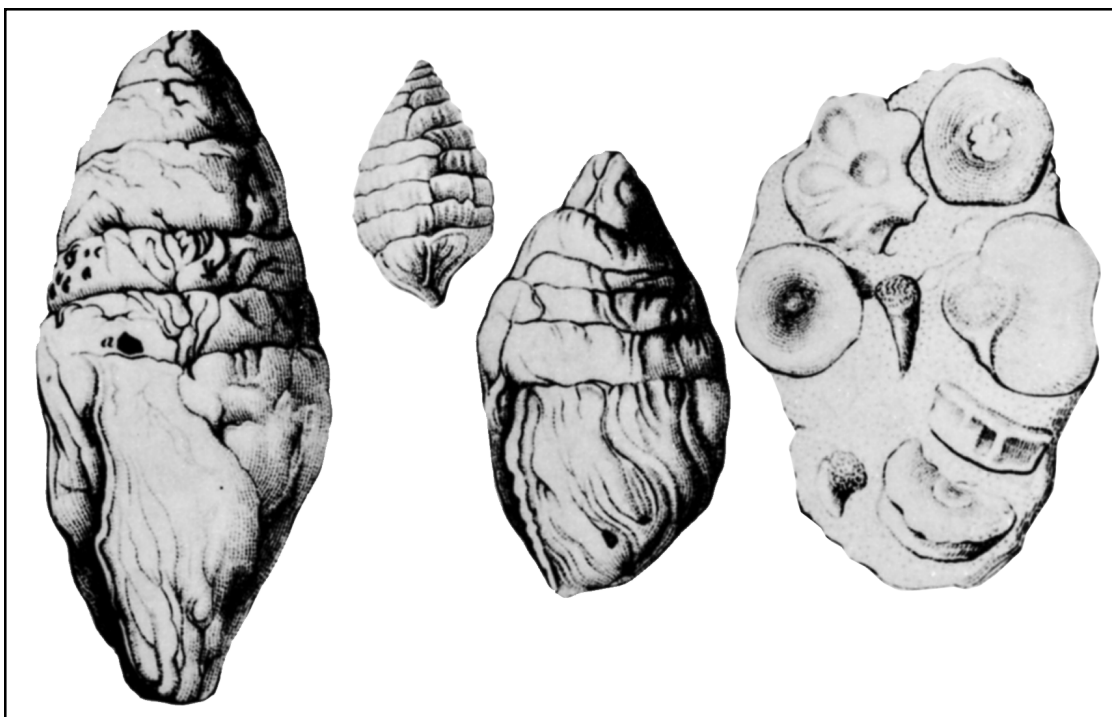


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Vertebrate Coprolites



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COPROLITES WITH PREY REMAINS AND TRACES FROM COPROPHAGOUS ORGANISMS FROM THE LOWER CRETACEOUS (LATE BERRIASIAN) JYDEGAARD FORMATION OF BORNHOLM, DENMARK

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Abstract—Two fragmentary coprolites from the Lower Cretaceous Jydegaard Formation of Bornholm, Denmark, represent the first record of coprolites from continental Mesozoic deposits in Denmark. Both specimens contain fish scale bone fragments of unknown affinity. Based on morphology, inclusions and the potential producers found in the Jydegaard Formation, we suggest they were made by either a turtle or a theropod with a piscivorous diet. One specimen shows pits and grooves in the surface, as well as two deep cylindrical burrows, made by coprophagous organisms.

INTRODUCTION

Deposits with Mesozoic continental vertebrates are rare in Denmark, and are only found in a few restricted outcrops on the Baltic Island of Bornholm (Fig. 1). Some of these vertebrate-bearing deposits are in the lowermost Cretaceous Nyker Group (Gravesen et al., 1982), comprising the Berriasian Rabekke Formation, which mainly consists of swamp and freshwater sediments, and is overlain by the interfingering Berriasian shallow marine Robbedale Formation and brackish to freshwater Jydegård Formation, that are interpreted as back barrier and lagoonal deposits (Noe-Nygaard et al., 1987; Noe-Nygaard and Surlyk, 1988), with the upper parts of the latter formation being of Valanginian age.

The Rabekke Formation (Gravesen et al., 1982), exposed just east of Arnager at the south coast of Bornholm (Fig. 1), has recently yielded a relatively rich micro-vertebrate fauna. It comprises abundant crocodile teeth (*Bernissartia* sp., *Theriosuchus* sp., and *Goniopholis* sp.) and fragments of turtle carapaces, scales and jawbone fragments of actinopterygians, postcranial remains of amphibians and primitive lizards, small dromaeosaurid dinosaur and perhaps bird teeth, and a single tooth of a multituberculate mammal (Lindgren et al., 2004, 2008; Rees et al., 2005; Schwarz-Wings et al., 2009). In addition to the small-sized body fossils, a trample ground with abundant cross-sections through large dinosaur tracks (up to 70 cm in length), and possible lungfish estivation burrows, have been described from the coast cliff (Surlyk et al. 2008).

