A crocodilian coprolite from the lower Oligocene Viborg Formation of Sofienlund Lergrav, Denmark

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A large, well-preserved vertebrate coprolite found in the clay pit Sofienlund Lergrav, Jylland, is identi-fied as crocodilian due to its size and morphology. The coprolite consists of several concentric layers wrapped around a more homogeneous core. Weak constriction marks are present on the surface. Dinoflagellate cyst contents of the coprolite indicate a mid-Lutetian to earliest Rupelian (middle Eocene to earliest Oligocene) age, which at Sofienlund Lergrav places it within the lower Oligocene Viborg Formation. The coprolite can thus be dated as approximately 33–34 Ma old. The Viborg Formation in Denmark represents a period with deposition of hemipelagic marine clay and formation of glaucony. The nearest shoreline was located *c.* 200 km north of the location of the present day Sofienlund Lergrav, and the climate was humid, warm-temperate to sub-tropical. The presence of a crocodilian coprolite is an important addition to the sparse Oligocene vertebrate fauna of Denmark, which previously only consisted of sharks and cetaceans.

Keywords: Coprolite, Palaeogene, Oligocene, vertebrate fauna, Denmark, Crocodilian.

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Coprolites are important palaeoecological indicators and are with increasing frequency included in palaeoecological analyses, as they can provide important additional information about extinct animals and their diet, in form of preserved inclusions of undigested prey remains (e.g. Thulborn 1991; Hunt *et al.* 1994; Northwood 2005; Prasad *et al*. 2005; Chin 2007; Souto 2008; Eriksson *et al*. 2011; Milàn *et al*. 2012a,b; Hansen *et al*. 2016). Coprolites are regarded as ichnofossils and were first recognised as fossil feces by William Buckland (1835) who coined the term coprolite. Today vertebrate coprolites are known from the Silurian to the present (Hunt *et al*. 2012). The Danish fossil record of coprolites is sparse, with only a few specimens known from the Lower Cretaceous of Bornholm (Milàn *et al*. 2012b), the Upper Cretaceous of Stevns Klint (Milàn *et al*. 2015), the Lower Paleocene (lower Danian) of Hammelev Kalkbrud (Milàn & Hunt 2016), the middle Danian of Faxe Kalkbrud (Milàn 2010) and Bed L2 of the Eocene Lillebælt Clay Formation (Heilmann-Clausen *et al*. 1985). A new specimen originating from the lower Oligocene Viborg Formation of Sofienlund Lergrav (Fig. 1) is thus the hitherto youngest coprolite from Denmark. The aim of this study is to describe the new-found specimen, identify its producer, and discuss its palaeoecological context.

Geological Setting

During the Palaeogene and Neogene, the North Sea Basin formed an epicontinental basin (Ziegler 1990). The carbonate deposition that dominated during the Late Cretaceous continued into the earliest part of the Palaeogene (early Paleocene). It was succeeded by deposition of deep marine clays during most of the Paleocene and Eocene (Nielsen *et al*. 2015 and references therein). Volcanic activity in the North Atlantic became extensive at the Paleocene–Eocene transition and resulted in sedimentation of ash-rich layers throughout the North Sea Basin and diatomites locally in parts of the eastern North Sea area (Pedersen & Surlyk 1983). During the Oligocene, the first

Fig. 1. Pre-Quaternary map of Denmark indicating the location of the clay-pit Sofienlund Lergrav in the Oligocene–Miocene deposits at the small town of Ulstrup (56° 23.4002´N, 09° 48.3961´E). Modified from Håkansson & Pedersen (1992).

prograding fluvio-deltaic systems were established south of the Fennoscandian Shield (Schiøler *et al*. 2007; Jarsve *et al*. 2014). These systems were restricted to a narrow rim around present-day Norway (Śliwińska *et al*. 2014). A branch of delta lobes that prograded deeper into the North Sea Basin are found south-west of present-day Norway (Jarsve *et al*. 2014). The eastern part of the North Sea Basin, however, remained fully marine, with a water depth at a minimum of 300 m and dominated by deposition of glaucony-rich mud. Late Oligocene – early Miocene inversion in the Central Graben and probably in the Norwegian-Danish Basin resulted in relatively shallow water in the eastern North Sea Basin (Rasmussen 2009). A coincident uplift of Norway during the Miocene (Japsen *et al*. 2010; Rasmussen & Utescher 2016) initiated major progradation of delta systems into the eastern North Sea Basin, and parts of the area covered by present-day Denmark became dry land.

