

Late Cretaceous coprolites from the Kristianstad Basin, southern Sweden

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Contents

1 Introduction.....	5
2 Coprolites and the fossil record	5
2.1 Morphology and composition	5
2.2 Paleoecological utility	6
3 Geological setting and stratigraphy.....	6
4 Materials and methods	7
5 Results	8
5.1 Systematic ichnology	8
5.2 Composition and inclusions	11
6 Discussion	12
6.1 Coprolite taxonomy	12
6.2 Producer	12
6.3 Taphonomy	15
7 Conclusions.....	15
8 Acknowledgements	15
9 References.....	15

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Abstract: Vertebrate coprolites from the Upper Cretaceous (Campanian) of the Åsen locality, Kristianstad Basin, southern Sweden, are described and illustrated. Their fecal origin was supported through chemical analyses revealing a calcium phosphate composition. Five specimens were chosen for detailed description and analyses and these were sub-divided into three different groups of ichnotaxa. Because of their heteropolar mode of spiralling, coprolites of one group are interpreted as being produced by macrophagous lamniform sharks. Two groups, each containing un-spiralled coprolites, are harder to attribute to a certain producer. One coprolite, containing invertebrate fossils of possible molluscan affinity, may have been produced by a bottom-feeding, durophagous shark or a pycnodont fish, both of which were common components of the Åsen fauna. Possible producers of the larger, un-spiralled coprolites include mosasaurs and plesiosaurs.

Keywords: coprolites, Cretaceous, Kristianstad, Åsen, spiral.

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Koproliter från Kristianstadbassängens yngre krita

URBAN MÅNSBY

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Sammanfattning: Vertebratkoproliter från de yngre kretaceiska (Campan) sedimenten vid Åsen, en lokal belägen i den nordliga delen av Kristianstadbassängen, har här beskrivits och illustrerats med det huvudsakliga målet att bestämma deras värdjur. Deras fekala ursprung kunde bekräftas vid en kemisk analys, emedan de huvudsakligen visades bestå av kalciumfosfat, ett ämne intimit förknippat med koproliter. Fem exemplar valdes ut för en detaljerad beskrivning och delades därefter in i tre olika grupper baserat på skillnader i morfologi och sammansättning. En grupp har kunnat kopplas till rovlevande hajar tack vare ett spiralvriddt mönster i koproliternas ena ände, och förekomsten av fiskrester inuti. De andra två grupperna, bestående av koproliter utan spiralform, är desto svårare att härleda till specifika värdjur. En koprolit innehållandes fossil av evertebrater, troligen mollusker, skulle kunna härstamma från särskilda haj- eller fisktaxa, vilka är kända för att äta skalbärande djur, t ex musslor. Andra tänkbara värdjur till de problematiska koproliterna är mosasaurier eller plesiosaurier (svanödlor), vilka båda ingår i den lokala kretaceiska faunan.

Nyckelord: koproliter, krita, Kristianstad, Åsen, spiralformade.

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1 Introduction

Coprolites, or fossilized feces, can provide valuable information with regards to feeding habits, digestive physiology and the trophic levels of ancient ecosystems. Coprolite studies have been conducted since the early 19th century, when Buckland (1829) identified unusual sedimentary bodies from Pleistocene cave deposits, previously interpreted as fossil fir cones, as fossilized hyena feces. Ever since the term was coined by Buckland, coprolites have been described from all Phanerozoic periods and every continent except Antarctica (Hunt et al. 1994). In a comprehensive review, Häntzschel et al. (1968) gathered more than 370 reports of coprolites of both vertebrate and invertebrate origin, and since then, several additional studies have been published. However, coprolites have generally received less attention than other fossils of equal abundance, despite their usefulness in paleoecological studies (Hunt et al. 1994).

Excavations of the marine Late Cretaceous strata of Åsen, southern Sweden, have yielded abundant vertebrate remains indicating a diverse marine fauna, including several shark and mosasaur taxa (Siverson 1993; Lindgren & Siverson 2004). In addition, numerous potential coprolites have been found in those strata. Most of them are small, more or less spherical to ellipsoidal lumps less than 1 cm in diameter, with no distinctive surface features. However, five specimens notable for their size and/or shape were chosen for closer examination and description. Based on a wide array of analyses these coprolites are described from a paleoecological context and potential producers are discussed.

2 Coprolites and the fossil record

Coprolites, i.e., fossilized feces, are trace fossils belonging to the group “bromalites”, which represent all fossilized material originating from the dietary tract of an organism (Hunt et al. 1994). In addition to coprolites, this group thus includes regurgitalites and cololites, i.e., dietary matter fossilized after extrusion through the oral cavity or fossilized in situ in the dietary tract, respectively. Sometimes the term coprolite has been used exclusively for fossilized vertebrate feces whereas fossilized droppings of invertebrates have been referred to as fecal pellets, strings, trains, or castings (Häntzschel et al. 1968; Thulborn 1991).

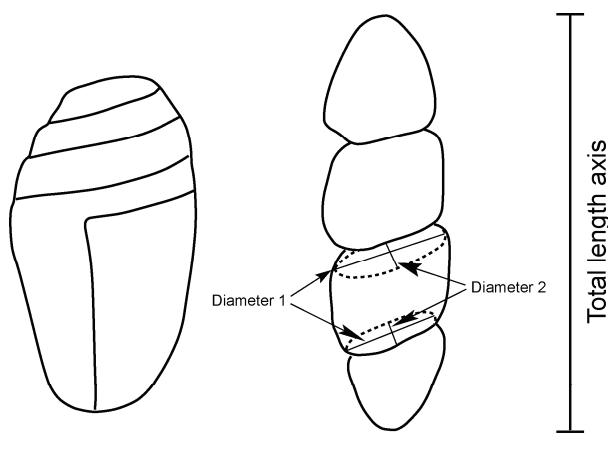
2.1 Morphology and composition

Coprolites can be recognized by many different features that distinguish them from sedimentary clasts, inorganic phosphate nodules or other types of fossils or concretions that potentially can be misinterpreted as coprolites. The morphology of coprolites produced by different organisms may differ significantly, just as the

wide variation of droppings seen among extant animals. In many cases, a coprolite can be identified directly on basis of its external morphology, as for example spiral-shaped specimens. This is a fairly common type of morphology (Häntzschel et al. 1968) that not only reveals the nature of the coprolite, but also assigns the producer to a fish taxon (Hunt et al. 1994). The mode of spiraling can be recognized as heteropolar or amphipolar (Fig. 1), depending on whether the coils are concentrated at one end of the coprolite or evenly spaced along its longitudinal axis. Dinosaur coprolites commonly also show a somewhat spiraled morphology (Thulborn 1991). However, they are considerably more irregular than the systematical spirals seen in fish coprolites.

Other common shapes include rounded, more or less spherical, ellipsoidal to cylindrical and rod-like forms (Häntzschel et al. 1968). The morphology of the ends of cylindrical coprolites can be used for classification, because they can be either rounded or pinched out. If both ends are similarly-shaped, the coprolite is termed isopolar, and, in the opposite case, anisopolar (Thulborn 1991). These terms should not be confused with heteropolar or amphipolar, which only refers to the mode of spiraling. Striations along the longitudinal axis of coprolites are a common feature (Hunt et al. 1994). Such features have been suggested to originate from impressions of the intestinal walls, puckering due to intestinal contractions or to have been imprinted by the anal valve during extrusion of the feces (Thulborn 1991). If the consistency of the fecal matter was sufficiently soft when extruded, the area resting upon the substrate, referred to as the ventral side, might be somewhat flattened. In such cases, the opposite side can be attributed to as the dorsal side.