The Jydegaard Formation exposed in inland quarries has yielded dromaeosaurian teeth, *Dromaeosaurides bornholmensis*, and a possible tooth crown from a juvenile sauropod (Bonde and Christiansen, 2003; Christiansen and Bonde, 2003), as well as fragments from carapaces of turtles, teeth of the crocodile *Pholidosaurus*, and abundant teeth and scales of the holostean fish *Lepidotes* and the freshwater shark *Hybodus* and some pycnodont jaws and small stem-teleosts (Noe-Nygaard et al., 1987; Noe-Nygaard and Surlyk, 1988; Rees, 2001; Bonde, 2004). For a complete review of the Mesozoic vertebrate faunas of Bornholm see Bonde (in press). This study documents the finds of two coprolites from the base of the Jydegaard Formation, and examines their content of prey remains as well as traces of coprophagous organisms.

MATERIAL AND METHODS

Two partial Lower Cretaceous coprolites were found in the exposure of the Jydegaard Formation in the now abandoned Carl Nielsen's Sandpit at Robbedale on Bornholm (55°04'49.15N, 14°45'00E) approximately 5 km southeast of Rønne (Fig. 1). The two specimens were found by Regitze Benthien and the "Fossil Projektet," during their systematic

excavations in the sand pit during the last few years. One specimen is on display (unnumbered item) in the at-the-experience-center NaturBornholm at Åkirkeby, Bornholm, and the other specimen is part of the collection of the Natural History Museum of Denmark (MGUH 29809).

As Computed Tomography scanning has proven a useful non-destructive technique to examine coprolites (Milån et al, this volume), one specimen was CT scanned at the Radiology Department at Dronning Ingrid's Hospital in Nuuk, Greenland. The CT-scanner used was a Philips Brilliance 64. Physical parameters for the scanning were 140kV and 600mA and a rotation time of 1.5 sec per slice. As the coprolite is a dense object, a kernel 80 was used to obtain a high resolution. The scanning was performed with a matrix of (X,Y) 0.63 mm x 0.63 mm and a reconstruction (Z) of 0.63 mm. Thus, the object is shown with isometric voxels, and proportions are kept as original. The machine's resolution could, however, not exceed 0.63 mm and detail structures smaller than this could not be reproduced faithfully. Subsequent data processing was made using AmbivU 3D Workstation, which can create cross sections of the scanned objects with 3D insight.

THE COPROLITES

So far, the Carl Nielsen's sandpit has yielded two partial coprolites. Both specimens are dark-colored and permineralized by phosphate, and abundant prey remains are visible on their surfaces.

Specimen 1

A partial coprolite measures 2.6 x 1.9 cm (unnumbered item, NaturBornholm). The fragment is from a cylindrical specimen that has split along its longitudinal axis. A high density of indeterminate bone fragments and fish scales are visible on the surface, and most of the fragments are oriented perpendicular to the long axis of the coprolite (Fig. 2A). On the surface, representing the split along the long axis of the coprolite, the scales and bone fragments appear less-well organized, but in equal amount (Fig. 2B). In axial view, the preserved part of the circumference is curved, indicating the specimen had an original cylindrical shape with a diameter of about 2.5 cm (Fig. 2C).

Specimen 2

The second specimen (MGUH 29809) has a cylindrical circumference with the largest diameter measuring 2.8 cm and the overall length of the coprolite is 4.4 cm. One end is complete, and the diameter is decreasing toward the rounded end. The other end of the specimen is broken off, exposing a cross section through the coprolite (Fig. 3). In the broken cross section, two distinct circular voids are present inside the coprolite. The voids have a diameter of 3–4 mm and extend, slightly curving about 1 cm into the coprolite (Fig. 3C).

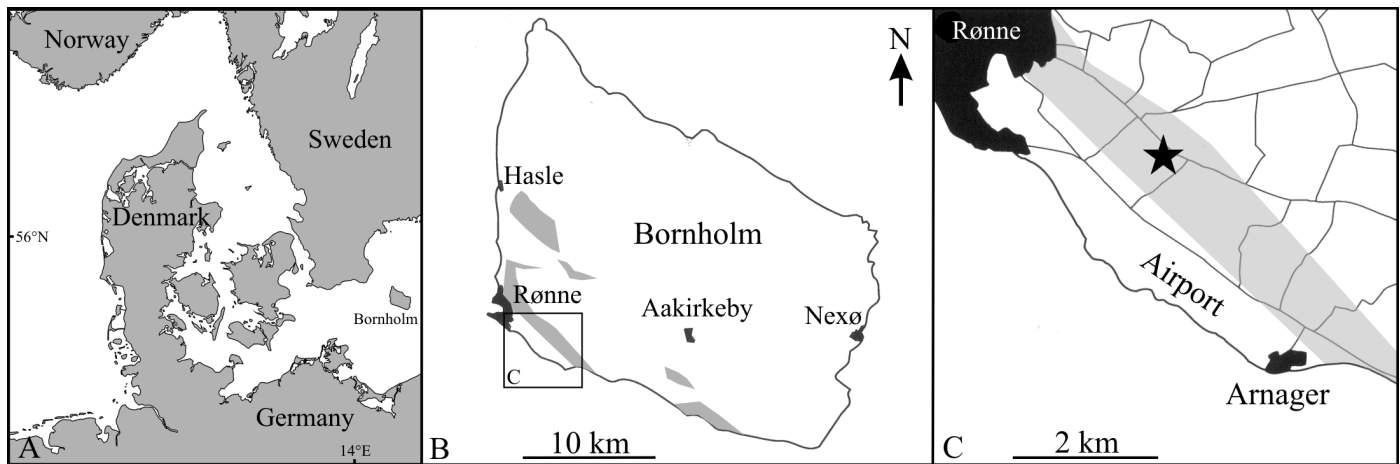


FIGURE 1. Location map. **A**, The Danish island Bornholm is situated in the Baltic Sea just south of Sweden (KMS G15-Ø). **B**, Map of Bornholm with the extent of the Lower Cretaceous Nyker Group sediments indicated in gray, based on Gravesen et al. (1982). **C**, The coprolite was found in a small exposure in the now abandoned Carl Nielsen's Sandpit (55°04'49.15N, 14°45'00E) at Robbedale, 5 km southeast of Rønne, indicated by asterisk. Modified from Rees et al. (2005).