The landscape was characterised by a coastal lowland with a few major wave-dominated delta systems (Rasmussen *et al*. 2010; Śliwińska *et al*. 2014). The fluvial systems that conveyed sediments to the sea were mainly the meandering type, but braided systems developed in the earliest early Miocene, associated with the inversion tectonism. Spit systems and barrier–lagoonal complexes formed in between the major delta lobes. The coastline was dominated by mangrove swamp, and on elevated areas in the hinterland sequoia and oaks vegetated the landscape.

During most of the Palaeogene and Neogene, the climate was warm temperate to subtropical. The annual precipitation was most of the time in the order of 1000–1500 mm (Utescher *et al*. 2009; Larsson *et al*. 2011). Temporal climatic deterioration occurred during the early and middle Oligocene and at the end of the Miocene.

Christensen & Ulleberg (1973) subdivided the succession in the clay-pit Sofienlund Lergrav into the Viborg Formation, the Ulstrup Clay, the Sofienlund Clay and the Sofienlund Sand. However, the regional study of Rasmussen *et al*. (2010) abandoned the upper three units and included the Ulstrup Clay in the Brejning Formation, which is late Oligocene in age, and included the Sofienlund Clay and Sand in the lower Miocene Vejle Fjord Formation. The Viborg Formation was deposited in a relatively deep marine environment (> 300 m of water) at a minimum of 150 km from the shoreline. A major hiatus separates the Viborg Formation from the Brejning Formation (Fig. 2). The hiatus was probably formed by deep marine currents (e.g. Hansen *et al*. 2004). Even though the Brejning Forma-

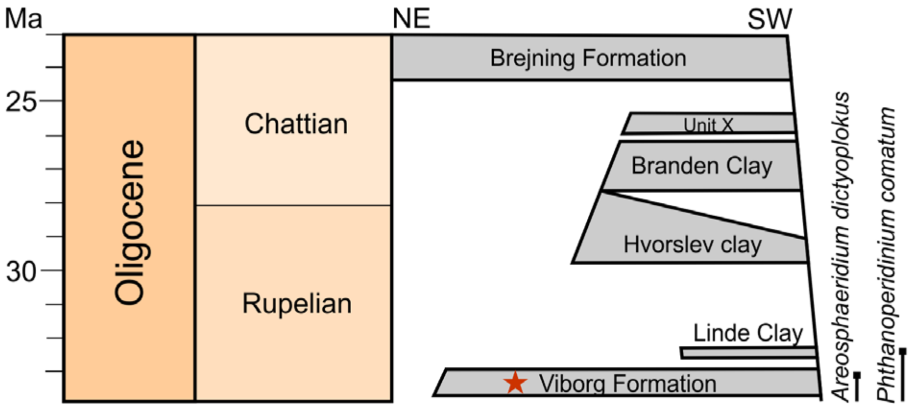

Fig. 2. Chronostratigraphy of the Oligocene sediments in a NE–SW transect through Jylland, Denmark. At Sofienlund Lergrav only the Brejning Formation and the Viborg Formation are present, separated by a major hiatus. The range of the dinoflagellate cysts retrieved from the coprolite places it within the Viborg Formation, indicated by an asterisk. Modified from Śliwińska *et al*. (2012, fig. 13).

tion was deposited in slightly shallower water, the shoreline was displaced farther north due to relatively high sea level during the late Oligocene. The shallowing of the water depth was a result of inversion of the Norwegian-Danish Basin. During the early Miocene the shoreline migrated from present-day Norway into the Danish area, and the Vejle Fjord Formation represents sediments deposited in a prodelta environment in front of the fluvio-deltaic Billund Formation.