Coprolites can vary in size from mm-sized rod-



Heteropolar

Amphipolar

Fig. 1. Illustration of a heteropolar spiral coprolite, with all the coils concentrated at one end, and an amphipolar spiral coprolite, at which the coils are evenly spaced along the coprolite length. Diameter 1 and 2, the longest and shortest, respectively, perpendicular to the coprolite length axis, is also featured. Modified from Hunt et al. (2004).

shaped specimens (Häntzschel et al. 1968) to the very large theropod dinosaur coprolites reaching over 40 cm in length and 15 cm in width (Chin et al. 1998). Among larger coprolites, a size range between 2 and 5 cm is the most common (Häntzschel et al. 1968).

Calcium phosphate is a characteristic chemical compound found in most coprolites analyzed (Häntzschel et al. 1968). Because calcium phosphate is the main component of bone, it is specifically associated with carnivore vertebrate coprolites (Dietrich 1951; Häntzschel et al. 1968). However, during diagenesis coprolites can become enriched in phosphates originating from phosphorous released into the pore water from decaying organic matter (Brenchley & Harper 1998). Thus invertebrate coprolites may show elevated levels of calcium phosphate (Häntzschel et al. 1968; Eriksson & Terfelt 2007). Although an anomalous concentration of calcium phosphate is a typical coprolite feature, it cannot be used as unequivocal evidence for a fecal origin, because authigenic phosphate nodules may form under certain conditions (Fountain & McClellan 2000; Marshall-Neill & Ruffell 2004).

While calcium phosphate is the mineral typically associated with coprolites, other common minerals replacing the organic matter and, hence, responsible for preserving coprolites, include, e.g., calcium carbonate, silica, iron and magnesium oxides and siderite (Häntzschel et al. 1968; Hunt et al. 1994). The texture of most phosphatic coprolites is extremely fine-grained, commonly distinguishing them from the surrounding sediment (Thulborn 1991). Coprolites are typically more firmly attached to the underlying than the overlying sediments, which tend to bulge over the feces.

If neither morphology nor composition provides sufficient information to reveal the identity of the fossil, possible inclusions of dietary residues can hint of its coprolitic status. Hard parts that might pass undigested, such as bones, scales, teeth, shells or cuticles, are found in many coprolites (Thulborn 1991), and are either visible on the surface, in thin sections, or, alternatively, in acid resistant residues of dissolved coprolites. Mineral grains or organic matter can also be adhered to coprolite surfaces, if the consistency of the dropping was sticky enough during the time of deposition. Such adhering material could potentially be misinterpreted as dietary components (Thulborn 1991).

2.2 Paleoecological utility

When studying coprolites, the main issue is to identify the producer (Thulborn 1991; Hunt et al. 1994). If the producer's affinity cannot be assigned, the utility of the coprolites for other paleoecological implications will be somewhat limited. However, if the producer's identity can be assessed with confidence, the coprolites can provide valuable information, particularly with regards to feeding habits. Coprolites without a known producer might also provide useful information, as many inclusions of organisms remain very

well preserved embedded in feces that are mineralized (e.g. Northwood 2005). In recent years, several innovative coprolite studies have been performed. Hunt (1992) recognized three different ichnofacies based on coprolites in a succession of Upper Triassic rocks of southern United States. The different facies were occurring in strata representing different depositional environments. Coprolite assemblages can hence be used to recognize different paleoenvironments and for correlation between different strata.

Prasad et al. (2005) were able to shed new light upon the early evolution of grass and grazers, by finding phytoliths of several different grass taxa in Maastrichtian titanosaur sauropod coprolites from India. These coprolites were ascribed to their producer because of their common occurrence associated with titanosaur sauropod bones. The total phytolith content of the droppings suggested a varied herbivorous diet, where grass was a significant constituent. This was an intriguing discovery since studies of titanosaur sauropod teeth give no implications of grazing.

Rodriguez-de la Rosa et al. (1998) performed another study where implications about the interaction between animals and plants were made. Angiosperm seeds found in Campanian coprolites of herbivore origin suggested that plants utilized indirect biotic seed dispersal due to herbivorous activity.

A single coprolite, attributed to *Tyrannosaurus rex* due to its very large size, stratigraphical and geographical occurrence, provided insight into its producer's mode of feeding and digestion (Chin et al. 1998). The level of fragmentation of the bones included implied that they were severely crushed during ingestion, and their very high grade of preservation contradicts the extensive digestion that could be expected according to the digestion of bone matter in extant crocodilians.

Evidences of producer and diet have also been received through extraction of DNA from well preserved late Quaternary North American coprolites (Hofreiter et al. 2001). In approximately 28,500 years old ground sloth coprolites, DNA evidence of pine forests in southern Nevada were extracted. In another study, evidence for meat from large mammals in 2,000 years old feces of Native Americans, could also be obtained through DNA extraction (Hofreiter et al. 2001).

3 Geological setting and stratigraphy

The Kristianstad Basin was formed during the Early Cretaceous to the early Campanian in the Late Cretaceous by downward tilting of the crystalline bedrock to the southwest, with faults forming the Nåvlingeåsen and Linderödsåsen horsts (Bergström & Sundquist 1978). The warm and humid climate of the latest Triassic to Middle Jurassic had prior to the formation of the basin led to an extensive kaolinization of the bed-