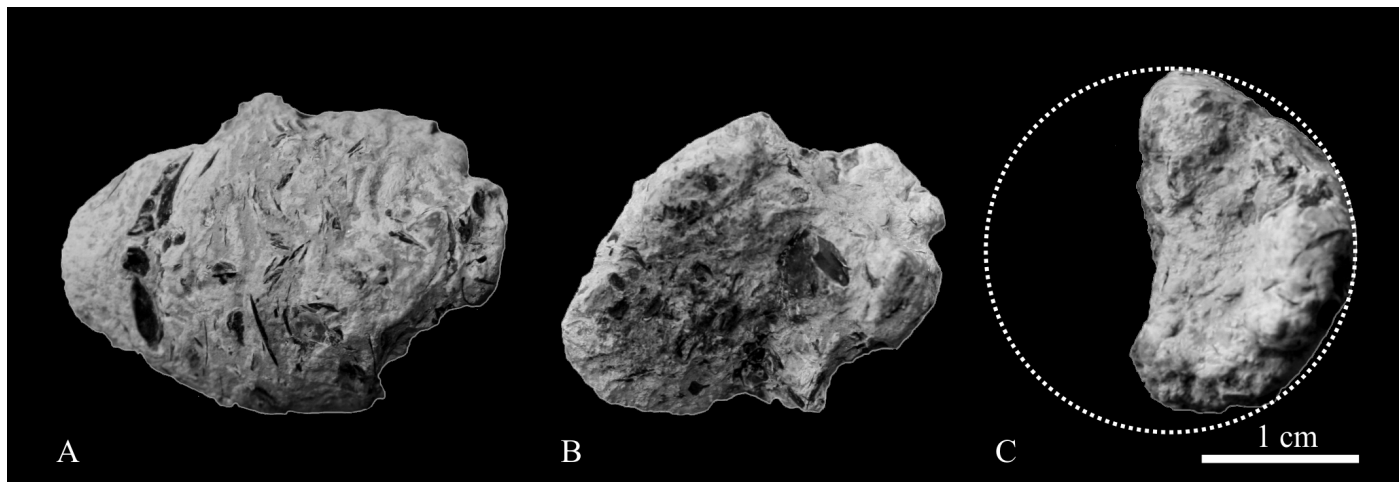


FIGURE 2. Fragment of coprolite (Unnumbered item, NaturBornholm). **A**, Several aligned bone fragments and fish scales are visible on the surface. **B**, View through the center of the coprolite showing a high density of scales and bone fragments. **C**, Axial view of the fragment, with the estimated unbroken circumference indicated by dotted line.

The surface is smooth, and a ganoid scale of the semionotid fish *Lepidotes* is visible in the surface of the coprolite (Fig. 3A). Several groups and rows of small pits are located around the surface, and on one side, three parallel grooves are present (Fig. 3B).

COMPUTED TOMOGRAPHY SCANNING

CT images of MGUH 29809 show a high density of small internal voids 0.5–2 mm in size, as well as several unidentified inclusions, possible prey remains (Fig. 3D). The two large voids can be traced to their full extent into the coprolite, and are revealed to be of almost constant diameter with a rounded end. One of the voids goes almost straight in, while the other is slightly curved towards the other, so that their ends converge towards the middle of the coprolite (Figs. 3C,D, 4).

DISCUSSION

The Lower Cretaceous continental vertebrate fauna from Robbedale, Bornholm is fairly diverse but represented by very fragmentary specimens (Bonde, 2004), so every new type of fossil helps to expand our knowledge of the fauna. The two coprolites with abundant prey items add further information to the picture in the form of evidence of large piscivorous carnivores, thus giving the first clues to the food

web. It further shows a complicated taphonomic history of these feces having been either dropped on land (a sandy beach), partly eaten by insects, and then deposited in the lagoonal water, or another scenario where the feces being dropped in the coastal water, drifting to the beach where insects infested it, and then finally buried in the lagoon (depending on the model for the “creator” chosen below).

Origin of the Feces?

The coprolites are elongated, cylindrical with smooth surface, with no evidence of internal coiling, and in shape similar to coprolites found in the Wealden of Southern England which have been attributed to crocodiles or small theropod dinosaurs (Goldring et al., 2005). Based on the knowledge of the local fauna, the possible makers of the coprolite are crocodylians, turtles, dromaeosaurids, sauropods, large fishes and hybodont sharks (Rees, 2001; Bonde, 2004, in press; Rees et al., 2005; Schwarz-Wings et al., 2009). The presence of fish bones and scales in the coprolite excludes an herbivorous animal, like a sauropod, as the maker of the coprolite.

