites from this region and time interval. These data can, in turn, provide insights into the affinity of the scat producer and nature of their prey, as well as having taphonomic and palaeoenvironmental implications.

Geological setting

The Late Cretaceous was a time of fluctuating sea levels which occasionally reached around 200 m higher than today (Miller *et al.* 2005; Müller *et al.* 2008, and references therein). In the Late Cretaceous, as a result of a prominent transgression (e.g., Vajda & Solakius 1999; Wilmsen 2007), the Münster Basin in what is nowadays North Rhine-Westphalia (north-western Germany) became part of an extensive epicontinental sea north of the Rhenish-Bohemian island, which (in Central Europe) separated the Tethys from the boreal realm. Today, the Münster Basin is manifested by a wide syncline with deposits locally exceeding 2000 m in thickness. Cretaceous sediments, with a stratigraphic range from lower Cenomanian to upper Campanian, are mainly underlain by Carboniferous deposits and partly covered by Cenozoic sediments (Fig. 1; Kronimus *et al.* 2008). The coprolites documented herein derive from three Cretaceous localities within the Münster Basin: The Rauen quarry (Mülheim-Broich), Lünen-Nordlünen (former Robbert brickyard) and Lüdinghausen-Seppenrade (former Pilgrim brickyard; see Appendix).

The Rauen quarry is located on the eastern flank of Kassenberg, a hill on the western shore of River Ruhr within the Broich district of the city of Mülheim an der Ruhr (Figs 1 and 2). The quarry has been excavated for Carboniferous shale and sandstone for more than one hundred years, and is still active on a small scale (Kasielke 2011). Upper Cretaceous sediments unconformably overlie Carboniferous sediments, and were first described by Kahrs (1927). He mentioned the extremely rich occurrence of fossils in ochre to reddish limestones (“Rotkalk”), found in wave-cut pockets within the Carboniferous sandstone and as matrix within a conglomerate bed, overlying deeply eroded Carboniferous shale between two sandstone ridges. This was interpreted by Kahrs (1927) as a barrier beach, which he called “Strandwall”. Nowadays, the “Rotkalk” is defined as a special facies of the Essen Greensand Formation (Hiss 2006a). A comprehensive list of fossils and references was provided in 1995 by Scheer & Stottrop (1995). Since then, a highly diverse gastropod fauna has been described (Kiel & Bandel 2004), the first occurrence of marine turtles from this facies revealed (Sachs *et al.* 2016), and roveacrinid crinoids studied (Hess & Thiel 2015). The first biostratigraphic subdivision of the “Rotkalk” on the basis of ammonites was provided by Hancock *et al.* (1972) and Wiedmann & Schneider (1979). This was later revised by Kaplan *et al.* (1998) to range

from the basal *Mantelliceras mantelli* Zone (*Neostlingoceras carcitanense* Subzone) into the upper part of *Mantelliceras dixonii* Zone of the lower Cenomanian.

Several phases of successive sea level changes have been identified in the Upper Cretaceous strata in the Rauen quarry (Fig. 3; Scheer & Stottrop 1995, and references therein). The thick glauconitic Plenus Marl was deposited (during Phase 5) following a hiatus corresponding to the late lower Cenomanian to early late Cenomanian. Compared to the “Rotkalk”, little work has been done on the fossil content of this unit, which in the western localities of the Ruhr area forms the upper part of the Essen Greensand Formation. As the Plenus Marl could be found overlying the “Strandwall” in the above mentioned wave-cut pockets, Kahrs (1927) included both of these units in what he called “Klippenfazies” (cliff-facies). The glauconitic Plenus Marl is characterized by the occurrence of the belemnite *Praeactinocamax plenus* (Blainville 1827) and has been correlated with the *Metoicoceras geslinianum* ammonite Zone (Fig. 3). Unlike other localities, the Plenus Marl in the Rauen quarry (and especially its basal part) is rich in fossils. Invertebrate body fossils, including oyster-like bivalves, corals (*Synhelia gibbosa* and cf. *Moltkia*), and large quantities of excrement, were deposited during this phase, leading to extensive phosphate accumulation (Scheer & Stottrop 1995).

The Plenus Marl is overlain by what was traditionally called the Labiatus Marl (Phases 6–7) from the early Turonian, but which has later been defined as the Büren Formation (Hiss *et al.* 2006). This extensive transgression was followed by a regression that entailed a hiatus, which includes the middle Turonian (Phase 8), and resulted in the deposition of the Soest Greensand Member of the Oerlinghausen Formation (Phase 9). Dölling *et al.* (2017) proposed that this member should be transferred into the newly established Duisburg Formation, a move accepted by the German Subcommission of Cretaceous Stratigraphy in the autumn of 2017. A rich phosphatized fauna, which may be partly reworked from older strata, occurs near the base of the Soest Greensand Member. Lommerzheim (1976) provides a list of the faunal content, which includes several ammonites and nautiloids. The ammonite taxa are currently being revised by W. J. Kennedy (Oxford) and U. K. Kaplan (Gütersloh), and the fauna indicates the upper Turonian *Subprionocyclus neptuni* Zone in the upper Turonian (pers. comm. to U.S.). Younger Cretaceous sediments are not preserved in the Rauen quarry.

Most of the studied coprolites from Rauen derive from latest Cenomanian deposits (the Plenus Marl, upper Essen Greensand Formation), which correspond to sea level phase 5. Some of the specimens found in the late Turonian, Soest Greensand Member may represent reworked Cenomanian specimens as well.

The other two coprolite-yielding localities, Lünen–Nordlünen and Lüdinghausen-Seppenrade, expose strata from the main (deeper) basin that were deposited during the upper Santonian and lower Campanian (Fig. 1). In both localities, marly sediments belonging to the Emscher Formation are accessible. This marl locally begins in the Coniacian (Hiss, 2006b). The Emscher formation is composed of argillaceous and partly sandy grey marls. It is widespread in the entire Münsterland region, and is also well known from Lower Saxony and Saxony-Anhalt (Arnold 1964b; Hiss 2006b). The Lünen–Nordlünen and Lüdinghausen-Seppenrade localities are not as well investigated as the Rauen quarry. The local fauna indicates the *Bohemoceras arcus/Marsupites testudinarius* Zone of the uppermost Santonian (Kennedy & Kaplan 2000).

The former Pilgrim brickyard in Lüdinghausen-Seppenrade is poorly investigated, but the local succession belongs to the lower Campanian Emscher Formation (M. Hiss, pers. comm. to U.S.).