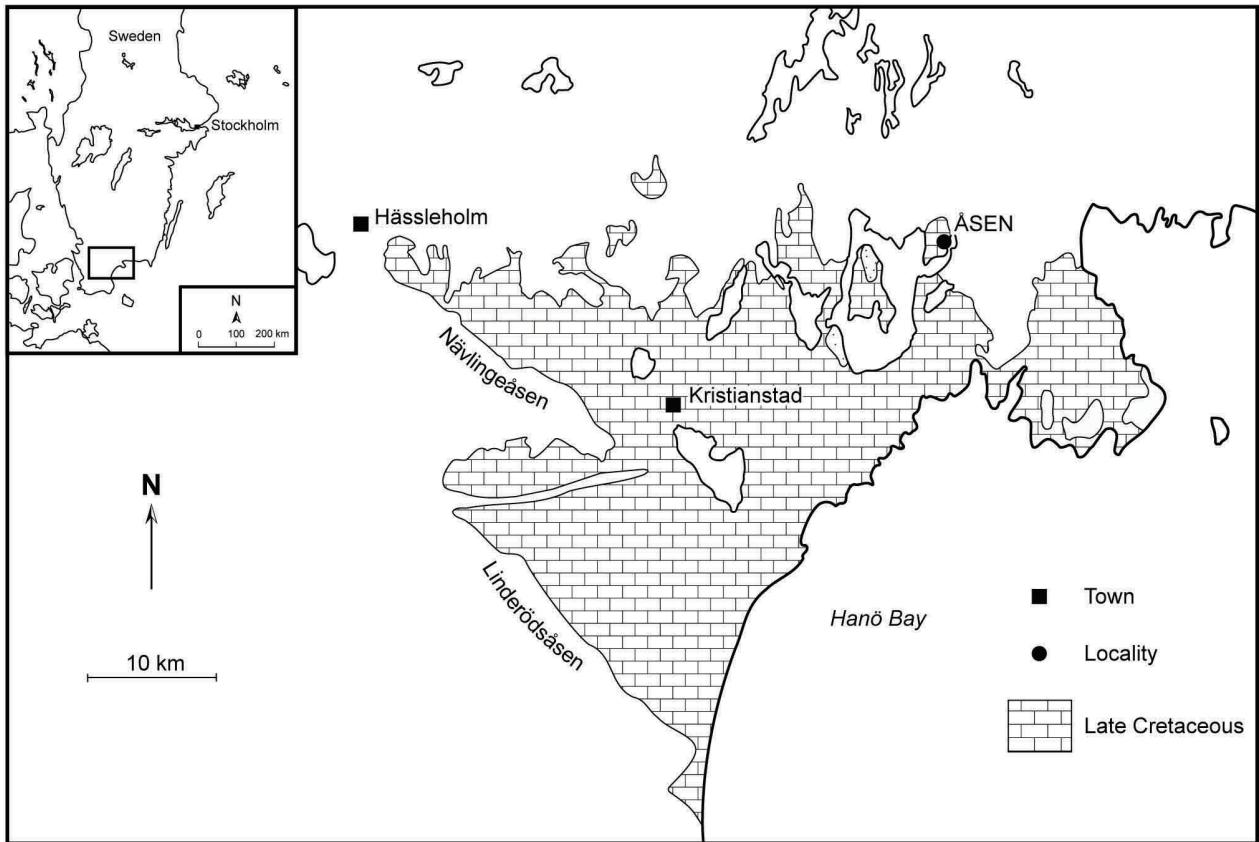


Fig. 2. Map showing the distribution of Late Cretaceous deposits of the Kristianstad Basin, and the location of the coprolite yielding Åsen locality.

rock in the area, resulting in a highly uneven topography where the more weathering resistant parts of the bedrock remained as paleohighs rising between weathered out troughs (Lidmar-Bergström 1982). Beginning in the late Early Cretaceous, the sea level transgressed during at least four occasions (Bergström & Sundquist 1978), resulting in an archipelago environment where bedrock highs formed low islands and peninsulas (Christensen 1984).

The Cretaceous marine sediments of the Kristianstad Basin are generally less than 200 m thick (Christensen 1984). In the southwest, the lateral distribution of these strata is sharply limited by the Nåvlingåsen and Linderödsåsen horsts, while their demarcation to the north is far more intermittent, with several outliers of upper Cretaceous strata (Lindgren et al. 2007). The basal part of the sequence is dominated by kaolinite and quartz rich sediments, whereas the succeeding deposition to a large extent constituted of calcareous bioclasts forming calcarenites (Erlström & Gabrielson 1992).

The Åsen locality is an old kaolin quarry now serving as a refuse dump. Its Cretaceous rocks are known both for their abundance in vertebrate fossils (Lindgren & Siverson 2002) and their diverse and exceptionally well preserved floral content (Friis & Skarby 1981; Koppelhus & Batten 1989). The exposed sequence is 15-20 m thick, consisting mainly of fluvi-

ally deposited clays with interbedded sands (Lundegren 1934). At the top of the sequence, there is an up to 3.5 m thick unit of poorly consolidated marine sands (Lindgren & Siverson 2002). An erosional surface sub-divides this unit into an upper and a lower part, and marks the boundary between the lower and upper Campanian (Lindgren et al. 2007). The strata underlying the erosional surface belongs to the local *Belemnelloccamax mammillatus* zone (uppermost lower Campanian), and are rich in reptile remains, belemnites and oysters. Among the animals, several mosasaur taxa have been reported from Åsen (Lindgren & Siverson 2004; Lindgren 2005), as well as plesiosaur remains (Persson 1967), and numerous different shark taxa (Siverson 1993).

The coprolites were collected from the second coquina bed, 1.5 m below the erosional surface (*sensu* Rees 1999). This bed was described by Lindgren et al. (2007) as a 10 cm thick storm deposit consisting of greenish, coarse grained quartz sand, rich in fragmented oysters, belemnites and vertebrate fossils.

4 Materials and methods

The five specimen selected from the coprolite collection were sub-divided into three different groups of ichnotaxa (ichnotaxon group 1 to 3, see below) based on overall morphology, surface texture, inclusions and

colour. The size of the coprolites was measured with a vernier caliper. Any characteristics providing information of the coprolites' taphonomic history, such as breakage, possible bite marks, borings, adhesions or desiccation cracks, were observed, noted and introduced into a database.

Because some of the specimens were going to be subjected to destructive analytical techniques, they were first moulded in order for plaster casts to be made if desired. Silicone moulds were made of specimen A, B and D, using RTV silicone for the two first-mentioned and silicone putty for the latter one.

Thin sections were made from two of the specimens belonging to group 1, for the study of internal structures and possible inclusions. Sawn-off pieces of the coprolites were embedded in transparent epoxy prior to being cut into slabs using a low-speed diamond saw. The slabs were mounted on glass slides using epoxy, and then ground to an appropriate thickness. The thin sections were studied under a Nikon Eclipse E400 POL binocular microscope and photographed with a Nikon digital camera.

Sawn-off pieces of two specimens belonging to group 1 were examined using a Hitachi S-3400N scanning electron microscope (SEM). An elemental mapping of the matrix was performed in order to evaluate their chemical composition.

Small pieces (approximately 1 cm³ each) of two specimens belonging to group 1 were dissolved in hydrochloric acid (HCl) in order to examine any potential palynomorph content, such as diatoms, pollen and spores, and cuticular fragments from plants and/or animals. The samples were cleaned from external contaminants in an ultrasound bath prior to dissolution in 4 M HCl. The solution was then rinsed through a sieve cloth with a mesh size of 18 µm. The resulting sample was fixed to a glass slide with transparent epoxy and studied under a Nikon Eclipse E400 POL binocular microscope. Since the remaining mineral grains of the residue were very few, no further dissolution in hydrofluoric acid was needed.

5 Results

5.1 Systematic ichnology

Ichnotaxon group 1

Fig. 3, 4, 5A-D

Description.- Various ellipsoidal shapes with a general diameter ranging from approximately 2,5 to about 6 cm. Overall shape varies from almost spherical to elongated with greatest diameter approximately twice that of the shortest diameter. Color varies from light grey to dark brown and surface texture is very fine grained. A pitted pattern of bowl-shaped depressions occurs on a somewhat flattened side of specimen C and D (Fig. 5C). Several Inclusions of bone fragments are visible on the external surface of specimen

B (Fig. 3G, H), and steinkerns of problematic invertebrates, probably of molluscan affinity, are present in specimen C (Fig. 4G, H). Parts of the surface of specimen B show shallow grooves of random orientation (Fig. 3I), and an approximately 2 mm wide and deep circular hole occurs in the same specimen (Fig. 3D, F).

Measurements.- See Table 1

Material.- Three loose specimens (B, C, D), one of which is broken along its longitudinal axis (B).

Occurrence.- The second coquina bed at Åsen, southern Sweden, described by Rees (1999).