Sharks and fishes generally produce coprolites that are coiled or spiral-shaped (Hunt et al., 1994; Sumner, 1994; Northwood, 2005), and sharks, with their more complex valves, produce characteristic heteropo-

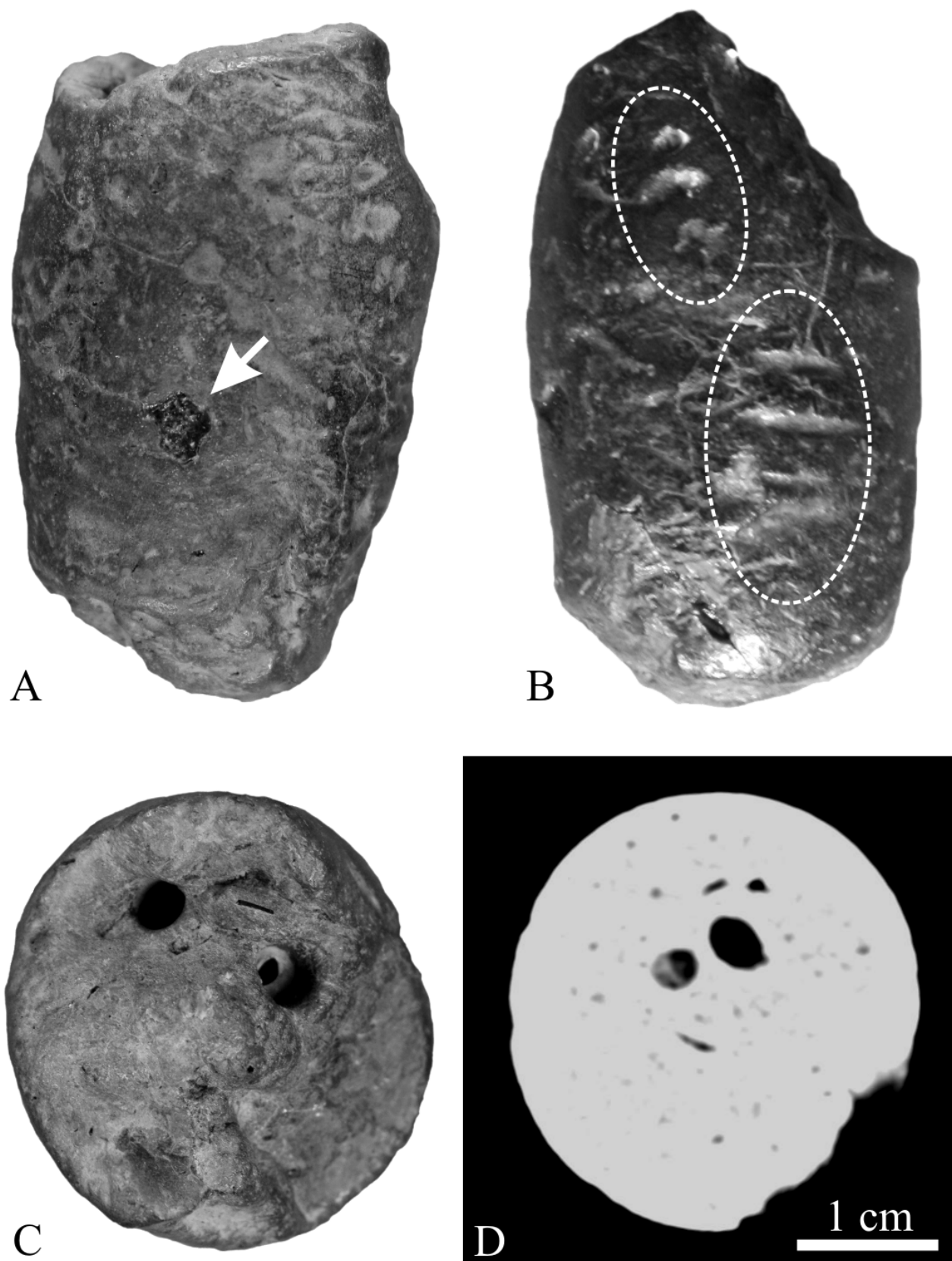


FIGURE 3. Fragment of large cylindrical coprolite (MGUH 29809). **A**, *Lepidotes* scale visible on the surface (arrow). **B**, Areas with high concentrations of pits and grooves are indicated by circled areas. **C**, Axial view of the broken end of the coprolite, showing the circular circumference and the two prominent burrows. **D**, Vertical CT image through the coprolite close to the termination of the two burrows. Notice the burrows have converged towards the middle of the coprolite. Several small gas vesicles are present towards the middle of the coprolite. All images reproduced to same scale.