Notes on the Late Cretaceous faunas of Germany

The Upper Cretaceous of the Münster Basin yields diverse invertebrate faunas; molluscs are notably abundant, but also vertebrates. Examples of the latter include rare turtle remains from the Cenomanian and Turonian (Diedrich & Hirayama 2003; Karl *et al.* 2012; Sachs *et al.* 2016), the mosasaur *Clidastes* from the upper Campanian of the Ahlen Formation, Beckum Member (Diedrich & Mulder 2004; Caldwell & Diedrich 2005), other marine reptiles, including ichthyosaurs and pliosaurs/plesiosaurs (Sachs 2000; Wittler & Roth 2000, Sachs *et al.* 2018) as well as a choristoderan, identified from an isolated vertebra (Reuss *et al.*, in prep.). Moreover, a wide range of cartilaginous and bony fish have been described from the basin (e.g. Marck & Schlüter 1858; Marck 1885; Marck 1894; Kaever 1985;

Müller 1989; Müller & Diedrich 1991; Scheer & Stottrop 1995; Müller 2008; Diedrich 2012; Müller 2014).

Lamniform and hybodont sharks, including *Cretoxyrhina mantelli*, *Isurus* cf. *angustidens* and *Ptychodus mammillaris*, have been described from the phosphatic beds of the Rauen quarry (Phase 5; Scheer & Stottrop 1995, and references therein), and these taxa are found throughout the entire Münster Basin. Kaever (1985) listed fish that occur in the upwelling-influenced greensands of the Münster Basin in the vicinities of Essen, Dortmund and Anröchte, including rare remains of *Xiphactinus* and *Berycopsis*. Moreover, Diedrich (2012) described trophic relations in fish assemblages across the Cenomanian-Turonian boundary and also mentioned the faunal components of the middle Turonian, with *Xiphactinus* and *Cretoxyrhina* as inferred top predators. *Xiphactinus*, the largest predatory bony fish at the time, could reach several metres in length, but was nonetheless preyed upon by *Cretoxyrhina*, the largest shark (Diedrich 2012). A similar trophic interaction between the two taxa is also indicated by stomach contents of a late Santonian-early Campanian *Cretoxyrhina* from North America, which contain remains of *Xiphactinus* (Shimada 1997).

The fauna of the middle Turonian phosphorites (Phase 8) includes poriferans, anthozoans, brachiopods, echinoids, pelecypods, gastropods, nautiloids, ammonoids, fish, and reptiles (Scheer & Stottrop 1995, and references therein). Coprolites, presumably deriving from fish (attributed to *Macropoma* sp.), have been described from these phosphorites (Wegner 1905; Scheer & Stottrop 1995), although some specimens may be reworked from older (Cenomanian) strata.

Materials and methods

The studied coprolite collection comprises 462 specimens stored at the Stiftung Ruhr Museum (formerly Ruhrlandmuseum) in Essen, Germany. The bulk of the material (>420 specimens) originates from the Rauen quarry. Most, if not all, specimens were either collected by museum staff in the 1920s or generously donated to the museum by Mr. Karl-Heinz Hilpert, who collected them over the last few decades. The fossils were subjected to a wide range of analytical methods (see below) performed at the Department of Geology, Lund University, Sweden (if not stated otherwise).

Photography and measurements

Selected specimens were photographed using a digital camera mounted on a table set-up with four external light sources. A few fossils were coated with ammonium chloride prior to photography in order to enhance the contrast. Measurements were taken with a vernier caliper.

X-ray fluorescence spectrometry (XRF)

A selection of coprolites, of different morphologies, and with or without visible inclusions, was analysed using XRF in order to semi-quantitatively assess their chemical composition. In addition, some sediment samples from Rauen quarry were analysed, as well as latest Santonian specimens of coprolites and their enclosing sedimentary matrix from Lünen-Nordlünen. A portable ThermoFisher Scientific Niton XL3t GOLDD+ instrument was used, with each analysis lasting 240 seconds. The NDTTr software package was used for analyses and processing of data.

CT-scanning

Computed tomography (CT) non-destructively allows 3D reconstruction of the internal coprolite structure and any inclusions (e.g., Villa & Lynnerup 2012; Milàn *et al.* 2012a). The CT-scanning was performed at the Department of Forensic Medicine, Copenhagen University. A Siemens Somatom +4 MDCT equipment was used and the parameters of the scan process were 120 kV and 200 mAs (highest possible ampere output for this medical scanner). The specimens were studied with perforating X-rays where an opposing detector plate collects values and creates a data set for processing. Because of the high density of the specimens a hard kernel 80 was used. To gain a high level of detail, the scanning was performed with pixel values (X, Y) of 0.5×0.5 mm; the reconstructed Z was 0.5 mm. This displays the object with isometric voxels (volumetric pixels), which provide truthful proportions of the specimens. The post-processing was performed at the

Anthropological Department of Copenhagen University using the software Mimics. The successive scans subsequently were stacked into 3D images that can be viewed from all directions.

Scanning electron microscopy (SEM)

A selection of ten specimens (including one piece of host rock) was studied in a Hitachi S-3400N Scanning Electron Microscope (SEM) in order to evaluate microscopic features and to search for inclusions. Prior to analysis, the coprolites were crushed with a hammer to reduce size, but also to expose fresh surfaces. The resulting fragments were mounted using double adhesive carbon tape onto glass slides, and subsequently coated with gold before being studied under SEM.

Thin sections

For the preparation of petrographic thin sections, the coprolites were initially sliced in transverse and/or longitudinal section using a slow-speed diamond saw. Because some specimens were rather brittle, they were embedded in transparent epoxy prior to sectioning. The resulting rock chips were then mounted on glass slides with epoxy, left to dry in an oven over night at 45 °C, and then ground to appropriate thickness.

Palynology

Six samples, four coprolites and two pieces of host rock, were sent to Global Geolab Limited, Alberta, Canada, for palynological processing. The aim was to date the samples, assess the paleoenvironment (proximity to land), and gain insight into the local Late Cretaceous vegetation. *Lycopodium* spores were added to the samples before processing with the intention to estimate productivity. A few additional sediment samples from the Rauen quarry were processed for palynomorphs with standard HF techniques as outlined in Vajda *et al.* (2013) at the Department of Geology, Lund University, Sweden.

Results

5.1 General coprolite characteristics

The coprolites vary from approximately 10 to 90 mm in length, and 5 to 28 mm in width. The largest are of Santonian age from Lünen-Nordlünen, and these specimens are retained in their host rock. The coprolites range from beige to dark brown in colour. Specific colour nuances are independent of coprolite morphology, sample locality and age, except for the A 0595 and A 0596 collection series (altogether comprising 44 specimens) of Middle Turonian coprolites from Rauen quarry that are all dark brown.

The coprolites are commonly anisopolar (i.e. the longitudinal terminations are of different shape), rod-like or ellipsoidal, and variably bent (Figs 4–6). However, a number of specimens are fragmentary and/or worn, rendering their original morphology difficult to assess. The majority of the coprolites appear to be spiral, although obvious coiling is only visible on the surfaces on some specimens (including most Santonian fossils). Of these, heteropolar coprolites (the spiral coils are concentrated to one end of the fossil, with the remaining part being composed of one large coil with a wide lip; e.g. Figs 4G, H, K, 5B) largely outnumber the possible amphipolar ones (with an even coiling throughout the length of the whole specimen; possibly Fig. 4I, J, M; see also Williams 1972; McAllister 1985; Hunt *et al.* 1994; Diedrich & Felker 2012).