Discussion.- This group is problematic because the coprolites assigned to it show rather diffuse morphologies lacking distinct features. Of the coprolites reviewed by Häntzschel et al. (1968), approximately 40 % have been described as round, oval or ellipsoidal, and could hence be assigned to this group on the basis of morphology. However, although the specimens share the same gross morphology, they show fairly different features when studied in closer detail. Specimen D, which was not examined with the same analytical methods as specimens B and C, differs most from the two others based on the macroscopic level, since it has a more coarse-grained texture and a darker colour. Even though it has an ellipsoidal shape, it might be interpreted as a spiral coprolite, since it viewed from certain angles looks somewhat spiralled (Fig. 5A). The coprolites of ichnotaxon group 1 may be produced by different animals, although being assigned to the same group due to a lack of more distinct morphological features.

Ichnotaxon group 2

Fig. 5E-I

Description.- The general shape is an elliptic cylinder with an approximately 5 cm major diameter, 4 cm minor diameter and a height of 3 cm. Ends are slightly concave and rougher than the smooth curved area. Colour is dark to medium brown. Surface texture consists of about 0.5 mm grains embedded in a mud-to silt-sized ground mass. One side of the curved (lateral) area of the cylinder shaped coprolite is flattened. Three grooves, approximately 2 mm wide and 10 mm long, oriented in the same direction, occur on the lateral area (Fig. 5I).

Measurements.- See Table 1

Material.- One loose specimen (A).

Occurrence.- The second coquina bed of Åsen, described by Rees (1999).

Discussion.- Matley (1941) described Upper Cretaceous coprolites from India with a presumed sauropod origin, that were broken into similar cylindrical segments as that of the specimen at hand. The puck-like morphology probably results from cleavage perpendicular to the longitudinal axis along a larger cylindrical fecal unit, likely formed during or prior to extrusion. Thulborn (1991) suggested that such segmentation originates from the squeezing together of fecal pellets within the animal's intestine. This implies

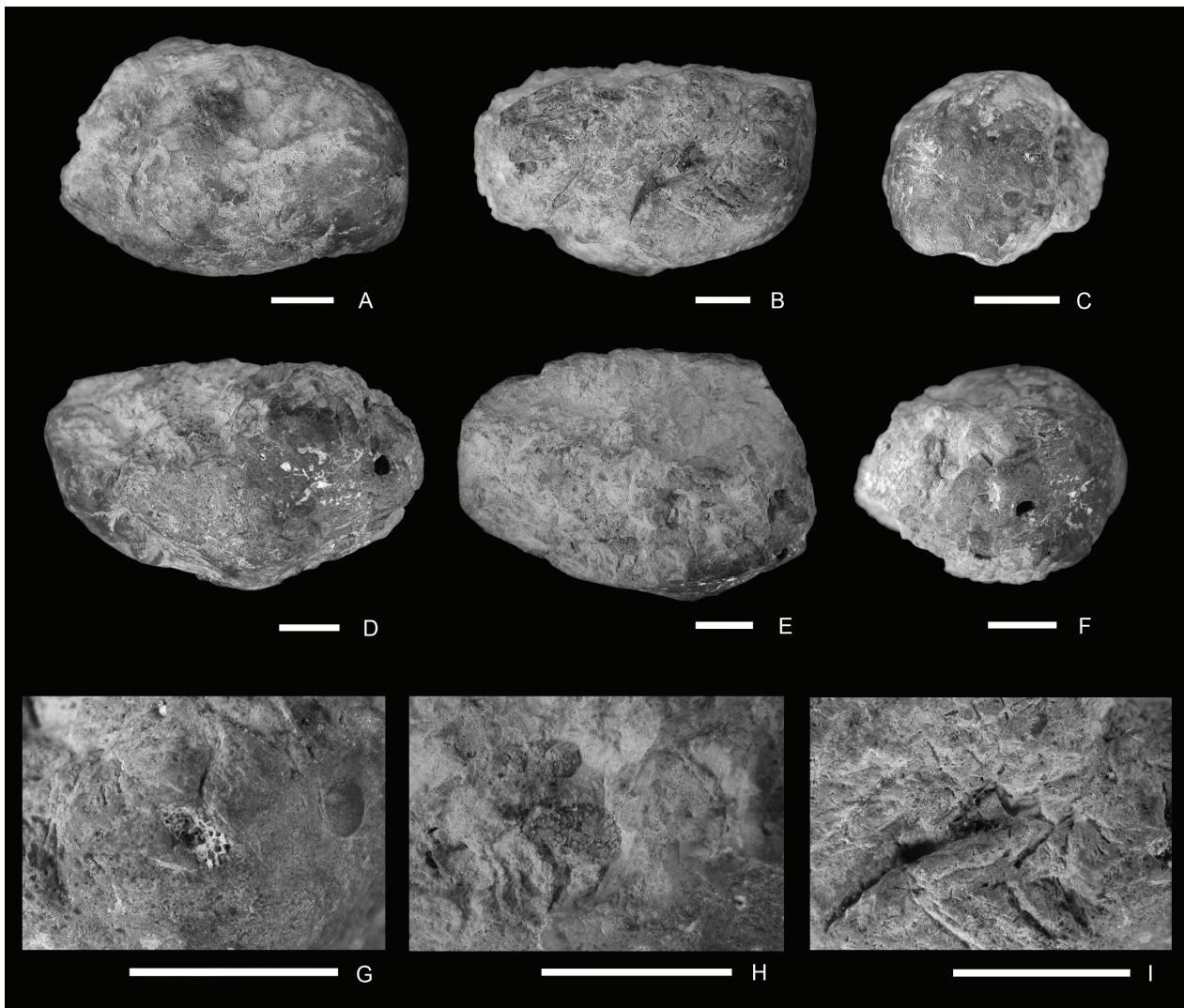


Fig. 3. Photographs of different views of the Åsen coprolite specimen B. A. Lateral view. B. Lateral view. Note that the upper part is broken off. C. End view. D. Lateral view. Note the circular hole present on the right side of the coprolite. E. Lateral view of a fracture surface. F. End view, also showing the circular hole. G-I. Close up photographs showing surface details; G-H. Bone-fragment inclusions. I. Surface striations. All scale bars: 10 mm. All pictures have been composed of multiple images using the CombineZM software.

that the specimen is only a part of a fecal mass of considerably larger size and volume, setting a higher limit for the size of the producer. It is likely that the grooves on the surface (Fig. 5I) are bite marks made by scavenging animals, as they correspond to bite marks in bone made by sharks (e.g. Schwimmer et al. 1997).

The flattened part of the curved area might correspond to the ventral side of the coprolite, which is also supported by the location of the possible bite marks on the resulting dorsal side. The smooth surface presumably results from weathering and/or erosion since the sand-sized grains are cut off at the surface.

Table 1. Measured size of the Åsen coprolites. For the ellipsoidal coprolites (B, C and D), the length refers to the maximum diameter, and to the length of the cylinder for the cylindrical coprolites (A and E). Diameter 1 and 2 refers to the longest and shortest diameter, respectively, measured perpendicular to the length axis.

