

# Upper Cretaceous coprolites from the Münster Basin (northwestern Germany) – a glimpse into the diet of extinct animals

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STAVROS ANAGNOSTAKIS

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**Abstract:** A large number of coprolites from three localities with Upper Cretaceous strata from the Münster Basin (northwestern Germany) have been subjected to a wide array of analytical techniques with the aim of shedding some light on ancient trophic structures and predator–prey interactions. The phosphatic composition, bone inclusions, size and morphology suggest that most or all coprolites were produced by carnivorous vertebrates, especially the late Santonian specimens (up to 90 mm) imply host animals of significant size. Based on the nature of the bone inclusions, the animals preyed principally upon fish, but may also have included turtles in their diet. Based on their gross morphology, the coprolite specimens are subdivided into eight different morphotypes. Possible coprolite producers include mosasaurs, bony fish and sharks, all of which have been recorded from the Münster Basin. A piscivorous shark producer is inferred for heteropolar coprolites and a bony fish producer for amphipolar ones. The presence of tracks and traces on several of the coprolites suggest handling by coprophagous vertebrates and/or invertebrates. Remains of epibionts are also common and have primarily been identified as brachiopods (*Isocrania*). The findings of this study highlight that a combination of multiple analytical techniques is the most comprehensive approach for unraveling the origin, composition and importance of coprolites in palaeoecosystem analyses.

**Keywords:** Coprolites, Upper Cretaceous, Münster Basin, Germany, carnivorous vertebrates.

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# Koproliter från sen kritatid i Münsterbassängen (nordvästra Tyskland) – en inblick i dieten hos utdöda djur

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**Sammanfattning:** En omfattande samling koproliter från tre lokaler med sediment från sen kritatid i Münsterbassängen (nordvästra Tyskland) har studerats med en mängd olika analytiska tekniker med avsikten att belysa urtida trofiska nivåer och relationen mellan rovdjur och bytesdjur. Den fosfatiska sammansättningen, inneslutningar av benmaterial, storlek och form tyder på att de flesta eller samtliga koproliter producerades av rovlevande vertebrater. Framför allt exemplaren av sen santonsk ålder (som mäter upp till 90 mm) tyder på värdjur av påtaglig storlek. Beninneslutningarnas karaktäristik tyder på att rovdjuret framför allt jagade fisk men att de även kunde inkludera sköldpaddor i sin diet. Baserat på koproliternas yttre karaktäristik delades exemplaren upp i åtta olika morfotyper. Tänkbara koprolitproducenter innefattar mosasaurier, benfiskar och hajar, vilka samtliga har rapporterats från Münsterbassängen. En fiskätande haj tros ha producerat de heteropolära koproliterna medan benfiskar bedöms ha producerat de amfipolära koproliterna. Förekomsten av märken och skårar på utsidan av flertalet koproliter tyder på hantering av koprofoga vertebrater och/eller evertebrater. Epibionter är också ett vanligt förekommande inslag och de flesta har identifierats som brachiopoden *Isocrania*. Den här studien visar att kombinationen av ett flertal analystekniker är det mest framgångsrika sättet att avslöja ursprung, sammansättning och betydelsen hos koproliter i analyser av dåtida ekosystem.

**Nyckelord:** Koproliter, sen krita, Münsterbassängen, Tyskland, rovlevande vertebrater.

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# 1 Introduction

Coprolites are fossilized excrements and belong to a group of ichnofossils known as bromalites (Hunt et al. 1994). Studies of coprolites began in the early 1800s, when W. Buckland unraveled the true nature of odd sedimentary bodies from Pleistocene caves of England and interpreted them as fossilized hyena feces, for which he also conceived the term coprolite (Buckland 1835). Prior to Buckland's conclusion those specimens had been interpreted as fossilized fir cones. Coprolites occur in different shapes and sizes, ranging from millimeter-scale to more than 40 cm in length (the larger ones have been attributed to theropod dinosaurs; Chin et al. 1998). Their composition is mostly phosphatic and they can be rich in organic material (bacterial remains, pollen and spores), as well as skeletal remains of invertebrates and vertebrates. Sometimes they are mistaken for gastroliths (swallowed stomach stones), otoliths (ear ossicles), pebbles, fruits, corals (Thulborn 1991), and fossil plants (e.g. Meyen 1983), but, when present, the inclusions of bones, organic material and scales are distinguishable features revealing their true nature (Sharma et al. 2005).

Coprolites have received less attention than other fossils, including both body fossils and other types of ichnofossils, even though they are found in many sedimentary rocks of both marine and non-marine origin (Hunt et al. 1994; Hunt & Lucas 2007). These fossils can provide valuable information on feeding habits, predator-prey interactions, digestive physiology

and the trophic levels of ancient ecosystems (e.g. Hunt et al. 1994; Chin & Gill 1996; Chin et al. 1998, 2009; Rodriguez-de la Rosa et al. 1998; Prasad et al. 2005; Eriksson & Terfelt, 2007; Eriksson et al. 2011). It should be emphasized, however, that it is usually difficult to connect coprolites with a specific host organism.

In this study a large collection of coprolites from Upper Cretaceous strata in Germany are examined. They were classified into different morphotypes (see below). Most specimens are from the Late Cenomanian and Middle Turonian of the Kassenberg quarry, whereas others are from the late Santonian of the Lünen-Nordlünen and early Campanian of Lüdinghausen-Seppenrade. The coprolites were found associated with diverse faunas comprising bony fish, sharks, reptiles, and several invertebrate taxa entombed in a Late Cretaceous shallow marine setting of the Münster Basin. The specimens were examined using a broad array of techniques in order to evaluate their origin and composition. The results were then used to decipher trophic levels and animal interactions.

## 2 Geological setting

The Late Cretaceous was a time of significant alternating sea-level rises and falls, where the sea-level occasionally was almost 200 m higher than it is today, resulting in extensive shallow-marine areas (Fig. 1; Torsvik & Van der Voo 2002). Specifically in the

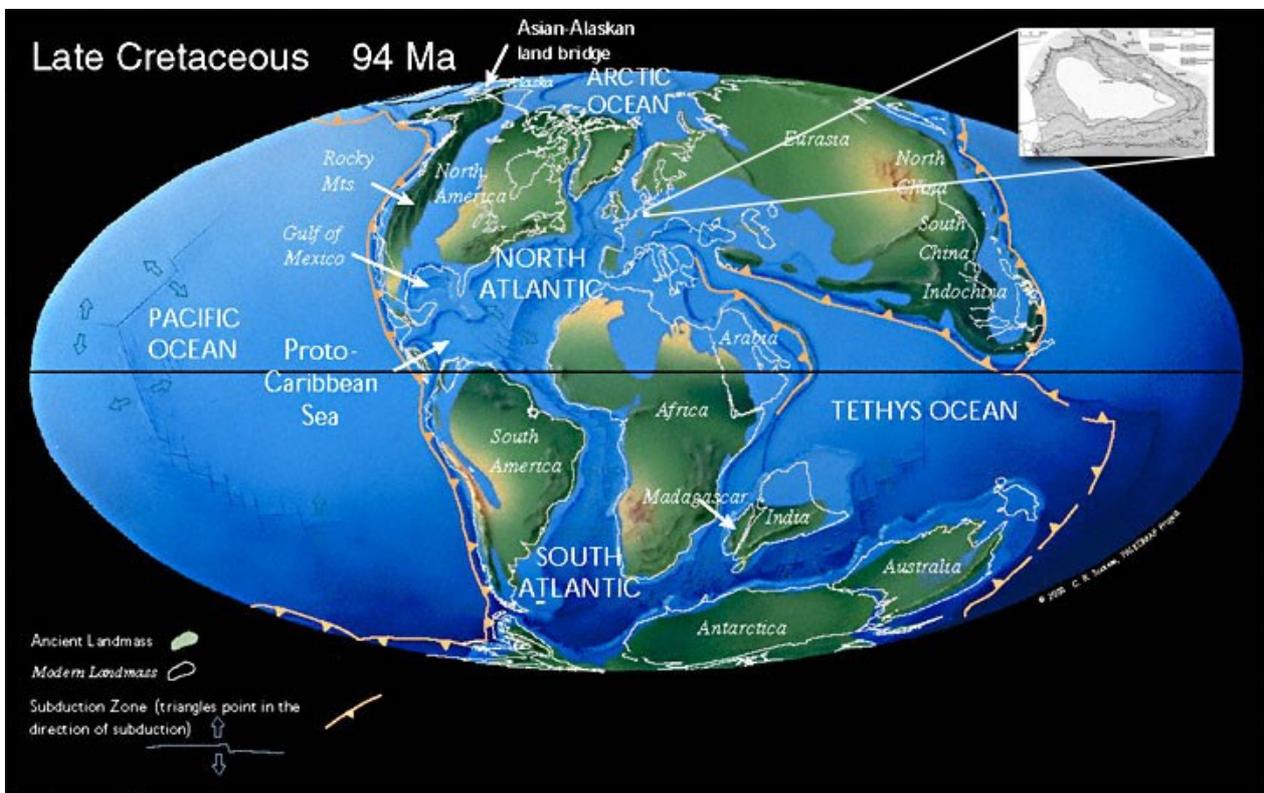


Fig. 1. Paleogeographic reconstruction of the world during the Late Cretaceous with an inset map showing the location of the Münster Basin. Inset map is magnified in Fig. 2 (adopted from <http://www.scotese.com/> the Scotese paleomap project).