Material and methods

A well-preserved coprolite was found in the collection of the Natural History Museum of Denmark (NHMD-227230), with the only information being that it was found in Sofienlund Lergrav but without any reference to a specific formation, or date of collecting. To determine the stratigraphic age, a small sample was extracted from the outer coil of the coprolite and analysed for dinoflagellate cysts. The sample was processed using HCl to dissolve calcareous matter and HF to dissolve silicates. The acid treatment was followed by neutralisation with water. The residue was filtered on a 6μm nylon mesh and mounted on a glass slide using glycerine gel. The organic particles, including the dinoflagellate cysts, were studied using a normal light microscope.

Description of specimen

The specimen is 66 mm long and 31 mm in widest diameter, tapering towards the ends (Fig. 3A). One end appears complete while other end is broken. Just prior to the break, the specimen has a circumferential constriction mark, which coincides with a bend at an angle of approximately 150° (Fig. 3B).

The colour of the specimen is light brown, and the outer surface is smooth but covered with small pits, grooves and irregularities. Parts of the outer surface layer are missing, exposing a perfectly smooth layer underneath (Fig. 3A). The internal architecture of the specimen is visible at both ends which show a massive, apparently structureless core of the specimen, measuring 11 mm in diameter at the rounded termination and 19 mm at the broken, incomplete end. Around the structureless core, several thin, concentric layers are deposited successively. Each layer is between 0.5 and 2 mm in thickness, and the thickness is unevenly distributed around the specimen (Fig. 3C). The texture of the individual layers is homogenous with no apparent inclusions of any kind.

Microfossil dating

A small sample extracted from a loose part of the outer coil of the coprolite was analysed for its dinoflagellate cyst content in order to provide a dating. The sample comprised a very sparse dinoflagellate cyst assemblage including the following taxa: *Areosphaeridium dictyoplokus*, *Phthanoperidinium comatum* and *Areosphaeridium michoudii*. The co-occurrence of these taxa indicates a mid-Lutetian to earliest Rupelian (middle Eocene to earliest Oligocene) age. As the coprolite was found at Sofienlund Lergrav where the Viborg Formation of earliest Oligocene age is the oldest deposits outcropping, it must be assumed that the coprolite came from that unit. The occurrence of *A. michoudii*, which has a last occurrence in the Eocene, indicates that the single occurrence of this taxa is due to reworking. Reworking of Eocene deposits into the Viborg Formation is a well-known phenomenon (Śliwińska *et al*. 2012).

Discussion

Origin of the feces

Identifying the exact producer of a coprolite is a challenging task with many possible uncertainties, as feces from many unrelated animal groups can appear to be very similar, due to diet and mode of egestion. To further complicate the picture, feces from the same animal can show a wide morphological variation as well (e.g. McAllister 1985; Chin 2002; Chame 2003; Milàn 2012).

The known Oligocene vertebrate fauna of Denmark is limited to small cetaceans (Ravn 1926; Hoch 2000; Bonde *et al*. 2008) and sharks, where one find of a tooth from *Carcharocles angustidens* suggests a length of the shark of up to 10 m (Bonde *et al*. 2008). Marine mammals including cetaceans usually have very liquid feces with a water content of up to 90 percent, which would be classified as diarrhea (Lewin 1999) and thus unable to be preserved as coprolites. This makes a cetacean origin of the coprolite unlikely. Coprolites from sharks and other actinopterygians are very common in the fossil record and are distinct in being spiral-coiled, reflecting the spirally valvular intestines of actinopterygians, and giving the coprolites the superficial appearance of a coiled pinecone (Williams 1972; McAllister 1985; Hunt & Lucas 2012). While the size of the Sofienlund coprolite is in agreement with a large shark, the morphology excludes a shark as a producer. The best morphological match for the Sofienlund coprolite is a crocodilian. Crocodilian coprolites are generally sausage shaped and circular in cross section, with few structures visible on their outer surface except for occasional striations or traces from coprophageous organisms (Souto 2010; Milàn 2012). A study of the morphological variation within fresh feces from 10 species of extant crocodilians demonstrated that a commonly occurring feature of crocodilian feces is circumferal constriction marks and a bend between 120° and 150°; their internal structure is composed of concentric layers of various thickness around a central core of a more homogenous mass (Milàn 2012; Milàn & Hedegaard 2010) (Fig. 3D, E). Crocodilian feces are devoid of any bone or shell remains as the digestive system of crocodilians effectively dissolves any bone or shell remains of their prey (Fischer 1981), leaving only hair and feathers behind (Milàn 2012). The total body length of a crocodile can be estimated from the diameter of the feces (Milàn 2012). In this case a diameter of 31 mm corresponds to a crocodile with a body length of around 260 cm (Milàn 2012).