Specimen	Ichnotaxon 1			Ichnotaxon 2	Ichnotaxon 3
	B	C	D	A	E
Length (mm)	57	37	41	30	15
Diameter 1 (mm)	40	35	30	52	11
Diameter 2 (mm)	34	28	26	41	11

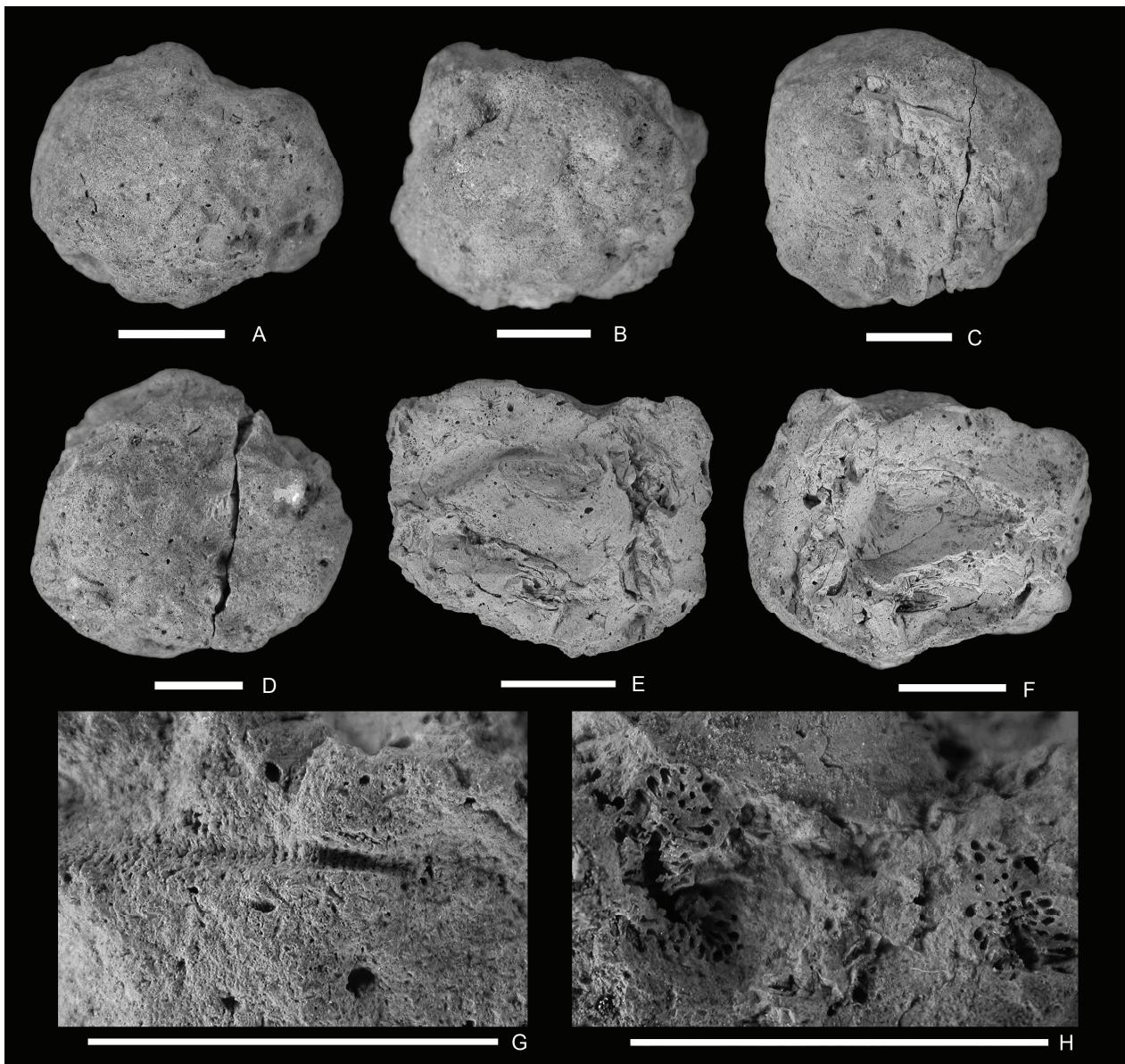


Fig. 4. Photographs of different views of the Åsen coprolite specimen C. A-D. Overview showing gross morphology. E-F. Surface views of a fracture through the specimen (fracture seen in photos C and D). G-H. Close up photographs showing surface details; G. Problematic invertebrate on the coprolite surface. H. Problematic invertebrates on the fracture surface. All scale bars: 10 mm. All pictures have been composed of multiple images using the CombineZM software.

Ichnotaxon group 3

Fig. 6

Description.- Heteropolar 1-2 cm long spiral-shaped coprolites. Diameter is approximately 1 cm. Cross section reveals a spiral folding of the lamina, which are folded into four to five coils (Fig. 6B, C). The surface of the coprolites shows small white longitudinal undulating, in some cases branching, striations, which are cut by the coils. Exterior color is light yellowish brown, and surface texture is very fine grained. Inclusions of fish bones and scales are visible on the lateral surface (Fig. 6D-F).

Measurements.- See Table 1

Material.- One loose complete specimen (E) and some broken-off fragments.

Occurrence.- The second coquina bed of Åsen, described by Rees (1999).

Discussion.- The coprolites of this group clearly show a heteropolar spiraling, and all fragments show the same macroscopic features as the complete specimen. Similar heteropolar coprolites have been described from the Upper Triassic Chinle Group of Arizona and Texas (Hunt 1992), however, those have a more elongated shape with the coils not as concentrated in one end compared to the specimens described here.