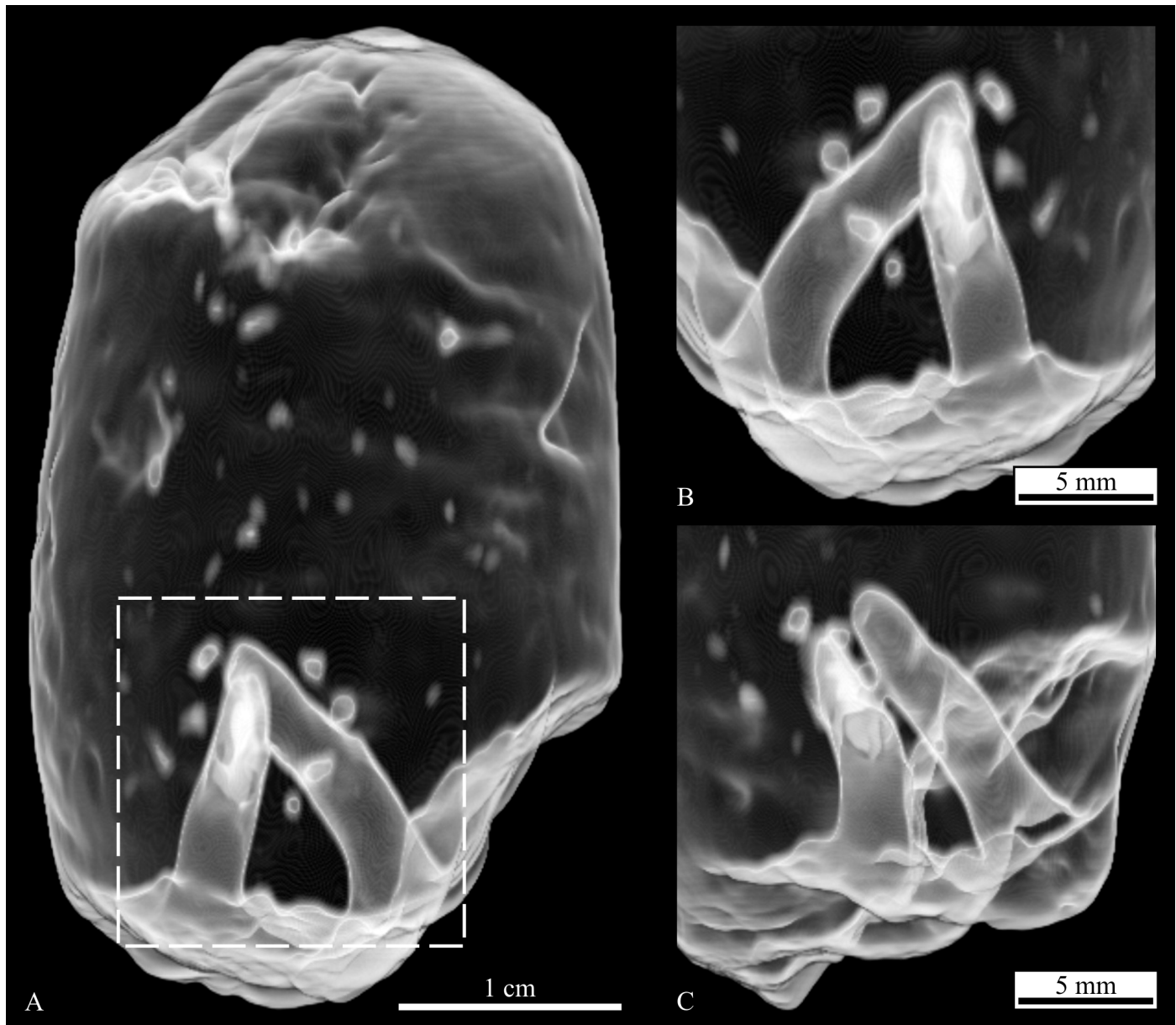


FIGURE 4. **A**, Three dimensional CT generated transparent image of MGUH 29809, showing the extent of the two burrows. The area with the burrows is indicated by dash-lined box. **B**, Cropped image showing the orientation of the two burrows. **C**, Same image from another angle. Notice how the burrows converge towards each other within the coprolite.

lar spiral coprolites (McAllister, 1985). There is no evidence of coiling or spiral shape in the examined specimen, and therefore we exclude a shark and fishes as the possible producer.

Based on their external morphology, the specimens look very similar to crocodylian coprolites. Crocodylian feces are typically elongate and cylindrical to slightly flattened in cross-section, composed of fused concavo-convex units (Young, 1964; Sawyer, 1981; Thulborn, 1991; Souto, 2010; Milàn, this volume). This is a general shape for crocodylian coprolites (Chin, 2002; Chame, 2003; Stuart and Stuart, 1998). The presence of visible fish scales and bone fragments, however, does not fit with a crocodylian origin. Extant crown group crocodylians have a very effective digestive system, with a hydrochloric acid concentration that exceeds mammalian carnivores by a factor of 50 (Coulson et al., 1989), that decalcifies and dissolves all bone tissue completely before excretion (Fischer, 1981; Coulson et al., 1989; Trutnau and Sommerlad, 2006; Milàn, this volume). However, the crocodylian genus *Pholidosaurus* found in the Jydegaard Formation (Bonde 2004) falls outside crown-

group crocodylians (Schwarz-Wings et al. 2009), and we do not know when the strong stomach acid evolved among the crocodylians. So it is possible that stem-group crocodylians did not possess the same effective stomach acids, and thus would not have dissolved the bones and scales to the same degree as extant crocodylians.

Another possibility is that the coprolites are from turtles. Coprolites associated with turtles are cylindrical tapering masses (Souto, 2008), and fresh scat from snapping turtles, *Chelydra serpentina*, are reported as ropy, tubular or pelletoidal in shape with diameters of 1-2 cm, with hair and bones from the prey animals, in this case rats, present inside (Farlow et al., 2010). Among the extant marine turtles like *Caretta caretta*, examination of the digestive tract has shown that fish bones are not digested and can be expelled in the feces (Plotkin et al., 1993), and fossil gut contents of Cretaceous sea turtles from Queensland, Australia, showed abundant bivalve shells that were only slightly corroded from gastric acid (Kear, 2006).