5.2 Surface structures

The coprolite surface textures range from almost smooth and glossy (e.g., Fig. 4M; probably in part due to reworking, abrasion and/or geochemical differences related to secondary mineral deposits or the original mucosal coating of the excrement; cf. Thulborn, 1991) to rough and sculptured/pitted (Figs 4, 5). Several specimens possess distinct circular holes, ranging from one to almost 8 mm in

diameter (Fig. 6A–C). Similar structures have been described from other Cretaceous deposits, and are linked to coprophagous activity (e.g., Eriksson *et al.* 2011; Milàn *et al.* 2012b, figs 3, 4). Other coprolite specimens have grooves and pits on their external surface (Fig. 4I, L). Additionally, distinct striations (e.g., Figs 4D, F, J, N, 5B, 6E–G) are seen on many coprolites from Rauen quarry.

Another conspicuous feature is the presence of encrusting organisms (epifauna) on some coprolites. Several specimens, exclusively from the Rauen quarry, show remains of seemingly monospecific assemblages of the encrusting bivalve *Atreta* (Fig. 4B, C, L). They are strikingly similar to, and most probably conspecific with, *Atreta* sp. 1 of Žitt & Vodrážka (2013, fig. 9A, C) from the lower Turonian of the Czech Republic. This bivalve is common in the Upper Cretaceous rocky-coast facies of Bohemia (e.g., Žitt & Nekvasilová 1996; Žitt *et al.* 2006; Žitt & Vodrážka 2013). The individual *Atreta* specimens in the material at hand are in variable states of preservation (compare, for example, Fig. 4B *versus* 4L) and they generally appear to be randomly distributed on the surface of the coprolites. Also, when multiple specimens occur on one coprolite their umbonal direction differs. In addition to *Atreta*, putative bryozoans or worm tubes were observed on some specimens (Fig. 4B).

5.3 Inclusions

Inclusions are common, particularly in coprolites from the Plenus Marl, uppermost Essen Greensand Formation (latest Cenomanian, Phase 5), of Rauen quarry. Inclusions can be observed on the external coprolite surface (Figs 4, 6), as well as internally in the thin sections (Fig. 7) and CT-scanning data (Fig. 8). The most conspicuous inclusions are bone remains in various stages of fragmentation (Figs 4E, F, 6E, H, J). At higher detail, some of these inclusions show distinct lamellar structures, which probably represent the cortical portion of the skeletal element (see e.g. Fig. 7C1, E1). The bone fragments appear to have been subjected to various degree of digestive corrosion: some specimens appear markedly corroded with rounded and polished edges (Fig. 7A), whereas others seem more-or-less unaltered (Fig. 7C).

In the CT data, the high-lighted (light green) parts in specimen A 0972/3 and A 5921/2 likely represent bone material (Fig. 8A, A1, B1, B2). Conversely, the bright areas in specimen A 1019 are similar to the adjacent rock matrix (Fig. 8C1) and are most likely too dense to represent bone material.

5.3.1 Palynomorph inclusions

Assemblages of dinoflagellates, green algae, fresh-water algae, pollen, spores, and amorphous organic matter were identified in the acid-resistant residues of the coprolites and host sediment (Fig. 9). The palynomorphs are well-preserved but sparse, indicating a well-oxygenated marine environment. Dinoflagellates dominate the assemblages, followed by green algae, spores and pollen. Seven dinoflagellate taxa were identified, of which *Achomosphaera ramulifera* and *Exochosphaeridium cenomaniense* are age-diagnostic, indicating a Turonian and Cenomanian age, respectively. Recognized green algae include *Lecaniella jaenata*, *Pleourozonaria* sp. and *Tasmanites* spp. Spores and pollen are uncommon and only two conifer pollen grains were identified.

5.4 Internal architecture and coprofabrics

Scanning electron microscopy and energy-dispersive X-ray microanalysis revealed that most coprolites consist of a microporous fabric, with characteristic calcium phosphatic microglobules and cavities (Fig. 10A–C). The structures vary somewhat in size, but are generally approximately 2–4 µm in diameter (Fig. 10C). Comparable structures were described by Lamboy *et al.* (1994, fig. 2) from putative fish coprolites from various Cretaceous–Eocene phosphorites in North and West Africa, but have also been observed in primary, non-pelletal phosphorites from the Campanian of Israel (Soudry 1992, fig. 4). More recently, similar structures have been observed in terrestrial Triassic coprolites from Poland (Zatoń *et al.* 2015) and in Upper Permian specimens from Russia (Owocki *et al.* 2012; Bajdek *et al.* 2016). Lamboy *et al.* (1994) distinguished different types of microfabrics, and the coprolites studied here show a combination of these types. Most common are microgranular calcium phosphate (Fig. 10A) combined with a microporous texture (Fig. 10C); the latter probably represents

the internal part of the granules. In the host rock of specimen A 0972/4 (Fig. 10D), a dense microfabric similar to the botryoid-based fabric *sensu* Lamboy *et al.* (1994) is observed, and this architecture also occurs in specimen A 0922/61-80.3 (Fig. 10F).

Some specimens possess larger pits that may represent negative moulds of inclusions (Fig. 10E, F). String-like, ca 1 μm wide structures were observed in some coprolites (Fig. 10B). It cannot be excluded that these represent fossilised biofilms, although they could be much younger or even modern. No obvious bone or scale inclusions were observed under SEM, and the only shelly microfossil remain identified is a putative coccolith recorded from the Santonian coprolite-bearing host rock (Fig. 10D).

In thin section, all examined specimens show a dense, microcrystalline fabric. In addition to the above mentioned bone inclusions, the thin sections also revealed that most coprolites are internally coiled (see, e.g., Fig. 7B, and less distinct in 7D), even in specimens where this architecture is not readily observable from the external morphology.

The CT-scanning of the spiral-shaped coprolite A 0972/3 and A 5921/2 (Fig. 8A, B) revealed multiple internal layers, comparable to those of a coprolite from the lower Paleocene (Danian) of Denmark (see Milàn *et al.* 2012a). A similar internal layering was also identified in some specimens lacking apparent external spiraling (Fig. 8C-C2).

5.5 Chemical composition based on XRF

Typically, Ca (expressed as CaO, c. 15–50%) and P (P_2O_5 , c. 15–42%) form the bulk of the major-element chemistry of the coprolites, with Si (SiO_2 , c. 4–26%) representing an important additional element. All coprolites show enrichment of both Ca and P compared to the host rock (Fig. 11). Only a few coprolites (notably A 0972/3 and A 0972/4, from Lünen-Nordlünen) approach the sediment in average C and P content. Some specimens show elevated concentrations of Si, even exceeding that of the host rock. There is no clear systematic variation in Si concentration; coprolites from the same host rock differ in Si content and the concentrations can vary greatly within a single specimen.