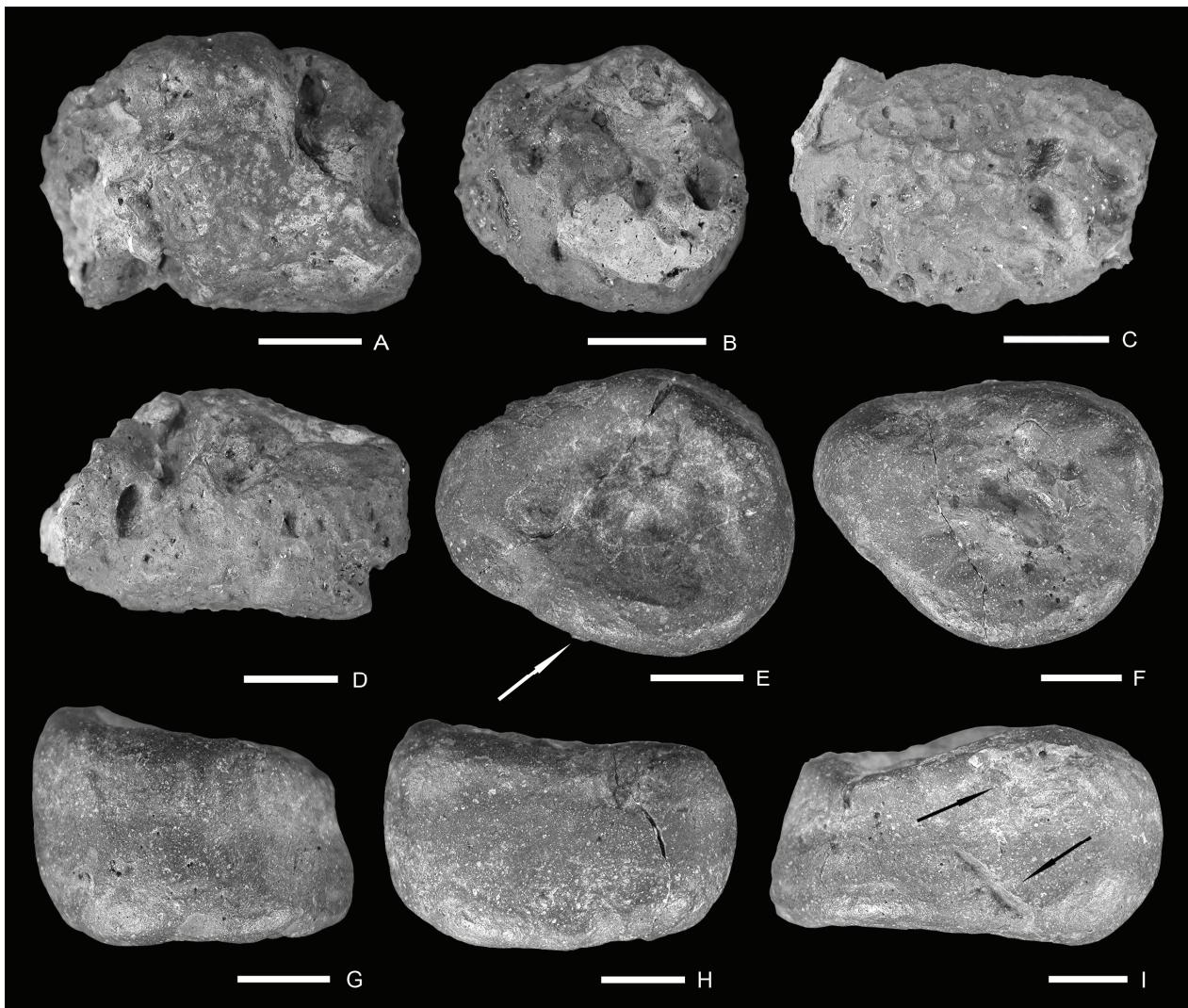


Fig. 5. Photographs of different views of the Åsen coprolite specimens D (A-D) and A (E-I). A. Lateral viewed at an angle where the coprolite may be interpreted as spiral. B. End view. C. Bowl shaped depressions on the possibly ventrally flattened side. D. Lateral view. E. View of flat/concave surface. Arrow pointing at a possibly adhering mineral grain. F. View of flat/concave surface. G-H. View of curved/later area. I. View of curved/lateral area. Arrows pointing at grooves interpreted as bite marks. All scale bars: 10 mm. All pictures have been composed of multiple images using the CombineZM software.

5.2 Composition and inclusions

The thin section analysis reveals a composition of silt- to sand-sized grains within a phosphatic microcrystalline groundmass of the coprolites (Fig. 7). The main differences between the two studied thin-sections were a more homogenous composition in specimen B (Fig. 7A), and the presence of silt- to sand-sized grains of an opaque mineral in specimen C (Fig. 7B). These grains are commonly occurring evenly-spaced in elongated narrow voids.

The results of the chemical analysis performed in the SEM clearly show that both analyzed specimens primarily are composed of calcium phosphate, although the peaks in carbon implies a high content of calcium carbonate as well (Fig 8). The elemental map-

ping shows distinct elevated levels of iron and sulfur in specimen C (Fig. 9B, C) revealing that the heavy mineral grains present in this coprolite are pyrite. The microstructure in specimen B also proved to be far more homogenous than in specimen C, which showed minute wrinkle structures and invertebrate steinkerns of possible molluscan affinity (Fig 9A, D).

Both the samples from specimens B and C were fully dissolved in the hydrochloric acid within a couple of hours. The acid resistant sample residues yielded abundant cuticular fragments of probable arthropod origin (S. Lindström, Lund, pers. commun. 2009; Fig. 10), grains of a sulfide mineral (only present in specimen C) and quartz grains in low abundance.

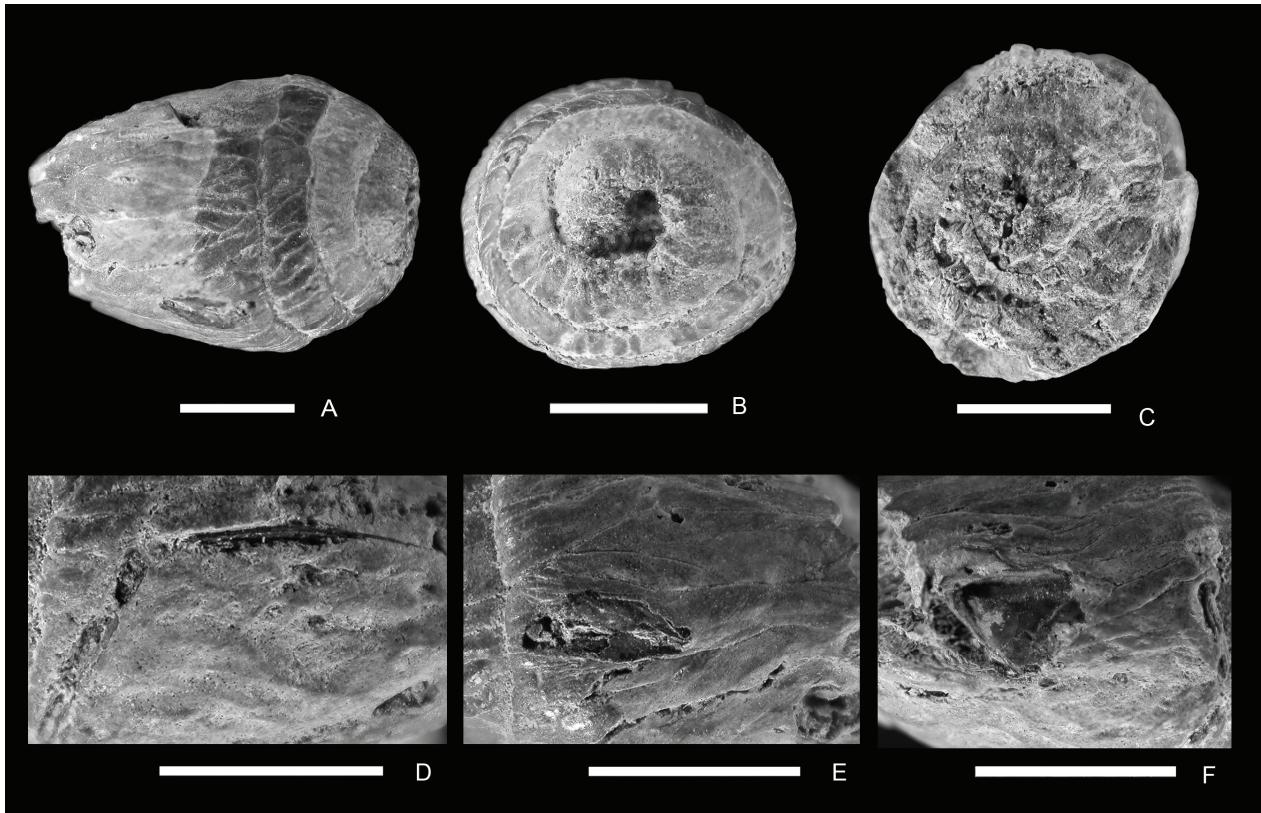


Fig. 6. Photographs of different views of the Åsen coprolite specimen E. A. Lateral view B. End view. C. Fracture surface, perpendicular to the longitudinal axis, showing the spiral folding of the lamina. D-F. Close up photographs showing surface details; D-E. Bone fragment inclusions. F. Fish scale inclusion. All scale bars: 5 mm. All pictures have been composed of multiple images using the CombineZM software.