Theropods are present in the fauna in the form of dromaeosaurids

(Bonde and Christiansen, 2003; Christiansen and Bonde, 2003; Bonde 2004, in press). *Dromaeosaurides bornholmensis* had an estimated body length of about 3 meters (Bonde and Christiansen, 2003), and could thus be a likely candidate for the coprolites. No dromaeosaurids have any apparent specializations that could be attributed to a piscivorous diet, but it is likely that some dromaeosaurs with their sickle-shaped, and highly mobile claw on the second pedal digits, could have used this for catching fishes in the shallow waters at the beach. A somewhat “similar” case has been claimed for *Baryonyx* from the English Wealden (Charig and Milner, 1997). In this case *Baryonyx* is supposed to have caught the heavy scaled fishes using the large claw on its thumb as a “spear.” Functionally the potential of the pedal claws of some larger dromaeosaurs being used in such a way at “spear fishing” must be at least as good as is the case of *Baryonyx*’ thumbs. It does help the case of *Baryonyx*, however, that *Lepidotes* has been found also as stomach contents of the single specimen of *Baryonyx*. No stomach content has been found in dromaeosaurs so far.

Plesiosaurs (and ichthyosaurs, exclusively marine) have not been found in the Jydegaard Formation, while pterosaurs are very uncertain, but the two groups are known from the contemporary Wealden deposits of northern Germany (Bonde, 2004) and the UK, and one or two plesiosaurian teeth have been found in a glacially-redeposited “Wealden” block in a gravel quarry on the Danish Island Fyn (erratics transported from Kattegat or from the Baltic Sea region - Niels Bonde, personal observation). Unfortunately there is no confirmed record of either plesiosaur or ichthyosaur coprolites (Richard Forrest, personal communication, 2011). Buckland (1829) described possible ichthyosaur and plesiosaur coprolites from the Early Jurassic of Lyme Regis, southern England. However, most of these are clearly coiled and bear more resemblance to shark coprolites.

We cannot entirely exclude plesiosaurs (ichthyosaurs) or pterosaurs as the possible producers, but such an assignment would be purely speculative as their coprolites are so far unknown, or at least unrecognized in the fossil record. The presence of abundant prey remains in the coprolites makes it rather unlikely that they are from crocodylian makers. Size, shape and prey content of the coprolites are consistent with coprolites from turtles and theropod dinosaurs, so based on the available fauna and morphology of the investigated specimens we suggest that the coprolites originate from either a turtle or a theropod dinosaur with a piscivorous diet.

Traces of Coprophagy

The elongated voids in the large specimen (MGUH 29809) (Fig. 4) bear resemblance to burrows made by coprophagous organisms. Such coprophagy traces have been observed in coprolites dating to the Lower Triassic, in coprolites from Australia (Northwood, 2005). Minute networks of holes with a diameter around 0.5 mm are described in Late Triassic coprolites from Arizona, and are suggested to be the work of Diptera larvae, because dung beetles were too large to have produced such traces (Wahl et al., 1998). However, the Upper Cretaceous amber scarabs or the smallest members of the extant Aphodiinae are small enough to have produced traces with such a diameter (Kneil, 2006). Late Cretaceous coprolites from herbivorous dinosaurs from Montana show similar elongated burrows with diameters ranging from 1–31 mm, some of them interpreted as made by dung beetles (Chin and Gill, 1996). Marine bivalves have also been reported to produce burrows in coprolites, but these expand their diameter as they go into the coprolite (Tapanila et al., 2004), while the two burrows from Bornholm keep a constant diameter.

The small pits and grooves in the surface (Fig. 3B) are similar to what can be observed in feces from extant crocodiles that have been attacked by fly larvae (Fig. 5). In these cases the maggots have produced

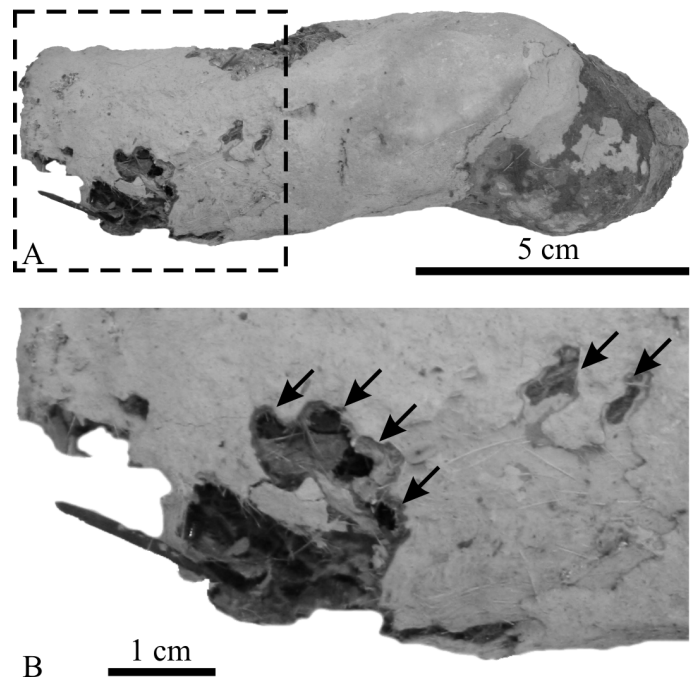


FIGURE 5. A, Scat from modern Dwarf Crocodile, *Osteolaemus tetraspis*, with burrows from fly larvae. B, The larvae have both produced shallow grooves and pits in the surface as well as tunnels into the scat (arrows). Notice the similarities with Figure 3B.