There is broad correspondence between the Si and Al concentrations in the coprolites. The specimens from Lüdinghausen-Seppenrade (A 5921/2) and Lünen-Nordlünen (A 0972/3, A 0972/4) contain relatively high concentrations of S and Fe (pyrite?), as do the host rocks. Low analysis totals for some coprolites may reflect a large organic component, with C being below the detection range of the XRF analyser. In sediment samples, low analysis totals are mainly considered to result from porosity and/or unevenness in the substrate, resulting in significant loss and scattering of X-rays.

6. Discussion

The coprolites show variable morphologies and states of preservation, suggesting that they derive from different producers and have different taphonomic histories. The largest and most well-preserved specimens are those of Santonian age from Lünen-Nordlünen; these show no signs of transportation and the occurrence of several large specimens (with spiral convolutions) suggest that some of the coprolite producers reached considerable size. By contrast, the Rauen specimens tend to be smaller and were, without doubt, produced by different (and/or smaller) animals. There is also a much higher relative number of abraded and reworked coprolites from the Rauen quarry as compared to that from Lünen-Nordlünen.

The initial consistency and composition of the faeces, the depositional setting and taphonomic history are all important factors contributing to the preservation of coprolites (e.g. Hunt *et al.* 1994; Chin *et al.* 2003; Eriksson *et al.* 2011). Rapid lithification seems to be essential for coprolite preservation, and microbes probably played an important role in this process (e.g., Lamboy *et al.* 1994; Seilacher 2002; Hollocher *et al.* 2010; Hollocher & Hollocher 2012; Qvarnström *et al.* 2016). It has also been proposed that spiral faeces in particular must undergo rapid burial and lithification in order to retain their original morphology (e.g., Northwood 2005). Such coprolites are particularly common from Late Santonian and early Campanian strata of the study area, suggesting environments with better preservation potential for faecal matter than those of Rauen quarry. However, many

coprolites from Rauhen quarry show a spiral internal architecture, although their fragmented and abraded state obscures such details when observed externally.

6.1 Inclusions

Coprolite inclusions can be useful to identify the diet and digestive system efficiency of the producer (Hunt *et al.* 1994; Rodríguez-de la Rosa *et al.* 1998; Chin *et al.* 2003; Qvarnström *et al.* 2017). Clearly, however, inclusions are more useful for identifying the affinity of the prey than that of the host animal (Chin 2002). Also the state of preservation of the inclusions depends on the digestive system of the host animal, mode of feeding, and exposure of the inclusions during diagenesis (e.g., Owocki *et al.* 2012; Zatoń *et al.* 2015; Qvarnström *et al.* 2016). Inclusions are abundant in the studied coprolites, particularly in the Rauhen specimens, and consist of bones and possibly scales of primarily actinopterygian fish, as suggested by their morphology, size, and histology (cf. Cohen *et al.* 2012). The well-preserved bony inclusions in some specimens (e.g., Fig. 7) suggest a short gut residence time and/or a limited ability to digest bone, whereas those with more corroded and rounded bone inclusions suggests longer residence time and/or more efficient gut tract for digesting bone (e.g. Owocki *et al.* 2012; Zatoń *et al.* 2015; Qvarnström *et al.* 2016). Extant crocodiles, for example, efficiently digest bone and their scat either lack visible bone fragments (Milàn 2012) or contain demineralized bone matrices (Fisher 1981). This implies that coprolites devoid of bone inclusions could derive from predatory animals, although the remains of the prey items are no longer identifiable.

The dominance of marine palynomorphs together with fern spores and angiosperm pollen grains indicate relatively near-shore marine conditions. This is further supported by the presence of green algae, indicating fresh-water influences. The scarce palynomorphs found in the coprolites were likely involuntarily ingested from the water or bottom sediments by the coprolite producer(s). It has been suggested that plant material in coprolites deriving from carnivorous (or omnivorous) animals could also be derived from the gut content of herbivorous prey animals (cf. Zatoń *et al.* 2015). However, it seems highly unlikely that the few palynomorphs recorded in this study were part of any major food source, and no macroscopic plant remains, indicative of an herbivorous diet, were identified. The palynomorph assemblages are dominated by typical Early Cretaceous taxa, but some reworked Triassic taxa were also identified. The latter indicate that Triassic strata were exposed, eroded and the weathering products transported into the basin during the Early Cretaceous.

6.2 Phosphatic composition

Coprolites from carnivorous vertebrates are far more abundant, or at least better known, in the fossil record than are those produced by herbivores (e.g. Chin 2002). Additionally, they are usually easy to differentiate from the latter because of their typical phosphatic composition and skeletal inclusions (Dietrich 1951; Lamboy *et al.* 1994; Chin 2002). Invertebrate coprolites also typically have considerable concentrations of calcium phosphate (Häntzschel *et al.* 1968; Eriksson & Terfelt 2007; Peel 2015), but are usually smaller in size. It should be noted that authigenic phosphatisation may also take place under other conditions (e.g., Fountain & McClellan 2000; Marshall-Neill & Ruffell 2004). Usually, however, such nodules can be differentiated from coprolites through their internal structures and lack of inclusions.

With regards to accessory compounds, there is a broad correspondence between Si and Al concentrations in the coprolites, indicating incorporation of siliciclastic matter or adherence of such to the surfaces of the fossils.

6.3 Morphology and producers

Per definition, coprolites represent fossilized faecal matter that was fully excreted from their host animals (e.g. Hunt & Lucas 2012). Because coprolites are generally not found in conjunction with body fossils of the host animal(s), the reconstruction of the coprolite–producer link is often problematic. However, there are some characteristics of the faecal matter that can be used to pinpoint the producer, or at least reduce the number of possible candidates.

The size and morphology of coprolites can provide clues about the producer's identity, although a substantial intraspecific variation (depending on, for example, diet and ontogenetic stage) must be taken into account. In addition, unrelated organisms can produce superficially similar droppings, and a single animal can produce differently shaped and compositionally varied faeces due to dietary changes (Thulborn 1991; Hunt *et al.* 1994; Eriksson *et al.* 2011; Stuart & Stuart 1998). Moreover, small faeces can be produced by large animals, but conversely it is difficult for small animals to produce large faeces (Hunt *et al.* 1994). The size range of the coprolites examined herein indicates vertebrate host animals as invertebrate faecal pellets generally are smaller than 5 mm in diameter (Häntzschel *et al.* 1968; Hunt *et al.* 1994).