6 Discussion

6.1 Coprolite taxonomy

Giving coprolites a proper taxonomic classification might be an elusive task, as discussed by Hunt et al. (1994). The feces from one single organism can differ substantially due to variations in diet, while unrelated organisms can produce very similar droppings. Due to the difficulties in assigning coprolites to a certain producer, applying Linnaean binominals to the coprolites can be deceptive. It could imply taxonomical differences within a group of feces produced by one and the same organism. Most coprolites studied never receive a taxonomic classification, which further limits the taxonomic assignment in future studies, due to the lack of detailed descriptive literature.

The use of morphotypes or ichnotypes instead of binomial designation might be an appropriate approach to describe and classify coprolites, and also avoiding the taxonomical fallacies that binomial classification may result in.

Specimens B and C, which were the most thoroughly analyzed specimens, showed fairly extensive differences even though their gross external morphology are quite similar. The texture of specimen B is very homogenous with inclusions of fish bones,

whereas specimen C has a far more heterogeneous texture, with irregular microstructures and inclusions of small invertebrates, and also a slightly different mineral composition with the presence of pyrite. As most coprolites have rather diffuse morphologies, these differences imply that morphological studies alone are not enough for classification of coprolites, unless for cases of very specific shapes that are diagnostic.

Despite the structural differences observed in specimens B and C, the chemical composition and inclusions of cuticles were closely similar, supporting a classification into the same group. As for specimens A and D, further analyses would be needed to assign a correct classification, although specimen A quite clearly differs from specimens of group 1 on a macroscopic level. The heteropolar spiralled coprolite and coprolite fragments of group 3 show very distinct morphological features, sufficient to assign them to a single group although no additional, destructive, analyses were performed.

6.2 Producer

Coprolite size can be a useful indicator of the size of its producer, however, it can only be used to approximate a lower limit of the producer's size (Hunt et al. 1994). The total mass of feces extruded in a single defecation event generally is larger among species of

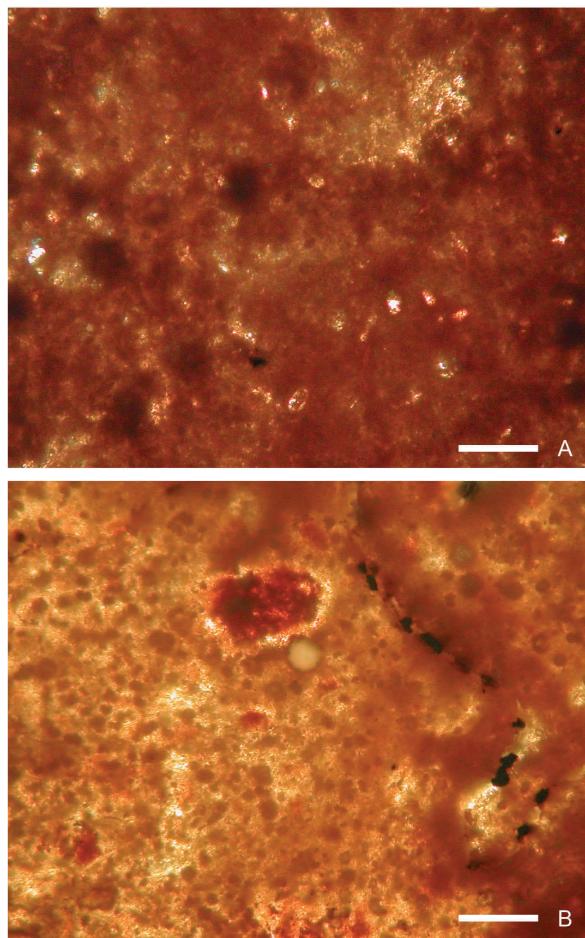


Fig. 7. Light microscope photographs of thin sections of two of the Åsen coprolites. A. Homogenous microcrystalline phosphatic groundmass in specimen B. B. Silt sized grains in a microcrystalline phosphatic groundmass., with evenly spaced pyrite grains in an elongated narrow void. Scale bars: 200 µm.

larger size. However, the individual bodies, or parts, making up the total fecal mass, might be as small as

the feces extruded by animals of significantly smaller size. Large coprolites are, however, unlikely to have a small producer due to their limiting sphincter diameter (Hunt et al. 1994).

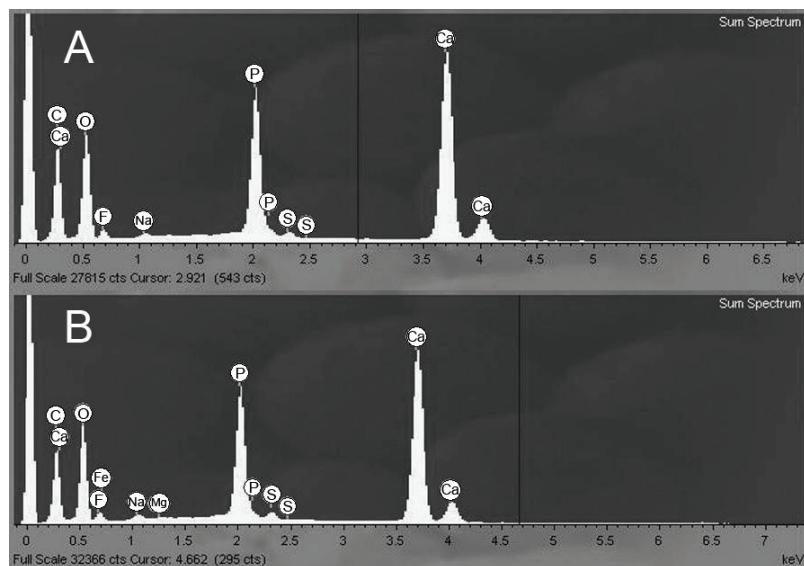
All of the coprolites examined are large enough to confirm a vertebrate producer, because fecal pellets produced by invertebrates generally are smaller than 5 mm (Häntzschel et al. 1968). The large diameter (4-5 cm) of specimen A indicates a producer of notably large size. As for the other specimens, at least the smallest vertebrates can be excluded, though further implications based exclusively on coprolite size would be ill-advised.