several rounded pits and elongated scrapes in the surface, as well as deep tunnels into the fecal mass. Similar pits and grooves are also known from specimens from the Upper Cretaceous of southern Sweden; these, however, were from a shallow water marine ecosystem (Eriksson et al., in press). Gas vesicles are a common feature of carnivore coprolites and have been reported in specimens since the Triassic (eg. Hollocher et al., 2005, 2010; Northwood, 2005; Harrell and Schwimmer, 2010; Souto, 2010).

CONCLUSION

The studied coprolites are the first record of coprolites from the Mesozoic of Bornholm, and add important knowledge to the sparse fossil record of continental Cretaceous vertebrates. The large specimen has been bored by coprophagous organisms, most likely dung beetles and fly larvae, which have left two deep burrows into the coprolite as well as small pits and grooves in the surface. Based on the available fauna, the external morphology and presence of abundant fish scales and bones within the coprolites, we cautiously suggest they were made by either a turtle or a piscivorous theropod dinosaur.

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REFERENCES

- Bonde, N., 2004, An Early Cretaceous (Ryazanian) fauna of "Purbeck-Wealden" type at Robbedale, Bornholm, Denmark; *in* Arratia, G. and Tintori, A., eds., *Mesozoic Fishes 3 – systematics, palaeoenvironments and biodiversity*: München, Germany, Verlag Dr. Friedrich Pfeil, p. 507-528.
- Bonde, N., in press, Danish dinosaurs: a review; *in* Godefroit, P., ed., *Bernissart Dinosaurs and Early Cretaceous Terrestrial Ecosystems*: Bloomington, Indiana, University Press. 464 p.
- Bonde, N. and Christiansen, P., 2003, New dinosaurs from Denmark: *Comptes Rendus Palevol*, v. 2, p. 13-26.
- Buckland, W., 1829, On the discovery of coprolites, or fossil faeces, in the Lias at Lyme Regis, and in other formations: *Transactions of the Geological Society of London, Second Series*, v. 2, p. 223-236.
- Chame, M., 2003, Terrestrial mammal feces: A morphometric summary and description: *Memoirs of the Instituto Oswaldo Cruz*, v. 98, p. 71-94.
- Charig, A.J. and Milner, A.C., 1997, *Baryonyx walkeri*, a fish eating dinosaur from the Wealden of Surrey: *Bulletin of the Natural History Museum, Geology Series*, v. 53, p. 11-70.
- Chin, K. and Gill, B.D., 1996, Dinosaurs, dung beetles, and conifers: Participants in a Cretaceous food web: *Palaaios*, v. 11, p. 280-285.
- Christiansen, P. and Bonde, N., 2003, The first dinosaur from Denmark: *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, v. 227, p. 287-299.
- Coulson, R.A., Herbert, J.D. and Coulson, T.D., 1989, Biochemistry and physiology of alligator metabolism *in vivo*: *American Zoologist*, v. 29, p. 921-934.
- Eriksson, M.E., Lindgren, J., Chin, K. and Månsby, U., in press, Coprolite morphotypes from the Upper Cretaceous of Sweden: Novel views on an ancient ecosystem and implications for coprolite taphonomy: *Lethaia*.
- Farlow, J.O., Chin, K., Argast, A. and Poppy, S., 2010, Coprolites from the Pipe Creek sinkhole (late Neogene, Grant County, Indiana, U.S.A.): *Journal of Vertebrate Paleontology*, v. 30, p. 959-969.
- Fisher, D.F., 1981, Crocodilian scatology, microvertebrate concentrations, and enamel-less teeth: *Paleobiology*, v. 7, p. 262-275.
- Gravesen, P., Rolfe, F. and Surlyk, F., 1982, Lithostratigraphy and sedimentary evolution of the Triassic, Jurassic and Lower Cretaceous of Bornholm, Denmark: *Geological Survey of Denmark Series B*, v. 7, p. 1-51.
- Goldring, R., Pollard, J.E. and Radley, J.D., 2005, Trace fossils and pseudofossils from the Wealden strata (non-marine Lower Cretaceous) of Southern England: *Cretaceous Research*, v. 26, p. 665-685.
- Harrell, S.D. and Schwimmer, D.R., 2010, Coprolites of *Deinosuchus* and other crocodylians from the Upper Cretaceous of western Georgia, USA: *New Mexico Museum of Natural History and Science, Bulletin* 51, p. 209-213.
- Hollocher, K.T., Alcober, O.A., Colombri, C.E. and Hollocher, T.C., 2005, Carnivore coprolites from the Upper Triassic Ischigualasto Formation, Argentina: Chemistry, mineralogy, and evidence for rapid initial mineralization: *Palaaios*, v. 20, p. 51-63.
- Hollocher, K.T., Hollocher, T.C. and Rigby, J.K., Jr., 2010, A phosphatic coprolite lacking diagenetic permineralisation from the Upper Cretaceous Hell Creek Formation, northeastern Montana: Importance of dietary calcium phosphate in preservation: *Palaaios*, v. 25, p. 132-140.