The coprolites from Germany include characteristic morphologies that have been assigned to specific host organisms by several authors. For instance, spiral coprolites are associated with animals with a spiral gut valve, i.e., most cartilaginous and some bony fish (Gilmore 1992; Hunt *et al.* 1994; Northwood 2005). Some authors (e.g., McAllister 1985, and references therein) described spiral coprolites as enterospirae, i.e. fossilised valvular intestines. Preserved valvular intestines are present in placoderm, chondrichthyan, actinopterygian, and probably acanthodian fossils (McAllister 1985, and references therein). Neumayer (1904) distinguished two main morphologies in his study on Permian spiral coprolites: heteropolar coprolites, which exhibit spaced coils concentrated to one end, and amphipolar coprolites, which have coils along the length of the specimen that are more evenly spaced. Due to differences in intestinal valves, it has been suggested that sharks are likely producers of heteropolar coprolites, and bony fish of amphipolar ones (cf. McAllister 1985). Even if such distinction is almost certainly too simplified, both sharks and bony fish were part of the Late Cretaceous vertebrate faunas of the Münster Basin (e.g. the chondrichthyans *Ptychodus* and *Odontaspis*, as well as the actinopterygian *Plethodus*, have been described from Rauhen quarry; see Scheer & Stottrop 1995), and droppings from animals of both taxonomic groups are most likely present in the material. A wide range of vertebrates has been found in the Münster Basin, including sharks, rays, bony fish, turtles, ichthyosaurs, pliosaurs, plesiosaurs, and mosasaurs. Many of these were carnivorous and thus potentially could be responsible for producing the coprolites at hand. However, cephalopods cannot be ruled out as producers of at least some of the coprolites (cf. Eriksson *et al.* 2011) since the Münster Basin housed a diverse ammonoid fauna and individual specimens could grow fairly large in size. Extant cephalopods are known as agile hunters, feeding largely on live prey, including fish, crustaceans and other cephalopods (Markaida & Sosa-Nishizaki 2003). However, whereas cephalopod remains (especially their sclerotized mouth parts) are well known from stomach, gut and faecal contents from a variety of animals, including ichthyosaurs, sharks and bony fish (e.g. Pollard 1968; Keller 1976; Uyeno & Tsutsumi 1991), coprolites with a confirmed cephalopod origin have yet to be documented.

6.4 External coprolite features

The various burrows, striations, pits and grooves observed on the coprolites probably derive from manipulation by coprophagous invertebrates and fish both preceding and after lithification (cf. Eriksson *et al.* 2011). The two distinct marks on a coprolite belonging to specimen-group A 1030/21-40 (Fig. 6I) possibly represent tooth marks, and the larger of them is similar to an inferred shark medial tooth impression on a coprolite from the Miocene of Maryland (Godfrey & Smith 2010). Extant sharks are not known to be deliberately coprophagous, but the marks could be the result of exploration of objects on the sea floor (see Godfrey & Smith 2010).

The circular holes (Fig. 6A-C) are likely made by invertebrates that either exploited the faecal matter or produced borings in the lithified coprolite. Coprophage traces have been observed in, for example, Lower Triassic coprolites from Australia (Northwood 2005) and Upper Cretaceous coprolites from Sweden (Eriksson *et al.* 2011). Even the largest burrows (e.g., Fig. 6A) could have been made by invertebrates since, for example, marine bivalves have been reported to produce borings in coprolites (Tapanila *et al.* 2004), as well as other hard substrates (Ekdale *et al.* 1984).

The grooves on the external surface of the coprolites may derive from actions of scavenging animals or possibly from the landing of faeces on a sharp object (Eriksson *et al.* 2011), or from erosion (see e.g., Figs 4I, L). The ridges and striations (Figs 4D, F, J, N, 5B, 6E-G) could

originate from impressions of the intestines and/or sphincter muscles. Small holes likely represent gas-escape features (Broughton *et al.* 1978; Northwood 2005; Hollocher *et al.* 2010).

6.5 Encrusters

Based on its inferred life strategies, the encrusting bivalve *Atreta* (e.g., Žitt & Nekvasilová 1996) attached to the coprolites when they were already lithified. Specimens of *Atreta* tend to be chaotically oriented on horizontal surfaces, but on oblique ones they commonly orient in a single direction (slope orientation). As such, they can be used as tools for recognising substrate position during encrustation (Žitt & Vodrážka 2013). However, the random distribution suggests that the bivalve marks represent different generations of attachment and that the coprolites have been moving, or rolling, to some extent on the sea floor, and that the faecal matter must have been lithified in order to withstand such transport. The variable, but relatively poor, preservation of the individual *Atreta* specimens, particularly in their umbonal parts, suggest that the organisms died before the substrate was buried and that that a rather prolonged time of exposure allowed post-mortem abrasion. The absence of epibionts on the Santonian specimens either suggests a different taphonomic history or environments unsuitable for *Atreta* or other encrusters.

6.6 Internal structures

As is evident from thin sections (Fig. 7) and CT-scanning data (Fig. 8), a spiral internal structure consisting of several layers is dominant among the coprolites. Along with the external morphology, these concentric layers indicate that the majority of the coprolite producers had a spiral gut valve; i.e., a structure that occurs in cartilaginous and some bony fish. The spiral architecture and presence of fish bone inclusions support an interpretation of the coprolite producers as piscivorous sharks or bony fish.

The microglobular coprofabric (Fig. 10) likely originates from phosphate precipitation at the surface of globular bacterial cellular bodies (e.g. Lamboy *et al.* 1994). Such microorganismal pseudomorphs are commonly found in coprolites, and there is an ongoing discussion whether they derive from the intestinal biota of the host animal or from the surrounding environment (e.g. Hollocher *et al.* 2010; Bajdek *et al.* 2015). DNA studies of subfossil human coprolites have demonstrated that preserved microbial DNA can be both intestinal and environmental depending on, for example, climatic variables in the depositional area (Tito *et al.* 2012; Cano *et al.* 2014). Regardless of origin, the autolithifying bacteria most likely facilitated early lithification of the faeces, and thereby drastically increased their preservation potential. Early bacterial-induced lithification has similarly been described as a key mechanism for the preservation of delicate inclusions (e.g. soft tissues) within coprolites (Chin *et al.* 2003; Qvarnström *et al.* 2016).

Conclusions

Coprolites represent common fossil elements in the Upper Cretaceous deposits of the Münster Basin (Germany), and the majority of the findings derive from the Plenus marl bed (upper Cenomanian) and the phosphorites (upper Turonian) of the Rauen quarry. Most specimens have spiral morphologies. Additionally, internal coiling is also present in several coprolites that lack such external characteristics. Thus, seemingly non-spiral coprolites can likely result from post-depositional alteration (e.g. abrasion), and thus may not necessarily reflect an absence of a spiral gut valve in the producer.

The texture of the coprofabric matrix is homogeneous with abundant phosphatic microglobular structures, which most likely result from microbial autolithification that facilitated preservation of the faeces. Many coprolites contain macroscopic bone inclusions showing variable stages of fragmentation and degrees of etching. This suggests differences in gut residence time and/or efficiency in breaking down skeletal elements.

Borings and other traces occur abundantly on coprolite surfaces and most of them suggest handling by coprophagous organisms. Encrusters are also common, most of which are identified as the bivalve *Atreta*. Their random distribution indicates that they represent different generations and that the coprolites were moving on the sea floor prior to final burial. There is no evidence for herbivorous host animals and the few plant palynomorphs extracted from the coprolites were likely ingested involuntarily. Rather, piscivorous sharks and/or bony fish presumably produced most or all coprolites, as indicated by their phosphatic composition, size, morphology, and abundance of fish bone inclusions.