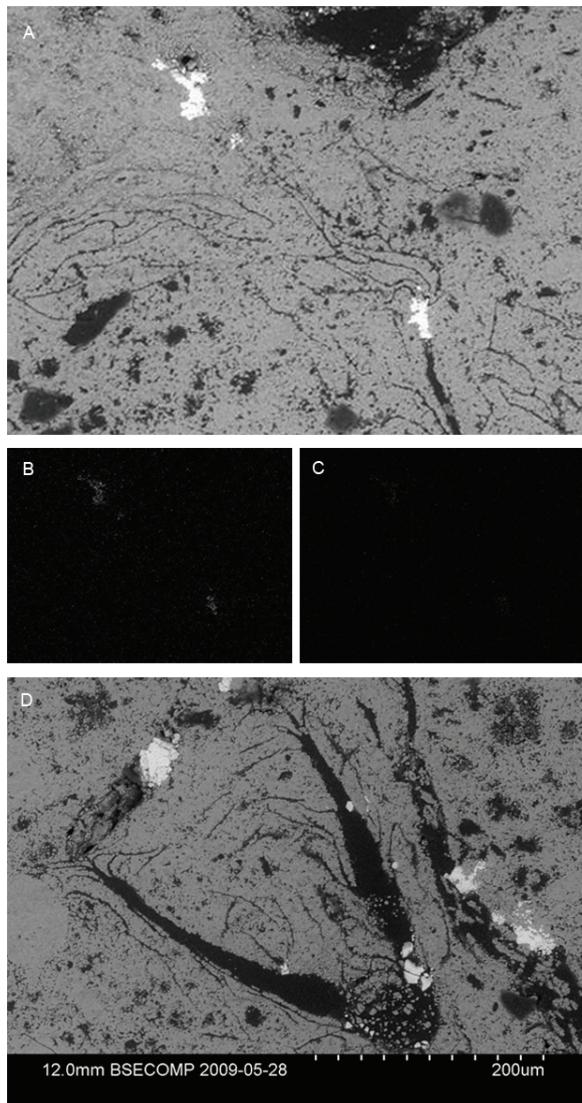
If present, one of the most useful characteristics for defining the producer's affinity is the spiral morphology of the coprolite. Spiral coprolites have long been identified as feces produced by primitive fish (Hunt et al. 1994; Northwood 2005). The spiralling is a result of the fecal matter passing a spiral intestinal valve, which has been seen in both extant taxa and fossil specimens (Williams 1972; Jain 1983). Also seen in experiments with extant taxa is that sharks, having more complex intestinal valves than bony fishes producing amphipolar feces, produce heteropolar feces similar to fossil heteropolar coprolites (McAllister 1985).

Due to their heteropolar spiral morphology, the coprolites of ichnotaxon group 3 most likely were produced by sharks. Siverson (1993) has recorded more than 60 different shark species in the Cretaceous sediments of the Kristianstad Basin of which approximately 40 have been identified at the Åsen locality. Of the certainly carnivorous sharks found, teeth from four different lamniform species are particularly abundant at Åsen; *Carcharias latus*, *Cretalamna appendiculata*, *Archaeolamna kopingensis*, and *Squalicorax lindstromi* (= *Squalicorax kaupi* sensu Siverson 1993) It seems probable that either of these taxa were responsible for the heteropolar coprolites at Åsen.

The chemical analysis showed a predominant

Fig. 8. Sum spectra received from the SEM chemical analysis of the Åsen coprolite specimens B (spectrum A) and C (spectrum B), showing the number of electron counts at different energy levels, corresponding to different elements. The anomalously high phosphorous content suggests a predominant calcium phosphate composition of the coprolites.





phosphatic composition in both specimens analyzed, which indicates that the coprolites were produced by vertebrate eating animals (Dietrich 1951; Häntzschel et al. 1968). Calcium phosphate is the primary component of bone and teeth, meaning that a diet in which bones are ingested results in phosphatic feces. However, phosphatization of fecal matter through microbial activity is a common way of preservation of coprolites, not necessarily requiring the presence of bone (Brenchley & Harper 1998). Thus, the phosphorous could be derived from organic material present in the surrounding sediments. Many coprolites contain higher concentrations of phosphate than the feces of the producer's extant relatives, suggesting a post depositional enrichment in phosphate (Northwood 2005).

The bones included in specimen B are with no doubt evidence for a carnivorous producer. The lack of visible bones together with the invertebrate inclusions in specimen C implies that it has been produced by a durophagous animal, although the invertebrates may have been unintentionally ingested. The cuticular frag-

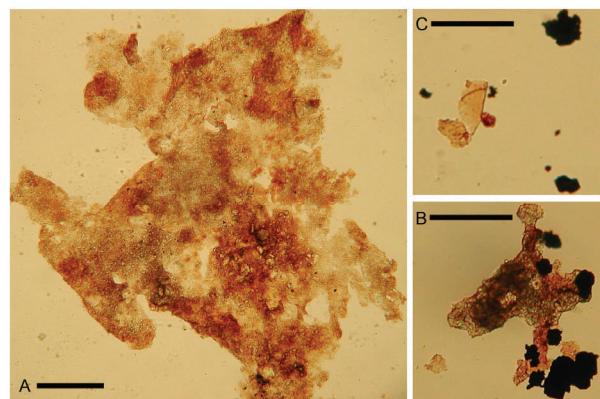


Fig. 10. Light microscope photographs of specimens recovered from the acid resistant residues of the digested coprolites. A. Larger cuticular fragment of possible arthropod origin from specimen B. B-C. Smaller cuticular fragments of possible arthropod origin and pyrite grains (black) from specimen C. Scale bars: 200 μ m.

Fig. 9. Backscattered electron images of a thin section of specimen C. The elemental maps (B: sulfur, C: iron) show the distribution of different elements of the area photographed in A; the brighter the colour, the higher concentration of the element. D. Unidentified inclusion of probable molluscan affinity.

ments present in both specimens may also result from inadvertent ingestion or derive from small organisms feeding on or dwelling in the feces.

Even though heteropolar coprolites have been attributed to sharks, all shark coprolites does not necessarily show a spiral structure. Hence, the non-spiralling Åsen coprolites could possibly also have been produced by sharks. The invertebrate inclusions in specimen C are consistent with the bottom feeding behaviour known from e.g. heterodont sharks or pycnodont fish (Edmonds et al. 2001; Poyato-Ariza & Bermúdez-Rochas 2009). Heterodont shark remains have been found in large abundance at Åsen (Siverson 1993). Mosasaurs or plesiosaurs, both represent taxa known from the Åsen fauna, may also be possible producers of the non-spiralling Åsen coprolites, because their size fit well with the relatively large size of some coprolites. However, the possibility that the coprolites were produced by an animal, not known from the Åsen fauna, should not be left out.

6.3 Taphonomy

Experiments with extant fish taxa have shown that the originally compact spiral faces start unravelling very soon after extrusion and that within 24 hours the feces resembles slightly spiralled loose strings or ribbons (Jain 1983). This suggests that the spiralled feces must undergo rapid burial in order to retain their original morphology, and, hence, provide a clue as to the mode of preservation of the Åsen coprolites, including specimens with a spiral morphology. Their preservation may also have been aided by phosphate enrichment due to microbial activity, in which case the mineralization would be facilitated by the anoxic conditions prevailing if the feces were buried.

7 Conclusions

The coprolites from Åsen represent several different morphologies and likely have been produced by different taxa. Even coprolites with similar gross morphology show a dissimilar content in terms of inclusions and microstructures, indicating different producers, or different feeding behaviors. The heteropolar spiraling in one of the coprolites together with inclusions of bones and scales suggest that it was produced by a vertebrate-eating shark. The morphologies of the other coprolites cannot be linked to any specific taxon, although all invertebrates and small vertebrates can be excluded due to the relatively large size of the coprolites. Bones included in one specimen are evidence for a vertebrate eating producer, whereas invertebrate inclusions in another specimen could indicate a durophagous feeding habit of the producer. The coprolites probably became preserved due to rapid burial coupled with phosphate mineralization through microbial activity.

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