Palaeoenvironment

The Viborg Formation containing the coprolite was deposited during the early Oligocene. The Norwegian-Danish Basin was generally sediment starved, as indi-

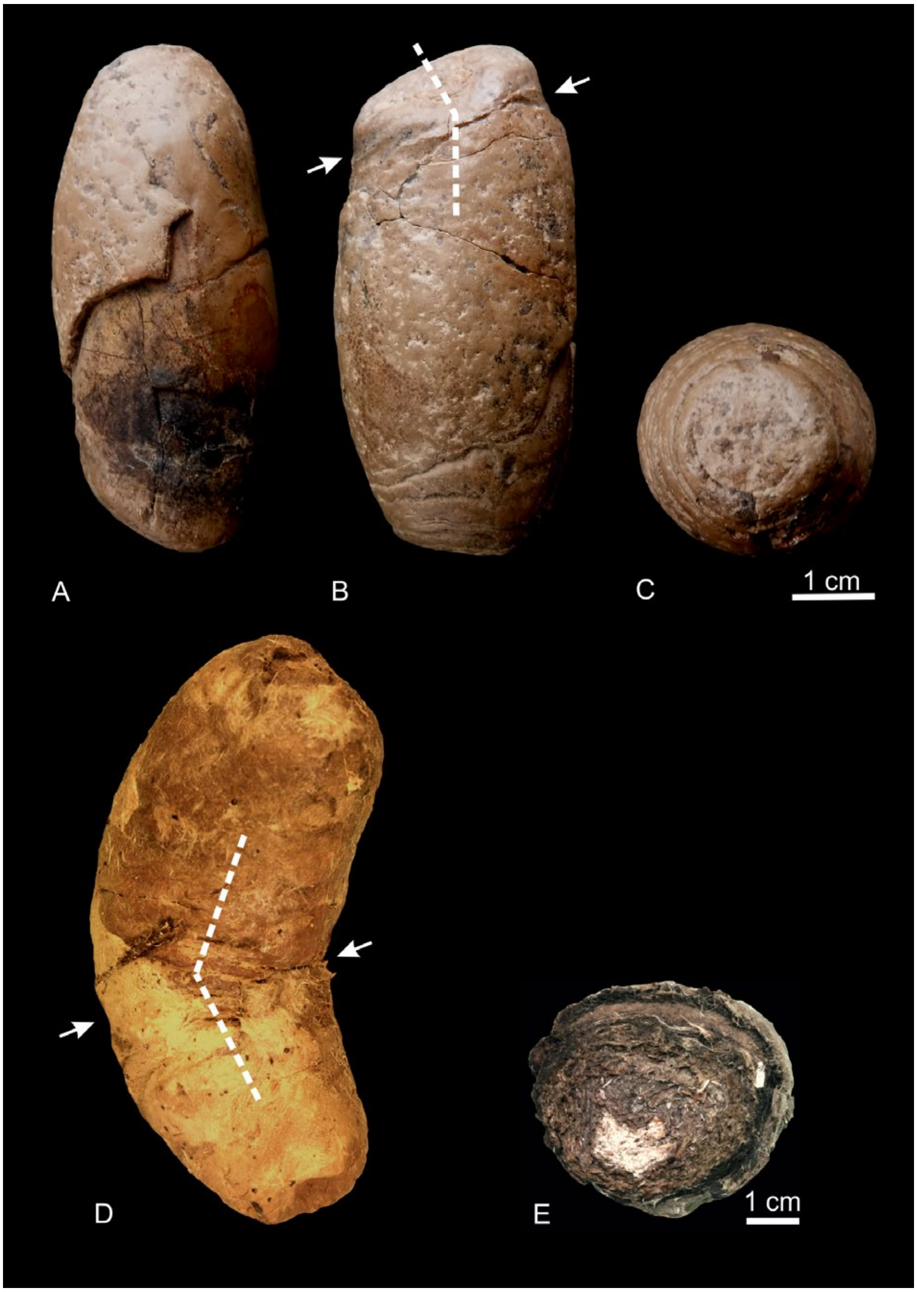

Fig. 3. The Sofienlund coprolite NHMD 227230 shown in three views, with comparisons. **A**: Lateral view where parts of the outer layer is broken off, revealing the inner, smooth surface. **B**: Lateral view showing the circumferal zone of constriction, indicated by arrows, and the 150° bending of the specimen at the zone. **C**: Axial view, showing the architecture of a dense featureless core wrapped in several millimetre-thick concentric layers. **D**: Fresh feces from a dwarf crocodile, *Osteolemus tetraspis*, showing a smooth surface and weak zone of circumferal constriction initiating a bend of 135°. **E**: Cross section of fresh feces from a dwarf crocodile, showing the typical layered internal architecture of crocodilian feces.

cated by the presence of glaucony, but progradation of a delta shoreline occurred south of the Fennoscandian Shield during the early Oligocene (Schiøler *et al*. 2007; Jasve et *al*. 2014). The shoreline was probably located 200 km to the north of the present-day Sofienlund Lergrav and the estimated depth of the water in front of the delta was more than 300 m based on the height of the clinoformal package around the Inez-1 well (Schiøler *et al*. 2007). Recent crocodiles are able to swim for considerable distances. A GPS-tagged saltwater crocodile (*Crocodylus porosus*) is reported to have swum 590 km in 25 days without going ashore (Campbell *et al*. 2010), and a juvenile saltwater crocodile has been observed to survive 4 months without feeding in fully marine conditions (Taplin & Grigg 1989). Lower Paleocene (Danian) records of crocodilian body fossils from Denmark and southern Sweden are also from sedimentary environments which represent deposition in excess of 100 km from the nearest shoreline (Troedsson 1924; Schwarz-Wings *et al*. 