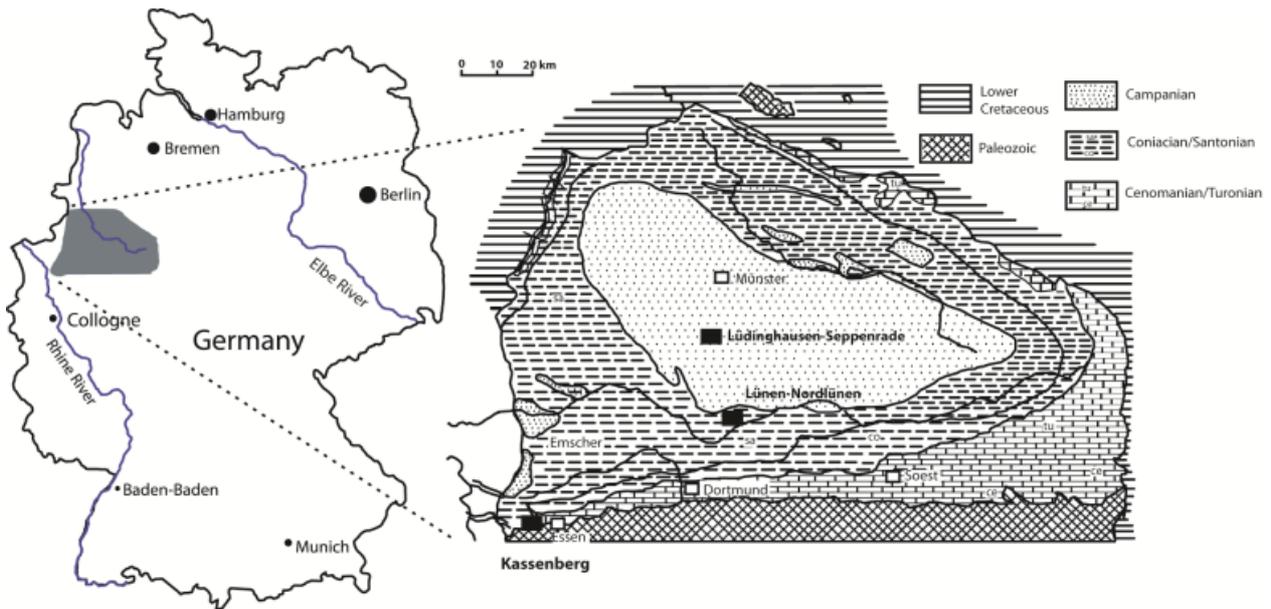


Fig. 2. Geological map of the Münster Basin, showing the distribution of Upper Cretaceous strata and location of the coprolite-yielding localities (modified from Walter 1995, after Arnold 1964b).

early Late Cretaceous (Cenomanian), “one of the most pronounced eustatic sea-level rises of the Phanerozoic occurred, resulting in the flooding of huge continental areas, which transformed them into peri- and epicontinental shelf seas across what is today Europe (e.g., north of the Early Cretaceous Tethys) and elsewhere” (Schneider et al. 2011, and references therein, p. 787). Northern Germany was a part of a wide epicontinental shelf which covered most of NW Europe (Wilmsen 2007). In the early Late Cretaceous the Münster Basin was a part of this epicontinental sea (of the pre-North sea Basin).

The collection of coprolites examined herein derives from three localities; that is the Kassenberg quarry, Lünen–Nordlünen and Lüdinhhausen-Seppenrade. The Upper Cretaceous of the Münster Basin in Northwestern Germany (Fig. 2) consists mainly of black shales, glauconitic sandstones and marls. Particularly, “the Cenomanian age was characterized by a general stepwise transgression culminating in the early Late Cenomanian” (Wilmsen 2007, p. 266); it was interrupted only by a major regression that occurred in the Middle Cenomanian. “This transgressive development is documented in a succession of inner shelf sediments (Essen–Grünsand and Herbram formations) overlain by mid-shelf marl-limestone alternations (Baddeckenstedt Formation) and outer shelf pelagites (Brochterbeck Formation)” (Wilmsen 2007, p. 266), which collectively form the bulk of the Cenomanian in northern Germany.

Kassenberg quarry is located near the town of Mülheim on the eastern flank of Ruhr Valley, in northwest Germany (Figs. 2 and 3). The quarry has been active for hundreds of years for the quarrying of both shale and sandstone, and it is still being operated (Kasielke 2011). The terrain is also a natural monument and a nature reserve (Kasielke 2011). During the

Cenomanian, Kassenberg was a cliff of Carboniferous sandstone in a near shore environment. The Cenomanian deposits consist mostly of sandstones, glauconitic sandstones and marls (Essen–Grünsand Formation). Pockets of Upper Cretaceous sediments are resting unconformably in pits and depressions (almost 0.5 m deep) in the Carboniferous sandstone (Hancock et al. 1972). Kahrs (1927) referred to these pocket sediments as “klippenfacies”; “The lower klippenfacies (Rotkalk) is a conglomeratic limestone with a very rich Cenomanian fauna” (Hancock et al. 1972, p. 445). This conglomerate is overlain by a light-coloured marl (Labiatus Marl) of Lower Turonian age. In the western part of the quarry, a glauconitic marl (Plenus Marl) of latest Cenomanian age, with pebbles and phosphatic nodules intervenes between the conglomerate and Labiatus marl (Hancock et al. 1972) (see Fig. 4). The Plenus Marl is the youngest member of the Essen–Grünsand Formation. It is characterized by the occurrence of the belemnite *Praeactinocamax plenus*



Fig. 3. Aerial photograph of the Kassenberg quarry (from <http://maps.google.gr/maps>).

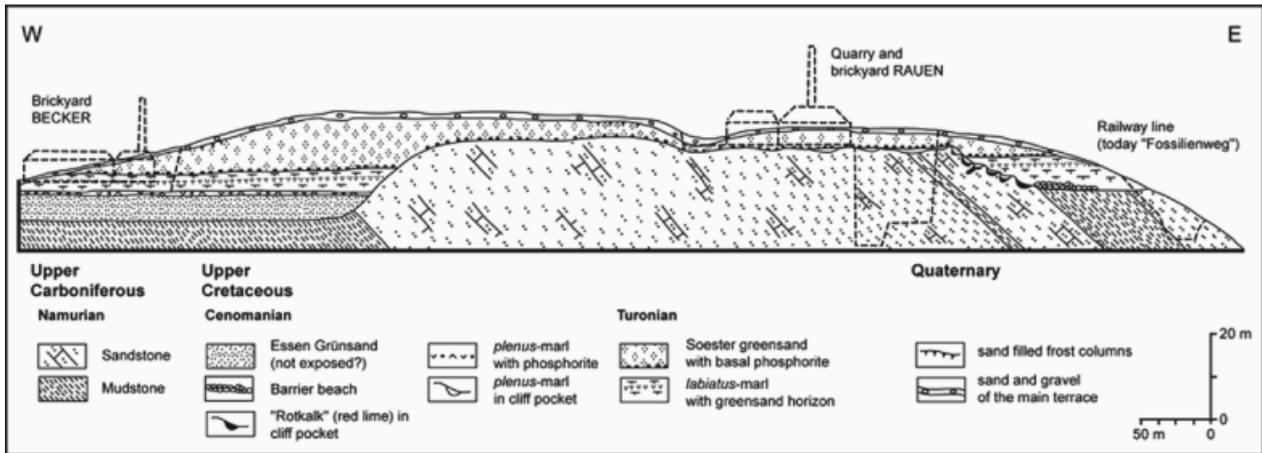


Fig. 4. Geological cross-section of the Kassenberg quarry (modified from Scheer & Stottrop 1995 and originally based on Kahrs 1927).

(Blainville 1827) and biostratigraphically is regarded as belonging to the *Metoiceras geslinianum* Ammonite Zone (see Fig. 5; U. Scheer, personal communication, 2012). Several different phases of successive sea-level change at Kassenberg have been identified (Fig. 5; Scheer & Stottrop 1995, and references therein). After a hiatus (upper Middle Cenomanian to lower Upper Cenomanian) sedimentation changed from greensand to glauconitic marls (Plenus Marl), with a thickness up to a few meters. This gap is presumably the result of a sea level change because after Phase 4 a major transgression occurred during the early Late Cenomanian (Phase 5; Fig. 5), although it was not the most extensive transgression recorded in the area. In fact, the most extensive transgression occurred in the late Early Turonian, corresponding to Phase 7. Phase 8 correlates with the Middle Turonian (Bochumer Greensand Member of the Oerlinghausen Formation). In this phase, the sea level fell again.

The other two coprolite-yielding localities, Lünen-Nordlünen and Lüdinghausen-Seppenrade, were during Cenomanian-Turonian time, parts of the main (deeper) basin. The coprolites from these two localities were extracted from the Emscher Formation. The formation is composed of a clayey and partly sandy gray marl, and is of an age ranging from the Coniacian to early Campanian. Coniacian and Santonian sediments of the Emscher Formation are widespread in the northern, central and eastern part of the Münsterland region (Arnold 1964a).

### 3 The Late Cretaceous faunas of Germany

The Late Cretaceous faunas of Germany are mainly comprised of marine invertebrates such as nautiloid and ammonoid cephalopods, belemnites and gastropods, but also reptiles (turtles and mosasaurs) and fish (sharks, bony fish and rays). Particularly the Münster Basin was a part of a wide epi-continental shelf with diverse marine faunas. In the Kassenberg quarry the Cenomanian

strata are well known and contain a diverse fossil fauna. Kahrs (1927) listed two species of poriferas, ten species of scleractinid corals, nine species of echinoids, 16 species of brachiopods, 65 species of bivalves, 77 species of gastropods (most of which

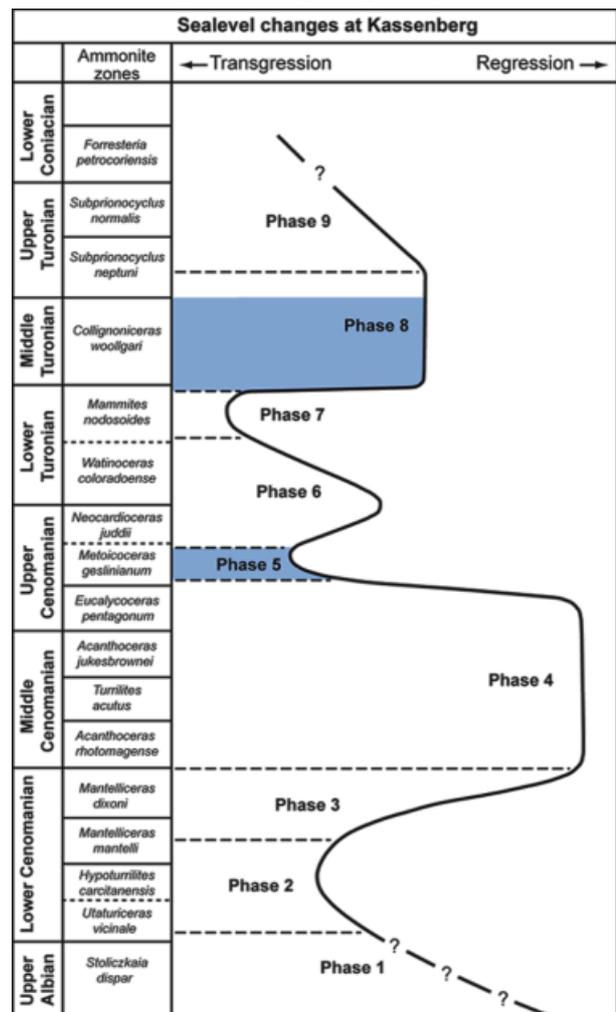


Fig. 5. Sealevel changes and ammonite zones at the Kassenberg quarry (modified from Scheer & Stottrop 1995). The intervals yielding coprolites studied herein are marked in light blue color.

remain undescribed), two species of ammonites, four species of serpulids, and one species of crab (see also Hancock et al. 1972). Wiedmann & Schneider (1979) described the entire cephalopod fauna at Kassenberg with four species of nautiloids and 21 species of ammonites, all of which are representative of the Lower Cenomanian, except for *Metoicoceras geslinianum* which is characteristic of the Upper Cenomanian. These fossils were extracted from a hard, yellow to red limestone cavity-filling in the Carboniferous sandstone (Kahrs 1927). Kaplan et al. (1998) studied the ammonites of these cavity-fillings and concluded that they were of Cenomanian age (see also Kiel & Bandel 2004).