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Appendix: Locality information

Mülheim-Broich, Rauen quarry

Topographic map 1:25.000, sheet 4507 Mülheim (co-ordinates system Gauß-Krüger r2560360/h5698580)

Stratigraphic range: lower Cenomanian – upper Turonian (Essen Greensand Formation, Büren Formation, Duisburg Formation)

Lünen-Nordlünen, former Robbert brickyard

Topographic map 1:25.000, sheet 4311 Lünen (co-ordinates system Gauß-Krüger r3398770/h5723150)

Stratigraphic range: upper Santonian (Emscher Formation)

Lüdinghausen-Seppenrade, former Pilgrim brickyard

Topographical map 1:25.000, sheet 4210 Lüdinghausen (co-ordinates system Gauß-Krüger r2598000/h5737600)

Stratigraphic range: lower Campanian (Emscher Formation)

Figures:

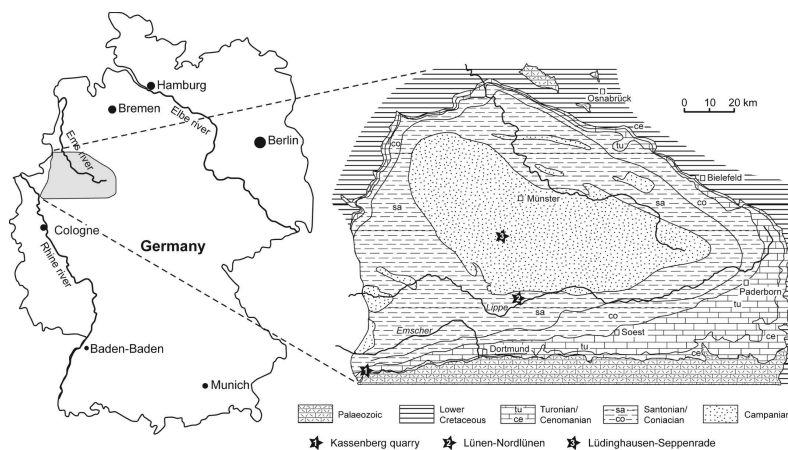


Fig. 1. Geological map of the Münster Basin, showing the distribution of Upper Cretaceous strata and location of the coprolite-yielding localities indicated by stars (map modified from Walter 1995, originally after Arnold 1964a).

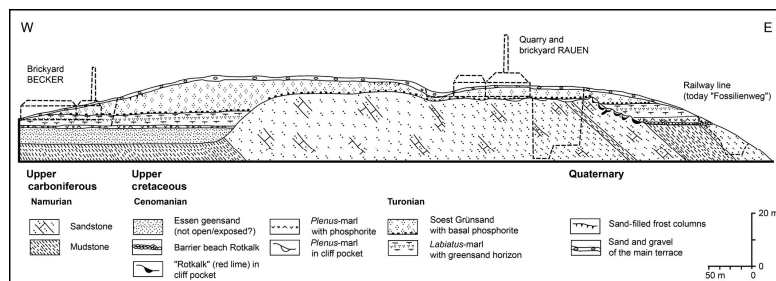


Fig. 2. Geological cross-section of the Kassenberg area (modified from Scheer & Stottrop 1995, originally based on Kahrs 1927).

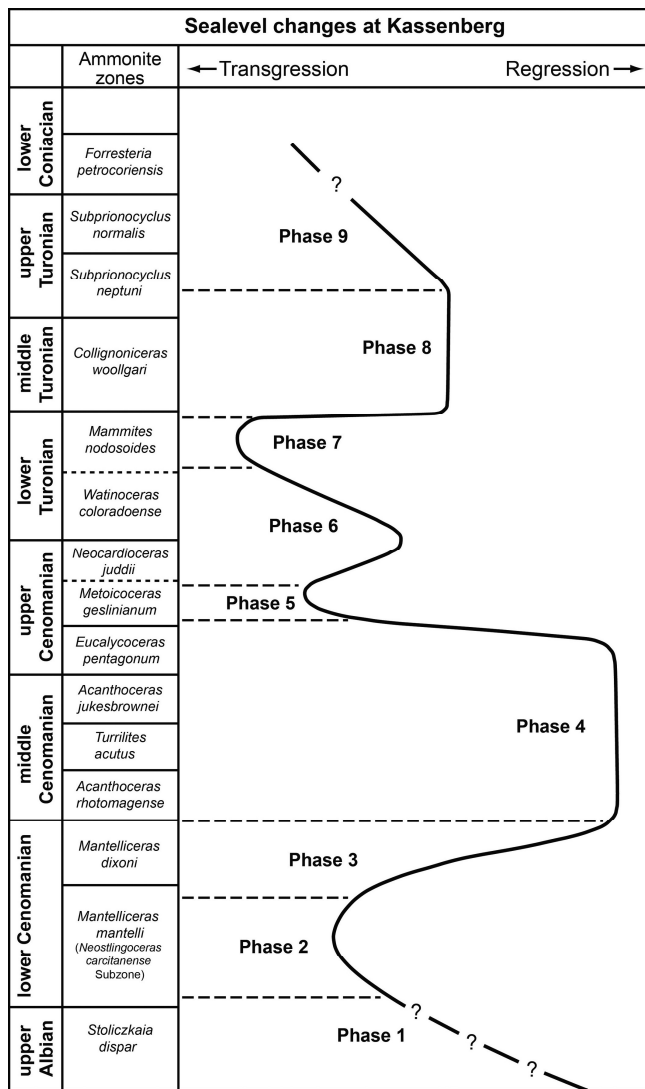


Fig. 3. Sea level changes and ammonite zones at Kassenberg (modified from Scheer & Stottrop 1995).



Fig. 4. Photographs of characteristic examples of different coprolite morphologies distinguished from the Upper Cretaceous of Germany. All specimens are from the Rauhen quarry, except for H, which is from Lüdinghausen-Seppenrade. All scale bars are 0.5 cm. A. specimen A 0596/1. B1-2. Specimen A 0596/12 in different views. C. Specimen A 2137/24. D specimens A 2137/21. E1-2. Specimen A 2137/3 in side and top view. F1-2. Specimen 0922/61-80.3 in different views. G. Specimen from collection group A 1030/41-60. H. Specimen A 5921/2. I. specimen A 2137/9. J. Specimen A 2137/13. K. Specimen A 0595/19. L. Specimen from collection group A 1030/1-20.20. M. Specimen A 0595/22. N. Specimen A 2137/1. Specimens D, G, H, M, N are distinctly spiral as based on the external morphology. Arrows in B, C, and L point at epibionts; larger arrows *Atreta*, smaller ones putative bryozoans.