- Hunt, A.P., Chin, K. and Lockley, M.G., 1994, The paleobiology of vertebrate coprolites; *in* Donovan, S., ed., *The paleobiology of trace fossils*: John Wiley and Sons, London, p. 221-240.
- Kear, B.P., 2006, First gut contents in a Cretaceous sea turtle: *Biology Letters*, v. 2, p. 113-115.
- Knell, F.-T., 2006, Fossil record of Scarabaeoidea (Coleoptera: Polyphaga): *Coleopterists Society Monographs*, v. 5, p. 120-143.
- Lindgren, J., Currie, P.J., Rees, J., Siverson, M., Lindström, S. and Alwmark, C., 2008, Theropod dinosaur teeth from the lowermost Cretaceous Rabekke Formation on Bornholm, Denmark: *Geobios*, v. 41, p. 253-262.
- Lindgren, J., Rees, J., Siverson, M. and Cuny, G., 2004, The first Mesozoic mammal from Scandinavia: *GFF*, v. 126, p. 325-330.
- McAllister, J.A., 1985, Reevaluation of the formation of spiral coprolites: *University of Kansas, Paleontological Contributions*, v. 144, p. 1-12.
- Milàn, J., this volume, Crocodylian scatology – A look into morphology, internal architecture, inter- and intraspecific variation and prey remains in extant crocodylian feces: *New Mexico Museum of Natural History and Science, this volume*.
- Milàn, J., Rasmussen, B.W. and Lynnerup, N., this volume, A coprolite in the MDCT-scanner – internal architecture and bone contents revealed: *New Mexico Museum of Natural History and Science, this volume*.
- Noe-Nygaard, N., Surlyk, F. and Piasecki, S., 1987, Bivalve mass mortality caused by toxic dinoflagellate blooms in a Berriasian-Valanginian lagoon, Bornholm, Denmark: *Palaaios*, v. 2, p. 263-273.
- Noe-Nygaard, N. and Surlyk, F., 1988, Washover fan and brackish bay sedimentation in the Berriasian-Valanginian of Bornholm, Denmark: *Sedimentology*, v. 35, p. 197-217.
- Northwood, C., 2005, Early Triassic coprolites from Australia and their palaeobiological significance: *Palaeontology*, v. 48, p. 49-68.
- Rees, J., 2001, Jurassic and Early Cretaceous selachians – focus on southern Scandinavia: *Lund Publications in Geology*, v. 153, p. 1-19.
- Rees, J., Lindgren, J. and Evans, S.E., 2005, Amphibians and small reptiles from the Berriasian Rabekke Formation on Bornholm, Denmark: *GFF*, v. 127, p. 233-238.
- Sawyer, G.T., 1981, A study of crocodilian coprolites from Wannagan Creek Quarry Minnesota: *Scientific Publications of The Science Museum of Minnesota*, v. 5, p. 1-29.
- Schwarz-Wings, D., Rees, J. and Lindgren, J., 2009, Lower Cretaceous Mesoeucrocodylians from Scandinavia (Denmark and Sweden): *Cretaceous Research*, v. 30, p. 1345-1355.
- Souto, P.R.F., 2008, Coprólitos do Brasil – Principais ocorrências e studio: *Publit*, Rio de Janeiro, 93 p.
- Souto, P.R.F., 2010, Crocodylomorph coprolites from the Bauro Basin, Upper Cretaceous, Brazil: *New Mexico Museum of Natural History and Science, Bulletin* 51, p. 201-208.
- Stuart, C. and Stuart, T., 1998, A field guide to the tracks and signs of southern and east African Wildlife: *Southern Books Publishers*, Cape Town, 310 p.
- Sumner, D., 1994, Coprolites from the Viséan of East Kirkton, West Lothian, Scotland: *Transactions of the Royal Society of Edinburgh, Earth Sciences*, v. 84, p. 413-416.
- Surlyk, F., Milàn, J. and Noe-Nygaard, N., 2008, Dinosaur tracks and possible lungfish aestivation burrows in a shallow coastal lake; lowermost Cretaceous, Bornholm, Denmark: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 267, p. 292-304.
- Tapanila, L., Roberts, E.M., Bouaré, M.L., Sissoko, F. and O'Leary, M.A., 2004, Bivalve borings in phosphatic coprolites and bone, Cretaceous-Paleogene, northeastern Mali: *Palaaios*, v. 19, p. 565-573.
- Thulborn, R.A., 1991, Morphology, preservation and palaeobiological significance of dinosaur coprolites: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 83, p. 341-366.
- Trutnau, L. and Sommerlad, R., 2006, Crocodilians. Their natural history and captive husbandry: *Edition Chimaira*, Frankfurt am Main, 646 p.
- Wahl, A.M., Martin, A.J.M. and Hasiotis, S.T., 1998, Vertebrate coprolites and coprophagy traces, Chinle Formation (Late Triassic), Petrified Forest National Park, Arizona; *in* Santucci, V.L. and McClelland, L., eds., *National Park Service Paleontological Research, Technical Report NPS/NRGRD/GRDTR-98/01*. National Park Service, Geological Resources Division, Lakewood, CO, p. 144-148.
- Young, C.C., 1964, New fossil crocodiles from China: *Vertebrate Palasiatica*, v. 8, p. 190-208.