The coprolites studied in this project are mostly of latest Cenomanian age; i.e., from the Plenus Marl Member of the Essen-Grünsand Formation, although some are of Middle Turonian age from the Bochum Greensand Member of the Oerlinghausen Formation. Based on the inferred sea-level changes at Kassenberg, the latest Cenomanian corresponds to phases 4-6 (Fig. 5; Scheer & Stottrop 1995, and references therein). According to Kahrs (1927), sharks, rays and belemnites (*Actinocamax plenus*) shared the open water. Only occasionally are ammonoid and nautiloid cephalopods found in the area (Scheer & Stottrop 1995). Before the upper Lower Turonian transgression (Phase 7), which represents the highest sea level stand of the cycle, a fossil rich basal conglomerate of Cenomanian age was deposited in potholes (Kasielke 2011). The fauna of the Middle Turonian phosphorites corresponds to Phase 8 and includes poriferans, anthozoans, brachiopods, echinoids, pelecypods, gastropods, nautiloids, ammonoids, fish, and reptiles (Scheer & Stottrop 1995, and references therein). From these strata coprolites presumably deriving from fishes (possibly *Macropoma* sp.) have also been described (Scheer & Stottrop 1995). Some coprolites found in the Middle Turonian sediments could be reworked, and if so, their age would most likely be latest Cenomanian (U. Scheer, personal communication, 2012).

As mentioned above, during Phase 5 warm water from the upper layers of the sea mixed with rising cold deep water currents rich in phosphate. Ammonites, sponges, snails, and large quantities of excrement were deposited in the carbonates and lead to marine phosphate accumulation and the preservation of a rich fauna (Scheer & Stottrop 1995). Lamniform and hybodont sharks, such as *Cretoxyrhina mantelli*, *Isurus* cf. *angustidens* and *Ptychodus mammillaris*, have been described from these phosphatic beds (Scheer & Stottrop 1995, and references therein) and these taxa are found throughout the Münster Basin. Kaeffer (1985) listed fish that occur in the upwelling-influenced greensands of the Münster Basin around Essen, Dortmund and Anröchte, with rare remains of *Xiphactinus* and *Berycopsis*. Moreover, Diedrich (2012, p. 253) described the fish assemblage of the Middle Turonian of the Münster Basin, “with *Xiphactinus* and *Cretoxyrhina* as top predators,” whereas teeth

remnants are from the “shark *Ptychodus mammillaris*”. The largest predatory bony fish, *Xiphactinus*, could reach several meters in length but was nonetheless itself preyed upon by *Cretoxyrhina*, which was the largest shark at this time (Diedrich 2012); stomach content of a late Santonian-early Campanian *Cretoxyrhina* from North America contains remains of a *Xiphactinus* (Shimada 1997). Reptiles have also been described from the Upper Cretaceous of northwest Germany and Münster Basin. Diedrich & Hirayama (2003) reported turtle remains from the Middle Turonian of northwest Germany and (Diedrich & Mulder 2004) subsequently reported the finding of an anterior portion of a mosasaur premaxilla assigned to *Clidastes* from the upper Campanian of the Beckum Formation.

## 4 Materials and methods

The collection of coprolites from the Upper Cretaceous of Germany studied herein consists of a total of 462 specimens which are stored at the Ruhrlandmuseum in Essen, Germany. Most, if not all, specimens have been collected by Mr. Karl-Heinz Hilpert (an amateur paleontologist), during the last few decades and handed over to the museum. In this study the specimens were subjected to a wide range of different analytical methods. Destructive analyses used include; thin sections for studies of coprofabrics, diagenesis, content and taphonomy, and digestion in acid for the recovery of potential acid resistant remains. Moreover, these analyses were coupled with non-destructive techniques, such as macroscopic and microscopic photography, Scanning Electron Microscopy (SEM), X-Ray Fluorescence spectrometry (XRF), size measurements and CT-scanning. The different methods are described in detail below.

### 4.1 Photography and measurements

The specimens were photographed using a Nikon digital camera mounted on a table set-up with four external light sources, at the Department of Geology, Lund University. Some specimens exhibiting interesting external traces were coated with ammonium chloride prior to photography in order to enhance their contrast. Size measurements of the coprolites were made with a vernier caliper.

### 4.2 X-Ray Fluorescence spectrometry (XRF)

X-Ray Fluorescence spectrometry (XRF) is a non-destructive method that allows identification of elements in materials. It is based on the fact that the wavelength of the X-ray emitted is unique for each element (Janssens 2004). The XRF analyses were performed on a representative selection of coprolite specimens at the Department of Geology, Lund

Table 1. List of specimens made into thin sections and for SEM studies.

SAMPLE NUMBER	AGE	MORPHOTYPES	LOCALITY
A2137/31	Latest Cenomanian	Rod-like bent (4)	Kassenberg
A2137/3	Latest Cenomanian	Fragment	Kassenberg
A1030/1-20	Latest Cenomanian	Irregular-kidney (6)	Kassenberg
A1030/21-40	Latest Cenomanian	Fragment	Kassenberg
A1030/41-60	Latest Cenomanian	Spiral (3)	Kassenberg
A1030/161-180.1	Latest Cenomanian	Oval- ellipsoidal (2)	Kassenberg
A0922/61-80.3	Latest Cenomanian	Sub-pyriform (5)	Kassenberg
A596/20	Middle Turonian	Rod-like (1)	Kassenberg
A595/1	Middle Turonian	Oval-ellipsoidal (2)	Kassenberg
Host rock (A0972/4)	Latest Santonian	From spiral (3)	Lünen-Nordlünen

University, using a thermoscientific NIKON instrument for revealing their chemical composition. Measurements were made with an element range of 60.0 in 3 steps for every sample, where each measurement lasted 240 seconds. A NDT software was used for the measurements and processing of the data.

### 4.3 CT-scanning

Computed tomography (CT) (Hounsfield 1973), is another non-destructive method which allows a 3D reconstruction of the internal structure and inclusions of a sample (Villa & Lynnerup 2012). 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. The scans were performed after “the salami principle”, which means that the scans are of successive thin slices, which subsequently are stacked into a long “sausage” which can be viewed from all orientations (orthogonal view). The object is studied with perforating X-rays where an opposing detector plate collects values and creates a data set from allegoristic data processing. A kernel 80 was used, which is a very hard kernel (high density in the object and high solubility). To gain a high level of details, the scanning was performed with pixel values (X, Y) 0.5 x 0.5 mm and the reconstruction (Z) was 0.5 mm. This displays the object with isometric voxels (volumetric pixels), which would provide trustworthy proportions of the object. The post-processing was performed at the Anthropological Department of Copenhagen University using the software Mimics. Many of the scans seem coarse, and that is due to the fact that many of them contain metals in some form. Metals create an artifact (Beam Hardening) which is hard to suppress in material of this small size.

### 4.4 Scanning Electron Microscopy (SEM)

Scanning Electron Microscopy (SEM) can provide elemental along with morphological data (Allen et al. 2002). SEM was used solely for examination of surface details at high magnification. A selection of 10 specimens (including one piece of host rock) was studied in a Hitachi S-3400N SEM at the Department of Geology, Lund University, in order to evaluate the microscopic texture and to search for inclusions. The specimens were first crushed with a hammer in order to get pieces with freshly exposed surfaces. The resulting fragments were mounted on double adhesive carbon tape onto a cover glass and subsequently coated with gold before being studied under SEM. The specimens examined are representative of six of the distinguished morphotypes (see below) while one of them comprised a piece of the host rock (see Table 1).

### 4.5 Thin sections

The petrographic thin sections were prepared at the Ceramic laboratory at the Department of Geology, Lund University. The coprolites were first sliced using a slow-speed diamond saw. Because some specimens were rather poorly lithified, they were embedded in transparent epoxy prior to being sliced. The resulting slabs were then mounted on glass slides with epoxy, left to dry in an oven over night, and then ground to appropriate thickness with a fine-grained diamond paste. In order to facilitate comparisons, the same specimens (comprising six morphotypes) that were studied also under SEM and thin sections were taken from each specimen (Table 1). The specimens were cut in both transverse and longitudinal section.

### 4.6 Palynology

Six samples were sent to Global Geolab Limited, Alberta, Canada, for palynological processing. Before

being shipped the samples were cleaned for approximately one minute in hydrogen peroxide and subsequently washed with distilled water in order to get rid of contaminants. Four of the samples represent coprolites and two are samples of the host rock containing the large Santonian spiral coprolites, number A0972/1 and A0972/4, from Lünen–Nordlünen. Two specimens from the Kassenberg quarry were of Middle Turonian age and the other two of latest Cenomanian age.

## 5 Results

### 5.1 Coprolite morphotypes and size

All coprolites, except for the Santonian specimens from Lünen-Nordlünen, range from 10 to 40 mm in length and up to 20 mm in maximum diameter. The Santonian specimens are considerably larger and range from 20 up to almost 90 mm in overall length. Moreover, the latter specimens are retained in their host rock. The specimens were sub-divided into different categories, or morphotypes, based on their gross morphology. It should, however, be noted that because many specimens are fragmentary they were difficult to

unambiguously assign to a specific morphotype. Among the 462 specimens, eight different morphotypes have been recognized (Table 2). These include the following:

*Morphotype 1:* Rod-like-elongated (Figs. 6J; 7E). The specimens are typically elongated with rounded edges. The largest specimens measure up to 40 mm in length but most of them are about 30 mm. Their diameter is up to 1/3 of their maximum length. Epibionts (*Isocrania* cf. *parisiensis*) are abundant on the surface of these specimens, as are various types of striations, pits and grooves. Bone inclusions are common and many of them are visible on the surface of the coprolites.

*Morphotype 2:* Oval-ellipsoidal-cone (Figs. 6A, E; 7C). These oval to ellipsoidal coprolites are the most abundant ones in the collection. They measure up to 35 mm in length and have a diameter of up to about 2/3 of their overall length. They commonly exhibit striations, epibionts, grooves, and pits, hence being closely similar to those of morphotype 1. Also as in morphotype 1, bone inclusions are abundant.