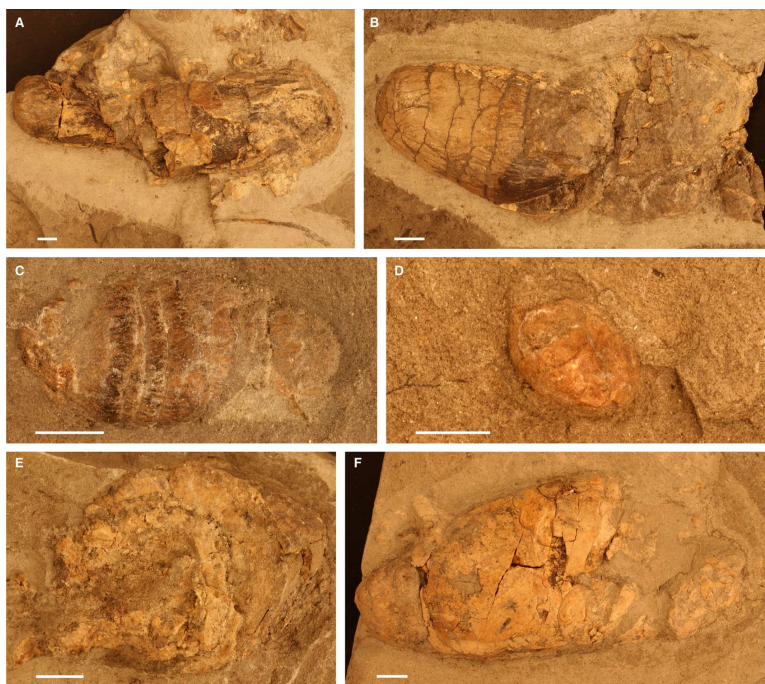


Fig. 5. Photographs of upper Santonian coprolites from Lünen–Nordlünen, all residing in their host matrix. All scale bars are 0.5 cm. A. Specimen A 0972/4. B. Specimen A 0972/3. C. Specimen A 0972/1. D. Specimen A 0982. E. Specimen A 0972/5. F. Specimen A 1019.



Fig. 6. Photographs of coprolites with distinct surface markings, burrows and inclusions. All scale bars are 0.5 cm, if not stated otherwise. A–D. Different views of coprolites with burrows; A. specimen

A595/20; B. specimen A595/12; C. specimen A596/21; D. specimen A596/16. E. Different views of bone inclusion and striations in specimen A1030/21-40.5. The inclusion is from two cross section views and probably derive from the same prey specimen. F and G. Different views of striations in specimens A0922/1-20.1 and A0922/1-20.2, respectively. H. Different views of bone inclusions in specimen A1030/141-160.2. I and II. Different views of possible tooth marks in specimen A0922/41-60.1; I. Overview showing gross coprolite morphology (dark elongate pit and striations in centre left of specimen are possible tooth marks) and II. Close up view. J and J1. Different views of an elongated fish vertebra in specimen A1030/21-40.1; J. Overview showing gross morphology and J1. Close up view.

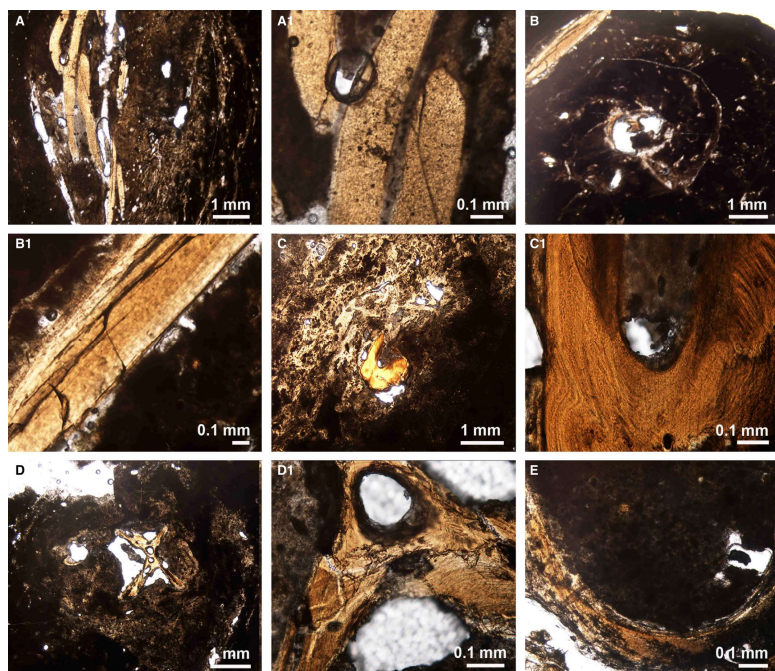


Fig. 7. Thin section photographs showing the coprofabrics, internal architecture and inclusions of selected coprolites. A. Longitudinal view of bone inclusions in coprolite specimen A0922/61-80.2 (A1 close-up of bone inclusion). B. Transverse view of bone inclusions in coprolite specimen A596/20, also showing the obvious internal coiling (B1 close-up of bone inclusion in upper left corner of B). C. Bone inclusion in coprolite specimen A1030/21-40 (C1 close-up of central bone inclusion in C, slightly rotated). D. Coprofabric and central cross-shaped bone inclusion in coprolite specimen A2137/3 (D1 close-up of central bone inclusion in D). E. Another bone inclusion in coprolite specimen A2137/3. Note the lamellar bone structure in shown in B and, particularly, C.