2014; Adolfssen *et al*. 2017), and presumed crocodilian coprolites are found in the middle Danian Faxe Formation of Faxe Kalkbrud (Milàn 2010). Therefore, it is not unlikely to find a crocodile coprolite at Sofienlund Lergrav despite its relatively long distance from the palaeo-shoreline. An alternative explanation is that the coprolite was produced onshore and subsequently transported by currents to its final resting place, or it could have been rafted by a floating root net and dropped to the sea bottom. A gneiss clast 25 cm in diameter and several pebbles have been found in the basal layer of the Sydklint Member, Brejning Formation at Siltstrup in northern Jylland (Heilmann-Clausen 1997). Land material transported by root nets and deposited as dropstones are thus well known in marine sedimentary environments (Bennett *et al*. 1996).

The sedimentological context of the specimen in the Viborg Formation, together with the morphology showing a featureless surface, a homogenous inner core wrapped in thin concentric layers, no prey remains, and a zone of constriction which initiates a 150° bend, strongly suggest a crocodilian origin of the coprolite, even though no skeletal remains exist to support it. The presence of crocodilians indicates that the climate during the deposition of the Viborg Formation was at minimum warm-temperate to subtropical.

Conclusions

A well-preserved coprolite from Sofienlund Lergrav in Jylland, Denmark, is identified as crocodilian in origin, based on its size and morphology. Dinoflagellate cysts extracted from the coprolite date it to the early Oligocene, which in Sofienlund Lergrav corresponds to the Viborg Formation, giving the coprolite an age of 33–34 Ma.

This is the first record of crocodilians in the Oligocene vertebrate fauna of Denmark, which previously only consisted of sharks and cetaceans.

The find indicates that the climate during deposition of the Viborg Formation was warm-temperate to subtropical.

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