*Morphotype 3:* Spiral (Figs. 6G-H; 7D, F; 8A-D, F). Most of the spiral coprolites are heteropolar, except for specimens A595/22 (Fig. 7F) and A0972/1 (Fig. 8B), which appear to be amphipolar. Coprolite A0972/5

Table 2. Coprolite morphotypes and characteristics.

Morphotype	Morphology	Number of specimens	Size	Inclusions	Surface traces
<b>Morphotype 1</b>	Rod-like elongated	57 + numerous fragments	Up to 40mm in the bigger one	Fish bones	Striations, scrapes, pits, grooves, burrows-holes, Epibionts
<b>Morphotype 2</b>	Oval-ellipsoidal -cone	62 + numerous fragments	Up to 35 mm in the bigger one	Fish bones	Pits, grooves, striations, burrows-holes, Epibionts
<b>Morphotype 3</b>	Spiral	7 or 8	24,2-86 mm	Possibly	Some grooves
<b>Morphotype 4</b>	Rod-like bent	5	19,7-30,9 mm	Possibly	Pits, grooves, mostly smooth surface, Epibionts
<b>Morphotype 5</b>	Sub-pyriform	11	18,2-34,8 mm	Fish bones, vertebrae	Striations, grooves, pits
<b>Morphotype 6</b>	Irregular, kidney	3	28,3-40,1 mm	No	Pits, grooves, Epibionts
<b>Morphotype 7</b>	Spiral, cigar-lens-shaped	1	24,28 mm	No	Pits, burrows-holes
<b>Morphotype 8</b>	Sub-pyriform-puck-shaped	1	30,2 mm	No	Some small pits and grooves, Epibionts



*Fig. 6.* Photographs of characteristic examples of the coprolite morphotypes distinguished from the Upper Cretaceous of Germany. A. Morphotype 2, specimen A596/1. B. Morphotype 8, specimen A596/12. C. Morphotype 4, specimen A2137/24. The arrows indicate epibionts. D and F. Morphotype 5, specimens A2137/21 and 0922/61-80.3. E. Morphotype 2, specimen A2137/3. G-H. Morphotype 3, specimens A1030/41-60 and A5921/2. I. Morphotype 6, specimen A2137/9. J. Morphotype 1, specimen A2137/13. K. Morphotype 7, specimen A595/19. Scale bars=0.5 cm. All specimens are from the Kassenberg quarry, except for H, specimen A5921/2, which is from Lüdinghausen-Seppenrade.



Fig. 7. Photographs of coprolite morphotypes 1-4 and 6 from the Upper Cretaceous of Germany. A. Morphotype 6, specimen A1030/1-20.20. B. Morphotype 4, specimen A2137/31. C. Morphotype 2, specimen A2137/17. D and F. Morphotype 3, specimens A0972/3 and A595/22. E. Morphotype 1, specimen A2137/1. Scale bars=0.5 cm.

(Fig. 8D) is fragmented and only its internal shape is visible. It is comprised of internal layers which is the reason for them to be included in the spiral morphotype. The specimens of this morphotype range from 24.2 mm to almost 90 mm in overall length with a diameter of 26.8 mm or almost 1/3 of their length. There are no obvious bone inclusions on their external surfaces, although the CT-scanning of the specimens A0972/3 and A5921/2 revealed internal structures of what appear to be bone (see below). Most of them have four or more visible coils and they lack striations.

**Morphotype 4:** Rod-like bent (Fig. 6C; 7B). This morphotype is represented by five specimens that are

between 19.7-30.9 mm in overall length. They are elongated and bent with a diameter that is about 1/3 of their length. Their surface is generally smooth and they lack striations, pits and grooves, except for one specimen (A0922/1-20.1) which exhibits very distinct striae (Fig. 9G). They do not contain visible inclusions but most of them show encrusting epibionts (*Isocrania* cf. *parisiensis*).

**Morphotype 5:** Sub-pyriform (Fig. 6D, F). Eleven specimens are assigned to this morphotype. The coprolites are elongated, although they are not bent as those of morphotype 4, and have one sharp edge. They range from 18.2 to 34.8 mm in overall length and their diameter is almost half of their length. This morphotype



*Fig. 8.* Photographs of upper Santonian coprolites from Lünen–Nordlünen. A, B, D and F. Morphotype 3, specimens A0972/4, A0972/1, A0972/5 and A0972/3, respectively. C and E. Morphotype 2, specimens A0982 and A1.019, respectively. Scale bars=0.5 cm.

has abundant skeletal inclusions, such as fish bones and vertebrae (see Fig. 6F). They commonly show grooves, pits and striations on their surface.

**Morphotype 6:** Irregular, kidney-shaped (Figs. 6I; 7A). Three specimens are included in this morphotype, all of which derive from the Kassenberg quarry. These coprolites have a morphology intermediate between the irregular and kidney shape *sensu* Häntzschel et al. (1968). They range from 28.3 to 40.1 mm in overall length and their width is almost one third of their length. There are no visible inclusions on their surface. The large pits and grooves distributed on the external surface of these specimens could be the result of abrasion, probably during reworking. Without these marks these coprolites could belong to morphotype 1. Only one specimen (Fig. 7A) exhibits epibionts.

**Morphotype 7:** Spiral, cigar-lens-shaped (Fig. 6K). Only one specimen represents this morphotype. Häntzschel et al. (1968) described both cigar-shaped and lens-shaped coprolites. The specimen at hand, however, has a morphology that is intermediate between these two categories. It is 24.2 mm in overall length and has a maximum diameter of 13.5 mm. The surface of this coprolite shows pits and small burrows. The general shape of the coprolite is spiral and hence it could be assigned to morphotype 3. This specimen is very similar to a coprolite described by Buckland (1835) from the Lyme Regis of Lower Lias of England. Hunt et al. (2007) assigned that specific coprolite of Buckland to *Liassocopros* ichnogenus.

**Morphotype 8:** Sub-pyriform, puck-shaped (Fig. 6B). This morphotype is represented by one specimen that measures 30.2 mm in length and 12.0 mm in maximum width/diameter. The shape of the coprolite is sub-pyriform with one sharp edge and is strongly pressed from both sides. Its external surface is mostly smooth with some small pits and grooves but no striations or other visible marks occur. It does, however, exhibit epibionts, possibly of *Isocrania* cf. *parisiensis*.

Overall, the color of the coprolites varies from beige to dark brown. Except for the A595 and A596 collections of Middle Turonian coprolites from Kassenberg quarry that are all dark brown, specific colors could not be linked to a certain morphotype, locality or age.

The first two morphotypes are representative of coprolites from the latest Cenomanian Essen-Grünsand Formation of the Kassenberg quarry. The spiral-heteropolar ones (morphotype 3) are from the latest Santonian of Lünen-Nordlünen and the early Campanian of Lüdinghausen-Seppenrade, respectively, with the exception of one specimen from the latest Cenomanian of Kassenberg. Because some or several of the Kassenberg specimens are reworked (U. Scheer, personal communication, 2012) they could represent also other morphotypes than the ones described herein. For example, the specimens belonging to morphotype 1 and 5 could derive from spiral and elongated specimens that have been abraded during reworking (Figs. 6D; 7F).

## 5.2 Surface structures

### 5.2.1 Epibionts

Epibionts are organisms that live on the surface of other organisms and they form a significant part of the fauna in many marine environments, preserving valuable ecological information (Lescinsky 2003). A large number of the coprolites from the Upper Cretaceous of Germany show remains of epibionts, most of which are identified as the brachiopod *Isocrania* cf. *parisiensis* (Figs. 6B, C; 7A). Curiously, epibionts were found exclusively on the specimens from Kassenberg quarry. Overall, the epibionts appear to be randomly distributed on the surface of the coprolites. Only rarely are they situated at one side of a coprolite.

### 5.2.2 Tracks and traces

Several specimens in the coprolite collection from Germany display a wide range of surface structures, such as pits, striations, grooves, borings and holes, on their external surface (see Table 2).

A number of specimens (Fig. 9A-C) from this collection exhibit distinct, circular smaller and bigger holes (up to 7.76 mm in diameter) very similar to those described by Milàn et al. (2012a) and Eriksson et al. (2011), whereas, a single specimen (A595/12) exhibits two circular distinct holes of different diameters. The holes in A595/20 (3.9 mm in diameter), A595/12 (7.76 mm in diameter for the big hole) and A595/15 (5.7 mm in diameter) are very similar to the ones described by Milàn et al. (2012a). Other specimens have holes or voids which are considerably smaller, e.g., A596/21 (2 mm in diameter) and A595/12 (1.4 mm in diameter for the small hole) (Fig. 9B, C). These are analogous to the ones described by Eriksson et al. (2011). Finally, the void in A596/16 (8.56 mm in diameter) is different from the ones described above. It is not circular, with a much bigger diameter, half of it is filled with sediment and it appears to be irregular (Fig. 9D).

Several coprolites also display other interesting external features. A2137/9 (Fig. 6I) and A1030/1-20.20 (Fig. 7A), both assigned to morphotype 6, exhibit large grooves and pits on their surface. Possible tooth marks are visible on the external surface of A0922/21-40 (Figs. 9I; 11). Distinct striations, such as those shown in Figures 6D, F, J; 9E-G and Figure 7E are observable in many coprolites from Kassenberg quarry.