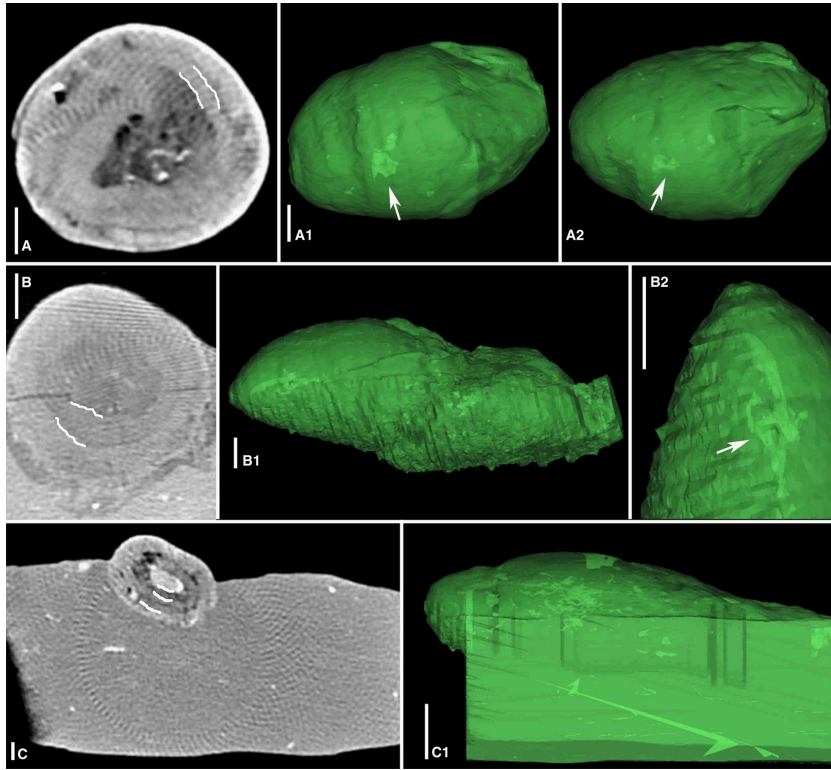


Fig. 8. CT-scanning images of coprolites. All scale bars are 0.5 cm. A. Transverse section showing the internal coiling in specimen A5921/2. A1, A2. 3D images showing the external side view of the same specimen. Arrow points to putative bone remains. B. Transverse section of specimen A0972/3 still in host rock sediment. B1, B2. 3D images showing external side views of the same specimen, virtually removed from the host rock. Arrows point to putative bone fragments. C. Transverse section of specimen A1.019 still in host rock sediment. C1. 3D image, external side view of the same specimen. Light-coloured areas probably do not represent bone inclusions. The white lines in A-C are added only to enhance the internal coiling.

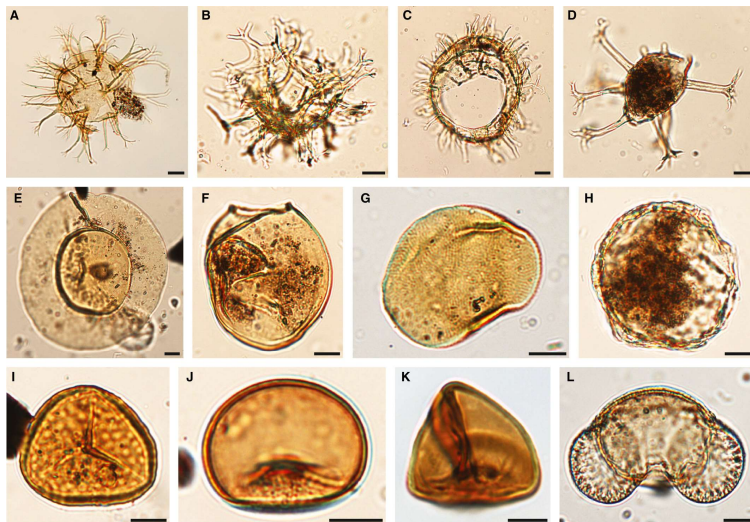


Fig. 9. Light micrographs of representative palynomorphs from coprolites and sediments of the Münster Basin: A. *Achomosphaera ramulifera* (from coprolite specimen A0972-1); B. *Spiniferites ramosus* (Soest Greensand Member); C. *Exochosphaeridium cenomaniense* (Bochum greensand basal); D. *Oligosphaeridium* spp. (Plenus marl); E. *Pterospermella eisenack* (Plenus marl); F. *Fromea amphora* (Bochum greensand basal); G. *Pleurozonaria* sp. (Bochum greensand); H. (Bochum greensand); I. (Bochum greensand); J. (Bochum greensand); K. (Bochum greensand); L. (Bochum greensand).

Lecaniella sp. (Bochum greensand); **I.** *Sestrosporites pseudoalveolatus* (Labiatus marl); **J.** *Laevigatisporites ovatus* (Labiatus marl); **K.** *Cyathidites minor* (from coprolite specimen A1030-21-40); **L.** *Pinuspollenites minimus* (Bochum greensand). Scale bars equal 10 μ m.

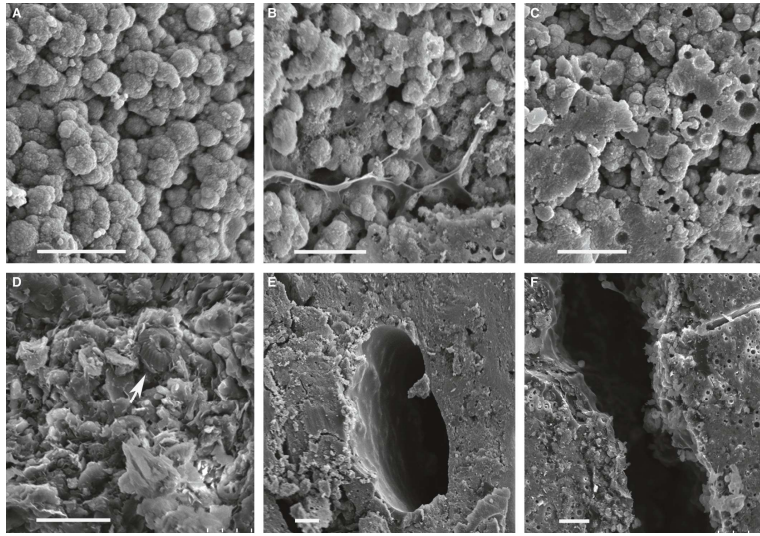


Fig. 10. SEM micrographs showing the microtexture of selected coprolites and coprolite-bearing host rock. All scale bars are 10 μ m. A–C. Calcium phosphate microgranules in coprolites; A, C coprolite specimen A1030/21-40; B. specimen A1030/161-180.1; note the string-like putative biofilm. Microgranules are particularly distinct in A and B, whereas in C also a microporous texture is evident; the circular voids/cavities most likely represent the internal part of the granules. D. Upper Santonian host rock of coprolite A972/3 (coccolith marked by white arrow). E, F. Negative moulds/cavities in coprolite matrix; E, coprolite specimen A2137/31, F. specimen A596/20.

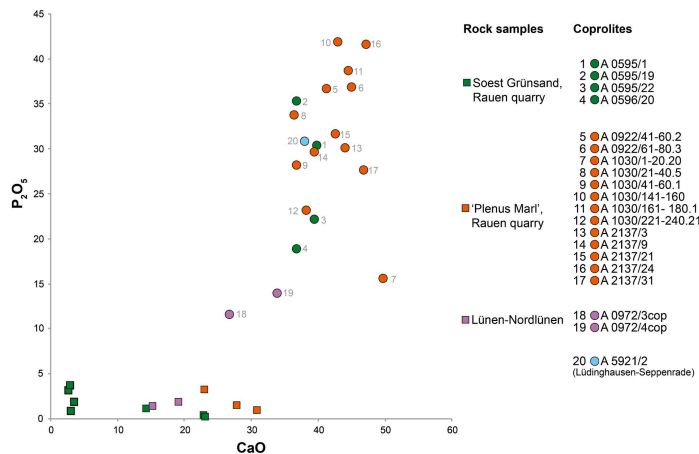


Fig. 11. CaO-P₂O₅ diagram showing samples from coprolites (circles) and the host sediment (squares) from the Rauen quarry (Soest Greensand Member and the Plenus Marl, Essen Greensand Formation) and Robbert brickyard, Lünen-Nordlünen, Emscher Formation.