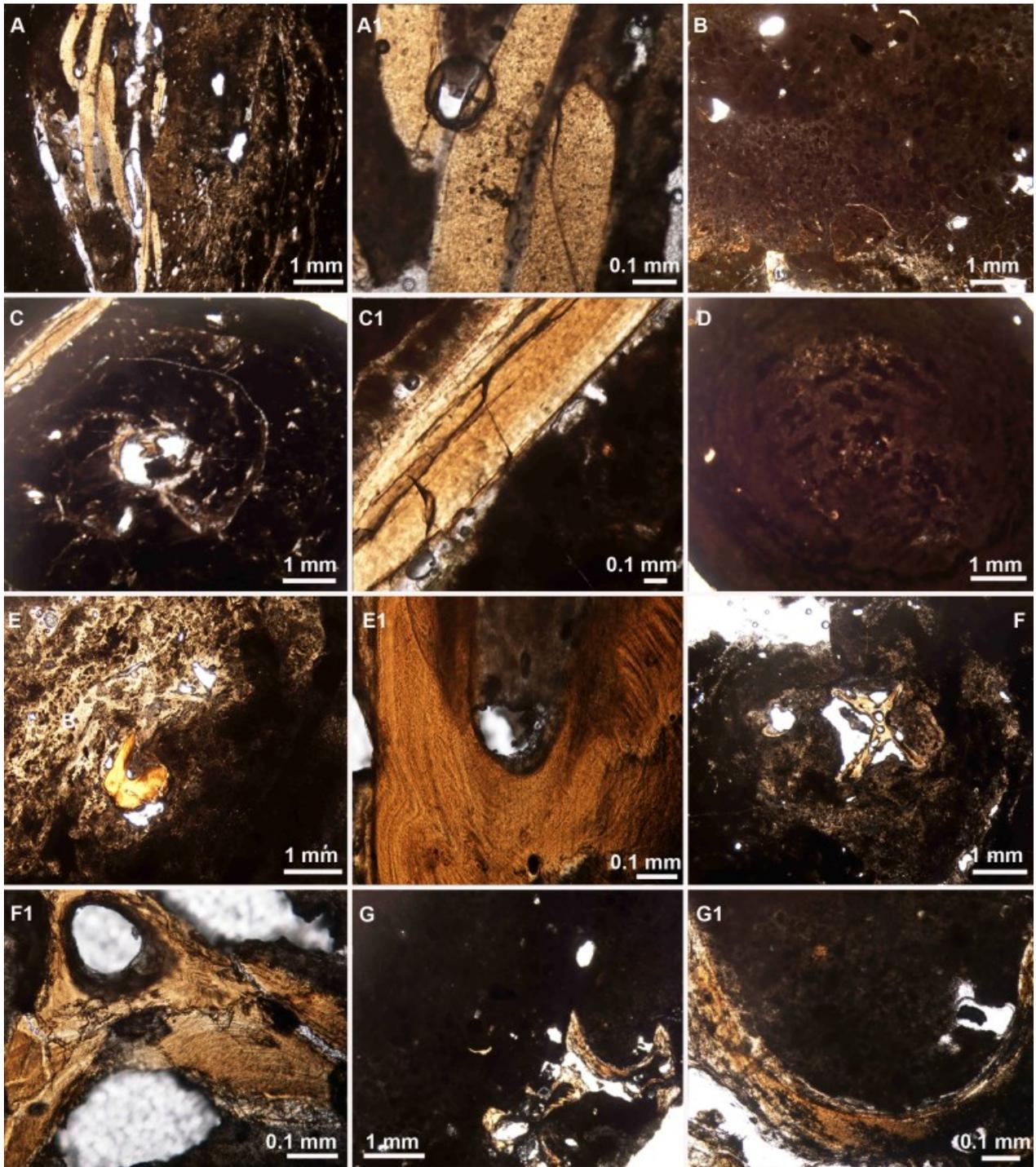
## 5.3 Inclusions

Thin section analyses, CT-scanning, macroscopic as well as microscopic inspection of the coprolites revealed the presence of a variety of inclusions, such as bones, scales and palynomorphs.

Thin section analyses revealed the presence of fragmented bones in the majority of the coprolites studied (Fig. 10), and also internally in specimens that



*Fig. 9.* Photographs of burrows and inclusions in the Upper Cretaceous coprolites. A-D. Different views of burrows in coprolites; 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. 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 I1. Different views of possible tooth marks in specimen A0922/41-60.1; I. Overview showing gross morphology and I1. Close up view. J and J1. Different views of an elongated vertebra most probably of a juvenile turtle in specimen A1030/21-40.1; J. Overview showing gross morphology and J1. Close up view. Scale bars=0.5 cm.

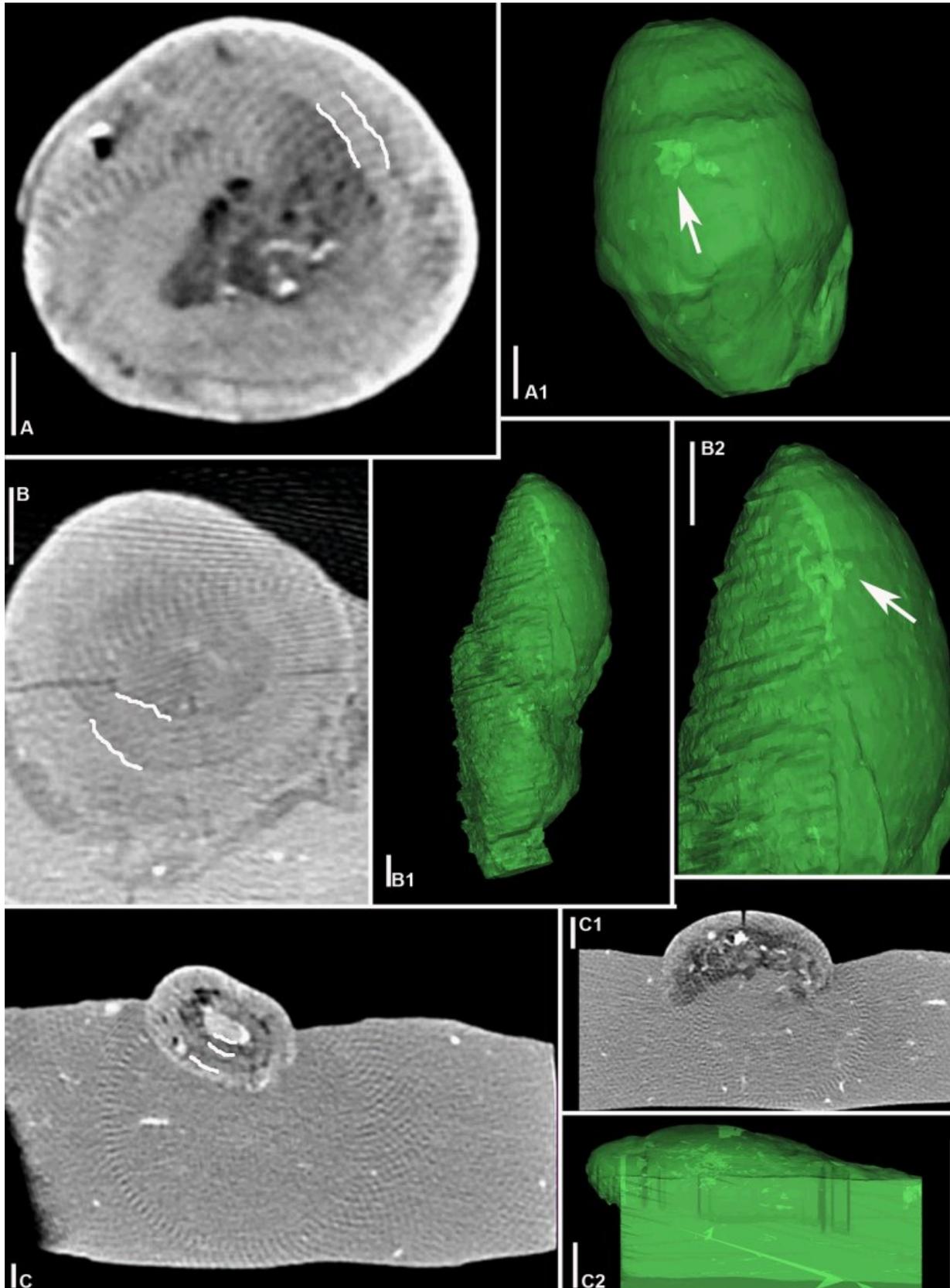


*Fig. 10.* Light microscope thin section photographs showing the microfibrils and coprolite inclusions. A. (longitudinal) and B (transverse) views of bone inclusions in specimen A0922/61-80.2. C. Transverse view in specimen A596/20 showing the obvious coiling. D. Transverse view of bone inclusion in specimen A1030/1-20, E. Bone inclusion in specimen A1030/21-40. F and G. Bone inclusions in specimen A2137/3.

seemed to lack such features based on observations of their external surface. These inclusions show layered or lamellar structures which probably represent the cortical part of the bone (see e.g. Fig. 10C1, E1). The coprolites that have bone inclusions belong to morphotype 5 and 6 (Table 1) and also some broken specimens occur that are difficult to assign to specific morphotypes. Only in A0922/61-80.3, which belongs

to morphotype 5, bone inclusions are also visible on the surface (Fig. 10C).

External surface inclusions, similar to those of specimen A0922/61-80.3, occur also abundantly in other coprolites. One of the most interesting and unusual bone inclusions was observed in coprolite specimen A1030/21-40.1 (Fig. 9J). It comprises an elongated vertebra exposed on the external surface of the



*Fig. 11.* CT-scanning images. A-C and C1. Transverse sections showing the coiling in spiral morphotype 3 coprolite specimens A5921/2, A972/3 and oval-ellipsoidal morphotype 2 specimen A1.019. A1, B1, B2. CT-scanning 3-D image showing the possible bone inclusion in morphotype 3 spiral specimens A5921/2 and A972/3. Arrows indicate bones. C2. CT-scanning 3-D image of specimen A1.019, light-colored areas probably do not represent bones. The white lines in A-C are added only to enhance the internal coiling. Scale bars=0.5 cm.

coprolite. This coprolite is from the Plenus Marl Member of the Essen-Grünsand Formation (Latest Cenomanian; Phase 5) of the Kassenberg quarry in which coprolites with bone inclusions are abundant. Because the inclusion-bearing coprolite is fragmentary it could not be unambiguously assigned to a specific morphotype. An additional and conspicuous inclusion was recorded from the same collection (coprolite A1030/21-40). This inclusion is visible at both ends and seems to extend through the entire length of the coprolite. This coprolite is fragmented with a length of 11.8 mm (Fig. 9E). The subpyriform coprolite (morphotype 5) from Kassenberg (A0922/61-80) exhibits many bone inclusions that are concentrated mostly in the one sharp surface of the specimen (Fig. 6F). The same pattern of bone inclusions concentrated to one edge is also present in specimen A1030/141-160 (Fig. 9H). This latter specimen seemingly lacks visible inclusions on its external surface; however, bone fragments are present on the side that is fragmented.

Many putative bone inclusions have been seen also during CT-scanning analyses. In specimen A0972/3 (Fig. 11B1, B2) some parts that are highlighted (light green) seem to represent bone inclusions. Similarly, the lighter colored areas in specimen A5921/2 could also represent bones (Fig. 11A, A1). Inversely, the bright areas in the specimen A1.019 are very similar with the bright areas in the matrix outside the coprolite (Fig. 11C2). Most, if not all, of these areas probably do not represent bone material, because Hounsfield Units are simply too high and identical with the Hounsfield Units of the bright object which is situated in the matrix outside the coprolite (see Villa & Lynnerup 2012).

### 5.3.1. Palynomorphs

Overall the coprolites were scarce in palynomorphs, mostly containing amorphous organic matter, dinoflagellates (largely marine plankton, although some taxa are known to inhabit freshwater environments) and some reworked bisaccate pollen grains. A selection of representative and overall well-preserved specimens is shown in Figure 12. It is problematic to assess the results since the coprolites were analyzed without access to their host rocks and vice versa.

## 5.4 Internal structures, microtexture and coprofabric

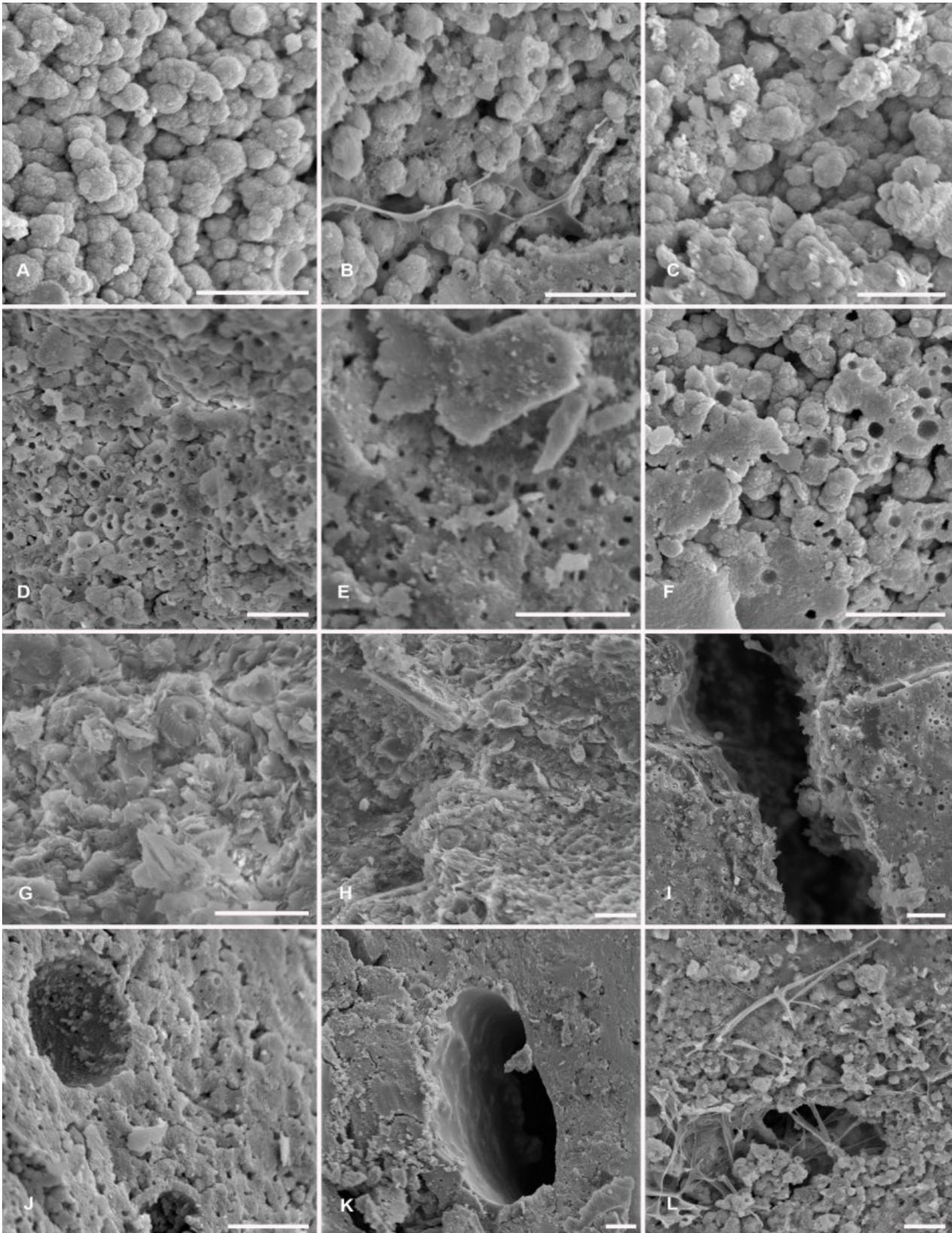
The specimens exhibit mostly homogenous and microporous structures as revealed by the thin sections and SEM studies (Figs. 10 and 13, respectively). Under SEM most of the coprolites show a porous structure that is surrounded by calcium phosphate microglobules. Calcium phosphate microglobules are visible in specimens A1030/21-40, A1030/161-180.1 and A595/1 (Fig. 13A-C). These structures are closely similar to the ones described by Lamboy et al. (1994) in fish coprolites of Cretaceous-Eocene phosphorites from Tunisia, Morocco, Senegal, Mauritania, and Egypt. Lamboy et al. (1994) distinguished two main types of fabrics: inframicroglobule based and botryoid. The inframicroglobule based is in turn subdivided into two types, one type consisting of granules of calcium phosphate and a second microporous one surrounded by inframicroglobules. The microporous structure consists of many small cavities of somewhat varying size, but generally ca 2 µm in diameter. The analyzed coprolites from Germany exhibit mostly or only the inframicroglobule based fabric and exhibit a combination of the two types distinguished by Lamboy et al. (1994). The most characteristic specimen revealing a combination of those two microstructures is A1030/21-40. This coprolite shows microgranules of calcium phosphate (Fig. 13A) combined with a microporous texture (Fig. 13F). Botryoid microstructures are clearly visible in the host rock of specimen A0972/4, (Fig. 13G, H) but they also occur in specimen A0922/61-80.3 (Fig. 13I). Within specimen A596/20 two slightly larger pits are also visible and may represent structures that are now missing (Fig. 13J). Some specimens, such as A1030/161-180.1, also show putative biofilms that probably represent younger (present-day?) structures (Fig. 13L). The only microfossil remain identified in SEM is a probable coccolith recorded in the Santonian host rock (Fig. 13G). Overall, most of the specimens exhibit a homogenous phosphatic (apatite) porous structure (Fig. 13D-F, J) and there are no obvious macroscopic bone or scale inclusions in the specimens, as revealed in the SEM study.

Also in thin sections the coprofabric was shown to be homogenous between the specimens; all of the ex-

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*Fig. 12 (opposite page).* Light microscope photographs of selected palynomorphs. A. Reworked bisaccate pollen grain from specimen A0922/21-40. B. Amorphous Organic Matter (AOM) and bisaccate pollen grain from specimen A1030/21-40. C. Reworked bisaccate *Alisporites* from the host rock of specimen A0972/4. D. *Cyathidites australis* spore from specimen A1030/21-40. E. *Cyathidites australis* spore from specimen A0972/1. F. AOM from specimen A0922/21-40. G. *Peripollenites elatoides* from specimen A1030/21-40. H. Dinoflagellate from specimen A0972/4. I. Dinoflagellate from specimen A595/10. J. *Baculatisporites comaumensis* spore from specimen A1030/21-40. K. AOM (possible contamination) from specimen A596/7. L. *Alisporites* pollen from A1030/21-40. M. Amorphous Organic Matter (AOM) from specimen A1030/21-40. N. Degraded wood from specimen A596/7. O. Bisaccate pollen from specimen A596/7. Scale bars=10µm. Note that the *Lycopodium* spores seen in figures A, B and I were introduced to the samples, by Global Geolab Limited, as reference material for calculations of relative abundance.





*Fig. 13.* SEM micrographs showing the microtexture of selected coprolites and coprolite-bearing host rock. A-C. Calcium phosphate microgranules in coprolites; A. specimen A1030/21-40; B. A1030/161-180.1 and C. A595/1. D-F. Microporous structures in coprolites; D. A2137/3; E. A2137/31; F. A1030/21-40. G-I. Botryoid microstructures; G and H. Upper Santonian host rock of coprolite A972/3; I. A0922/61-80.3. Note the coccolith in the centre of G. J and K. Hollow structures in coprolites; J. specimen A596/20; K. specimen A2137/31. L. Putative biofilms in specimen A1030/161-180.1. Scale bars=10  $\mu\text{m}$ .

aminated specimens showing a dense, microcrystalline fabric. Except for the many bone inclusions the overall structure of most coprolites appears coiled. For example in specimen A0922/61-80.3, which is of morphotype 5, the coiling is very obvious in transverse section (Fig. 10C). Similar, although somewhat less distinct internal coiling is seen also in specimens A595/1 and A596/20 (Fig. 10B) both assigned to morphotype 1, and in A1030/41-60 (morphotype 3). Specimen A595/1 shows a more homogenous, microcrystalline appearance (Fig. 13A).

The CT-scanning of the spiral coprolite specimen A0972/3 (Fig. 11B) revealed that its internal structure exhibits some degree of coiling and is composed of several distinguishable layers, closely similar to those of the coprolite examined by Milàn et al. (2012b) from the lower Paleocene (Danian) of Denmark. In specimen A1.019, the CT-scanning revealed an internal structure of the coprolite that deviates from its external features (Fig. 11C-C2). The coprolite gross morphology is oval-cylindrical, belonging to morphotype 2 (with a smooth external surface that lacks striations, grooves and pits) and is elongated with no apparent signs of spiraling. However, internally, the specimen seems to be spiraled and composed of different layers, suggesting some degree of coiling. Specimen A5921/2 is a heteropolar-spiral coprolite (morphotype 3) with oval-ellipsoidal elongated gross morphology. Its spiral gross morphology corresponds to the internal layering of the specimen (Fig. 11A, A1). The coprolite is composed of layers with obvious coiling in transverse sections.

## 5.5 Chemical composition

The specimens analyzed using XRF (see list of specimens in Table 3) represent different morphotypes and some of them contain visible bone fragment inclusions. Also, in two of the specimens (i.e., no. A0972/3 and A0972/4) which belong to morphotype 3 of latest Santonian age, analyses were made both for the coprolite and the enclosing host rock. The general composition of the most common oxides is shown in Table 3. Overall, the percentages of CaO and P<sub>2</sub>O<sub>5</sub> are high in the examined specimens (Fig. 14). The dominating elements are Ca, P and Si. CaO values range from 15% to almost 50%. P<sub>2</sub>O<sub>5</sub> also has high values of almost up to 42% in the coprolites. However, the two Santonian coprolites are the exception with lower values of CaO and P<sub>2</sub>O<sub>5</sub> (Fig. 15). The analyses of the Santonian coprolites showed P<sub>2</sub>O<sub>5</sub> values from 11 and 14%. These values are much lower than the ones for all the other specimens that range from 19 to 42%, but closely similar to specimen A1030/1-20.20 from Kassenberg (15%). There is also a significant difference in the amount of P<sub>2</sub>O<sub>5</sub> between the host rocks and their coprolites. Whereas the coprolites contain 11% (specimen A0972/3) and 14% (specimen A0972/4), as mentioned above, their host rocks show very low values of 1.4 and 1.9%, respectively (Table 3).

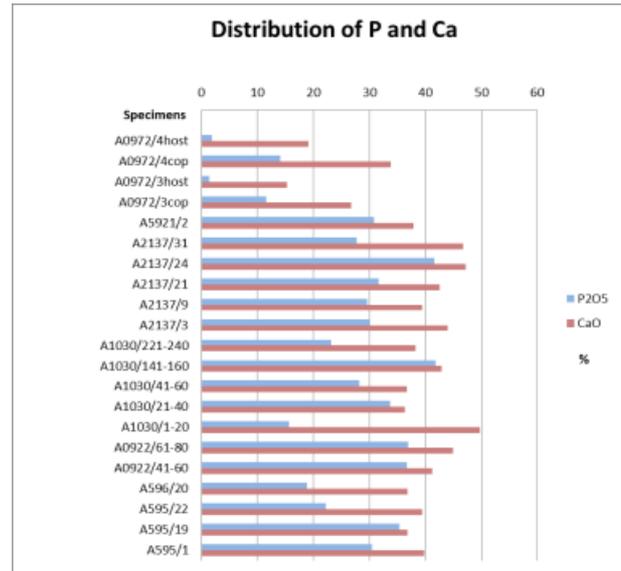


Fig. 14. Relative abundance of Ca and P oxides in selected samples from the collection.

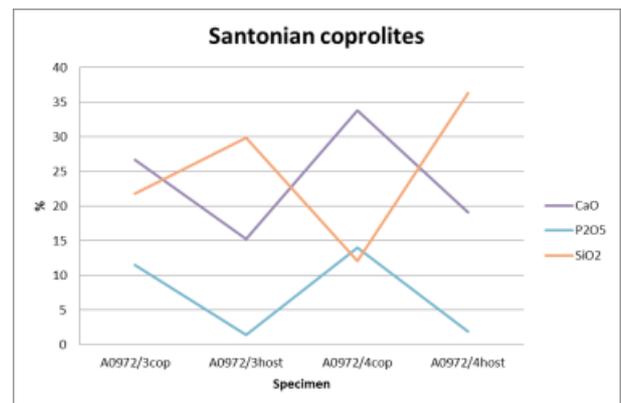


Fig. 15. Relative abundance of Si, Ca and P oxides in the upper Santonian coprolites.

## 6. Discussion

### 6.1 Diagenesis and taphonomy

The consistency and composition, the depositional setting and the degree of diagenetic alteration are important for the preservation of fecal material (e.g. Hunt et al. 1994; Chin et al. 2003; Eriksson et al. 2011). “Once deposited, two key factors essential for the preservation of coprolites seems to be rapid scat burial, followed by rapid lithification” (Eriksson et al. 2011, p. 466). It is also important to note the role of bacteria in the fossilization process. A large number of bacteria colonize the

Table 3. List of the major oxide concentrations in coprolites/host rock samples (in weight percent).

Coprolites	Fe <sub>2</sub> O <sub>3</sub>	CaO	K <sub>2</sub> O	Al <sub>2</sub> O <sub>3</sub>	P <sub>2</sub> O <sub>5</sub>	SiO <sub>2</sub>	SO <sub>3</sub>
<b>A595/1</b>	1,443468	39,75438	0,880019	3,411145	30,43246	12,91153	5,760372
<b>A595/19</b>	2,194421	36,78805	0,790954	3,011154	35,35898	10,68802	2,601549
<b>A595/22</b>	1,528042	39,47184	0,947703	3,66786	22,16887	11,60531	2,909058
<b>A596/20</b>	0,821792	36,75949	0,900135	3,139311	18,92166	12,80723	3,259773
<b>A0922/41-60.2</b>	0,422126	41,2887	0,331047	2,303897	36,6543	7,606532	1,893925
<b>A0922/61-80.3</b>	0,295042	44,98674	0,325463	1,838259	36,88793	5,192732	2,449396
<b>A1030/1-20.20</b>	0,847577	49,70995	0,821488	4,962204	15,61577	14,90741	1,711181
<b>A1030/21-40.5</b>	0,350292	36,38564	0,462287	3,075746	33,72475	10,1985	2,382386
<b>A1030/41-60.1</b>	1,507152	36,72827	0,84395	4,803385	28,17986	17,5917	3,088158
<b>A1030/141-160</b>	0,337755	42,87418	0,293003	2,24158	41,8918	7,477395	2,526312
<b>A1030/161-180.1</b>	3,461083	44,53227	0,626172	2,880411	38,67792	11,72614	2,705439
<b>A1030/221-240.21</b>	1,868857	38,22975	1,441104	7,8282	23,20517	26,38664	2,23505
<b>A2137/3</b>	1,334515	44,02575	0,474457	2,691443	30,15027	9,3721	1,825237
<b>A2137/9</b>	1,545045	39,43085	0,797994	3,413155	29,67758	14,18657	1,78446
<b>A2137/21</b>	1,192933	42,5756	0,997489	6,231317	31,67503	19,26448	1,936652
<b>A2137/24</b>	0,741997	47,19339	0,220985	1,528954	41,56605	3,62984	2,144237
<b>A2137/31</b>	1,280161	46,73621	0,308693	1,405383	27,68497	5,263864	1,671949
<b>A5921/2</b>	2,237338	37,90617	0,554649	3,822561	30,87943	15,19901	8,971283
<b>A0972/3cop</b>	3,635906	26,70645	0,96547	2,206189	11,52523	21,76607	7,845969
<b>A0972/3host</b>	2,653616	15,22837	1,461459	3,834039	1,421498	29,91618	6,978051
<b>A0972/4cop</b>	3,816244	33,85447	0,388719	1,571187	14,02767	12,07189	9,491305
<b>A0972/4host</b>	3,832488	19,143	1,57792	5,132271	1,883984	36,32676	6,055846

intestines of living vertebrates and help the process of lithification of the feces (Lamboy et al. 1994). According to Seilacher (2002, p. 237) “undeformed coprolites must have undergone selective prefossilization at a very early stage of diagenesis, long before the host sediment became lithified” and he suggested that the activity of bacteria led to the phosphatization of those coprolites.

It has been proposed that spiraled feces must undergo rapid burial and lithification in order to retain their original morphology (e.g., Northwood 2005). The presence of spiral coprolites mostly in the late Santonian and early Campanian specimens suggest environments with better preservation potential for fecal matter compared to those from Kassenberg. Many coprolites derived from Kassenberg are thought to be of a reworked spiral-heteropolar shape (morphotype 3), although they are assigned to different morphotypes. Many of these specimens are fragments and others are eroded. Differences in gross morphologies between the Kassenberg specimens and the late Santonian ones could be due to different taphonomic conditions. However, this is probably not the case for the various morphotypes recognized in Kassenberg specimens because they were all preserved under similar environmental conditions.

## 6.2 Host animals

The size and morphology of coprolites can vary substantially and strongly depend on the diet of the host animal; however, it is difficult for a small-sized animal to produce large feces (Hunt et al. 1994). Fecal pellets produced by invertebrates generally are smaller than 5 mm (Häntzschel et al. 1968). The coprolites examined herein show a variety of sizes, ranging from about 10 to almost 90 mm, and none of them is smaller than 5 mm. Therefore, an invertebrate producer of the coprolites at hand can probably be excluded and instead a vertebrate origin is suggested. The vertebrates that have been found in Kassenberg quarry and generally in the Münster Basin consist of fish and reptiles, including sharks, bony fish, rays, turtles (not recorded in Kassenberg) and mosasaurs, many of which were carnivorous (predators and/or scavengers).

### 6.2.1 Inclusions

Coprolite inclusions that consist of inorganic (bone) components that have been ingested by an animal, can be useful to identify the diet of the producer of the coprolite (Hunt et al. 1994; Rodriguez-de la Rosa et al. 1998). It should, however, be stressed that the inclusions are more useful for identifying the affinity of the prey animals than the host animal (Chin 2002). Several inclusions of specific taxa have been identified in coprolites (Chin 2002); mollusks (e.g., Speden 1969; Stewart & Carpenter 1990), fish (e.g., Zangerl & Richardson 1963; Waldman 1970), reptiles (e.g., Parris &

Holman 1978), and mammals (e.g., Martin 1981; Meng et al. 1998). Inclusions occur abundantly in the Upper Cretaceous coprolites studied herein but mostly in the Kassenberg specimens. These inclusions generally include fish bones and possibly scales. Those fish were probably preyed upon by bigger carnivorous fish or reptiles in the shallow Late Cretaceous seas of northwest Germany. The specific skeletal remains which have been studied herein, based on their characteristics, could be indicative of certain prey animals. For example, the visible layered or lamellar bone organization seen in thin sections (Fig. 10) is typical of bony fish (cf. Cohen et al., 2012). Based on its elongated morphology the vertebra recorded in coprolite specimen A1030/21-40.1 (Fig. 9J), may be from a juvenile turtle (J. Lindgren, personal communication, 2012). If this interpretation is correct, then this would constitute the first report of a turtle from the Cretaceous of the Kassenberg quarry. Except for the fish bones and the putative turtle vertebra another noteworthy inclusion is the vertebra most probably deriving from a fish in coprolite A1030/21-40.5 (Fig. 9E). The preservation of these inclusions depends on the digestive system of the host animal, mode of feeding, and exposure of the inclusions inside the coprolites during diagenesis. The lack of obvious signs of bone corrosion in the material at hand suggests that gut residence time was short and/or that the efficiency to break down bone of the host animal was limited.

In addition to inclusions of animal origin, dietary remains consisting of wood fragments, leaves and other plant remains have been recorded in many coprolites, primarily based on thin section analyses and palynological studies (e.g., Chin & Gill 1996; Northwood 2005; Prasad et al. 2005). Such remains obviously suggest an herbivorous diet of the coprolite-producing animal. All inclusions recorded in the Upper Cretaceous coprolites from Germany are most likely dietary remains except for some palynomorphs that could have been involuntary ingested by the coprolite producers (no macroscopic plant remains were identified). The palynological assemblages are dominated by typical Early Cretaceous taxa, but also some reworked Jurassic palynomorphs occur. These latter palynomorphs could have been transported into the basin by rivers that cut down into older sediments. These older sediments have then been mixed with the Cretaceous ones. The presence of Jurassic pollen grains in the coprolites could be explained by animals (involuntary) ingesting sediment during feeding.

Collectively this shows that coprolites along with their inclusions can provide additional taxonomic information to the body fossils from a specific locality.

### 6.2.2 Phosphatic composition

XRF and SEM analyses revealed the presence of high levels of calcium phosphate in the coprolites. The presence of calcium phosphate at high concentrations in the specimens is typical of coprolites, although, it

does not constitute proof in itself of biogenic origin as authigenic phosphate nodules may also form under specific conditions (Fountain & McClellan 2000; Marshall-Neill & Ruffell 2004). Calcium phosphate is the main component of bone and so, if present in coprolites, it can directly be linked with carnivore vertebrate hosts (Dietrich 1951; Häntzschel et al. 1968). However, invertebrate coprolites may exhibit considerable concentrations of calcium phosphate (Häntzschel et al. 1968; Eriksson & Terfelt 2007). Coprolites from carnivorous animals are far more abundant (or at least better known) in the fossil record than those of herbivore origin and they are usually easy to differentiate from the latter because they are typically phosphatic and often contain skeletal inclusions (Chin 2002). Especially carnivorous fish feces are usually phosphate-rich because of the large number of undigested fish skeletal remains (Lambooy et al. 1994). This fact along with the presence of many bone fragments in the coprolites from analysis of thin sections, external surface etc., further supports the idea of a carnivorous origin of the studied coprolites. Furthermore, the absence (except for a few palynomorphs) of herbivorous dietary remains, such as plants or parts of plants, further strengthens a carnivorous host animal interpretation.

### 6.2.3 Morphology

The morphology of droppings that related taxa can produce can vary significantly (Eriksson et al. 2011). However, organisms which are not related can also produce similar feces, but also a single animal can produce differently shaped feces because of changes in diet (Thulborn 1991; Hunt et al. 1994; Eriksson et al. 2011).

The Upper Cretaceous coprolites from Germany comprise typical morphotypes that have been assigned to specific host organisms by several authors. For example, spiral coprolites are commonly connected to primitive fish (Hunt et al. 1994; Northwood 2005) and/or intestinal valves (for example of sharks, lungfish, or gars; Gilmore 1992). Several authors (e.g. McAllister 1985, and references therein) described spiral coprolites as enterospirae, i.e. fossilized valvular intestines. Preserved valvular intestines are present in placoderm, chondrichthyan, actinopterygian and probably acanthodian fossils (McAllister 1985, and references therein). *Ptychodus* and *Odontaspis* (chondrichthyans) but also *Plethodus* (actinopterygians) have been described from Kassenberg quarry (Scheer & Stottrop 1995). Neumayer (1904) distinguished two main morphologies in his study on the Permian spiral coprolites; heteropolar coprolites exhibit spaced coils concentrated to one end, whereas amphipolar coprolites have coils along the length of the specimen and which are more evenly spaced. Because sharks have more complex intestinal valves than those of bony fishes, they produce heteropolar feces similar to fossil heteropolar coprolites in contrast with bony fish that produce amphipolar ones (cf. McAllister 1985). Therefore, the most probable

producers of the coprolites belonging to morphotype 3 are fish. For the heteropolar spiral coprolites a shark producer seems most likely. In contrast, because of the amphipolar shape of the two spiral specimens of morphotype 3, a shark producer should be excluded and a bony fish origin seems to be plausible. As noted above, sharks and bony fish were both part of the Late Cretaceous vertebrate faunas of Münster Basin.

The unique specimen representing morphotype 7 is similar to the spiral coprolite described by Buckland (1835) from the Lyme Regis of England. Its morphology could also be associated with a fish producer.

The general shapes of morphotypes 1 and 2 have been connected with invertebrates. For example, marine invertebrates (especially gastropods) are related mostly with ellipsoidal coprolites (e.g. Hancock et al. 1972) and/or other extant invertebrate taxa are related with rod-like and cylindrical coprolites (e.g. Ladle & Griffiths 1980). However, the size of the Upper Cretaceous coprolites of Germany is much bigger than invertebrate feces which are generally up to a few millimetres. It cannot be excluded, however, that large cephalopods could be responsible for producing some of the studied coprolites. The shape of crocodylian feces, which is typically elongate and cylindrical to slightly flatten in transverse-section (Milàn et al. 2012b, and references therein), could also be connected with these two morphotypes.

The morphology of morphotype 5 specimens could not be connected with specific producers. However, the presence of skeletal remains in morphotype 5, interpreted as bony fish bones (see Table 2) along with their size, provide information about the prey animals that could lead to certain assumptions for the predators too. Hence, possible producers of these coprolites include bony fish, sharks and reptiles.

As for the other morphotypes, their connection with certain taxa of fecal producers is problematic. Possible producers of these coprolites include sharks, bony fish and mosasaurs.

### 6.3 External coprolite features

Concerning the various trace fossils (burrows, putative tooth marks, striations and grooves) that occur in the coprolite specimens from Germany, these could be derived from coprophagous invertebrates and/or sharks or other fish after or prior to their lithification (cf. Eriksson et al. 2011). It is possible that the two distinct sharp marks in specimen A1030/21-40 (Fig. 9I1) could represent tooth marks originating from sharks. The bigger mark is similar to the shark medial tooth impression on coprolites from the Miocene of Maryland (Godfrey & Smith 2010). Extant sharks are not known to be deliberately coprophagous but this may be the result of shark predation and/or exploration (see Godfrey & Smith 2010). The holes (Fig. 9A-C, E) could be burrows from coprophagous invertebrates, whereas the more spherical and smaller ones could represent de-

compositional gas escape holes (Northwood 2005; Hollocher et al. 2010). Coprophagous traces, for example, have been observed in Lower Triassic coprolites from Australia (Northwood, 2005). Such holes/borings occur in several specimens in bigger or smaller sizes. The smaller holes (see e.g., Fig. 9B, C) possibly represent invertebrate burrows or borings as was suggested by Eriksson et al. (2011) for Upper Cretaceous coprolites from Sweden. Similarly the bigger ones (see e.g., Fig. 9A) could also have an invertebrate origin. For example, marine bivalves have been reported to produce borings in coprolites (Tapanila et al. 2004). These borings are excavations made in hard substrates, e.g., rocks or fossils (Ekdale et al. 1984).

The grooves on the external surface of the coprolites may well be from the action of scavenging animals or possibly from the landing of feces on a sharp object (Eriksson et al. 2011) or from the erosion of the coprolites (see e.g., Figs. 6I; 7A). The ridges and striations (Figs. 6D, F, J; 9E-G) could originate from impressions of the intestines while perforations could be gas-escape features (Broughton et al. 1978).

### 6.3.1 Epibionts

Epibionts identified as brachiopods, most probably belong to *Isocrania cf. parisiensis*, are present on quite a few of the Upper Cretaceous coprolites. Brachiopods have been reported by several authors from different units of the Kassenberg quarry, however, *Isocrania cf. parisiensis* has hitherto only been found in the Middle Turonian phosphorites which correspond to Phase 8 (Fig. 2) (see Scheer & Stottrop 1995, and references therein). Based on their life strategies (cf. Bassett 1984), these epibionts attached to the lithified coprolites and not to the soft feces. Their random distribution on the surface of the coprolites suggests that they represent different generations of attachment and that the coprolites have been moving or rolling to some extent on the sea floor, e.g., by current or wave action. The fecal matter must have been lithified in order to withstand such transport. The absence of epibionts in the Santonian specimens suggests different taphonomic conditions in this area or environments unsuitable for epibiont organisms.

## 6.4 Internal structures

As can be seen from the photographs of the thin sections (Fig. 10) and some of the CT-scanning images (Fig. 11), a spirally or whorl internal structure is dominant among the coprolites. According to Williams (1972), an intricate internal folding of the spiral coprolites most of the time represents mucosal folds of a shark's intestine (see also Broughton et al. 1978). CT-scanning revealed that many of the coprolites consist of several internal layers. These concentric layers probably result from the deposition of fecal mass inside the intestinal valve of the producer (Fig. 11A-C)

as was suggested by Milàn et al. (2012b). The presence of fish bones in the coprolites along with a spiral internal structure is an additional convincing clue that the producers of these coprolites are sharks or bony fish.

The coprofabrics are homogenous among the coprolites, exhibiting a micro-crystalline fabric. Therefore, no correlation between coprofabrics and distinguished morphotypes was found (cf. Eriksson et al. 2011).

The two main types of microtextures that were revealed in the SEM studies are the result of microbial processes (cf. Lamboy et al. 1994). According to Lamboy et al. (1994, p. 379) such microglobular structures represent "...phosphatised remnants of coalesced globular bacteria" and the botryoid microtexture is the result of phosphate precipitation around globular bacterial bodies which subsequently disappeared.

## 7 Conclusions

The main results of this study are summarized as follows:

- The Upper Cretaceous coprolites from the Münster Basin of Germany are sub-divided into eight different morphotypes based on their gross morphology. Coprolites form common fossil elements in the Plenus Marl bed and the phosphorites corresponding to phases 5 and 8 at Kassenberg quarry.
- Most of the specimens seem to be derived from carnivorous (predatory or scavenging) animals based on their phosphatic composition, bone inclusions, size and morphology. Moreover, there is no evidence for herbivorous host animals and the few palynomorphs deriving from plants were most likely ingested involuntarily.
- The host animals preyed principally upon fish based on the texture and lamellar organization of the bone inclusions. The bone inclusion tentatively assigned to a turtle shows also that these reptiles were prey animals in the Late Cretaceous Münster Basin. This is the first turtle recorded from the Kassenberg quarry.
- The size of the coprolites, and especially those of late Santonian age, indicates that the host animals were of considerable size.
- Macroscopic inclusions are abundant in many of the coprolites and even in specimens that seemingly lack such by visual external inspection, as revealed by thin section and CT-scanning studies.
- A spiral internal morphology was revealed in several coprolites, although it does not necessarily correspond to their external gross morphology. Especially, the spiral-heteropolar gross morphology (internal and external) of almost all the larger upper Santonian coprolites proba-

bly indicates a shark origin. Similarly, the other smaller coprolites may have been produced by other host animals. In this case a shark origin could probably be excluded because of their different gross morphology. Instead, a reptile origin seems more plausible.

- The abundance of skeletal inclusions along with the absence of obvious corrosion and the homogenous coprofabrics among the coprolites, suggest that gut residence time was short and/or that the efficiency to break down bone of the host animal was limited.
- Tracks and traces are common on the external coprolite surfaces and most of them suggest handling by coprophagous invertebrates and possibly vertebrates.
- Epibionts are common and many of these are identified as *Isocrania*. Their random distribution on the surface of the coprolites suggests that they represent different generations of attachment and that the coprolites have been rolling on the sea floor.
- Palynomorphs are rare in the coprolites and include Cretaceous as well as reworked Jurassic taxa. The presence of dinoflagellates in the coprolites and also in the host rock samples, along with several of the body fossils reported, confirms that the coprolite-yielding palaeoenvironment was shallow-marine.
- Microtexturally the coprolites proved to be homogeneous with phosphatic minute microglobular structures and botryoid microtexture resulting from microbial activity that most likely aided in the preservation of the feces.
- The combination of several different analytical techniques is powerful for understanding coprolite origin, composition, and their inclusions. Especially, CT-scanning offers a non-destructive tool for understanding the internal structures and concealed inclusions in valuable specimens.

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