

A diverse ichnofauna of small coprolites from the Eocene Lillebælt and Røsnæs Clay Formations, Hinge claypit, Denmark

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The majority of Palaeogene coprolite localities are in nonmarine strata. We describe a new, large and diverse ichnofauna of small-sized vertebrate and invertebrate coprolites ranging from 0.5 – 14 mm in length, from the marine Eocene of Denmark that includes several new ichnotaxa. The ichnofauna derives from the early – middle Eocene Røsnæs Clay Formation (R6) and Lillebælt Clay Formation (L2) in the active claypit at Hinge, middle Jylland, Denmark. The vertebrate coprolites represent six morphotypes and 6 new ichnotaxa – *Kylindrocopros hingeensis* igen. et isp. nov., *Kathemacopros duffini* igen. et isp. nov., *Osteocopros frandseni* igen. et isp. nov., *Commacopros dentziendiasae* igen. et isp. nov., *Kranocopros lucasi* igen. et isp. nov. and *Hingecopros lillebæltensis* igen. et isp. nov. We recognize a new ichnospecies of *Kylindrocopros*, *K. rakshitae* igen. et isp. nov. from the Eocene of the United States. *Funiculocopros sinuosus* igen. et isp. nov. is a member of the invertebrate coprolite ichnofamily Lumbricariidae and is the only post-Mesozoic example. This assemblage includes a rare co-occurrence of vertebrate and invertebrate coprolites.

Keywords: Coprolites, vertebrate, invertebrate, Eocene, Denmark

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<https://zoobank.org/urn:lsid:zoobank.org:1F5DA356-EAB2-4F63-995B-3F100C2C835F>

The majority of Palaeogene coprolite localities are in nonmarine strata, although the largest individual sample sizes are from marine deposits (Hunt & Lucas 2016). Palaeogene phosphorites yield marine coprolites over a wide area of the South Tethyan Phosphogenic Province (STPP) from northwest Africa to the Middle East, including Iraq, Jordan, Egypt, Algeria, Senegal, Mali, Morocco, Algeria, Togo and Nigeria (Hunt & Lucas 2016). The marine Eocene is characterized by very high numbers of specimens (> 1000 specimens) of coprolites, notably the early Eocene Potapaco Member of the Nanjemoy Formation, Virginia (Dentzien-Dias *et al.* 2021) and the upper Eocene Yazoo Clay, Louisiana (Stringer & King 2012), both in the United States, and from the middle Eocene Fürstenau Formation of Germany (Diedrich

& Felker 2012). The latter two coprofaunas consist principally of heteropolar spiral coprolites. Other marine coprolites from the Palaeogene occur in the Paleocene of Denmark (Milàn 2010, 2018; Milàn *et al.* 2012; Milàn & Hunt 2016), the Oligocene of Germany (Weiler 1922; Zotz 1928; Martini 1965), Oligocene of Denmark (Milàn *et al.* 2018), Oligocene of Poland (Bajdek & Bienkowska-Wasiluk 2020) and the Paleocene and Eocene of France (Meillet 1842) and Belgium (Buckland 1835).

Here we describe a large and diverse ichnofauna of small vertebrate and invertebrate coprolites from the Eocene of Denmark that includes several new ichnotaxa. Abbreviations are: LGP-G, Laboratório de Geologia e Paleontologia of the Universidade Federal do Rio Grande Brazil; NMMNH, New Mexico Museum

Geological setting

A succession through the Eocene Røsnæs and Lillebælt Clay formations is exposed in the active claypit at Hinge, middle Jylland (Fig. 1). The Røsnæs Clay and Lillebælt Clay formations are part of a slightly shallowing upwards overall setting going from deposition in undifferentiated bathyal zone of the underlying Røsnæs Clay Formation, to an upper bathyal to neretic setting for the overlying Søvind Marl Formation (King 2016). The interpreted water depth for the deposition of the Lillebælt Clay Formation, varies however, from deposition in an undifferentiated bathyal zone (King 2016) to only upper

bathyal zone (Thomsen *et al.* 2012) and deposition at 100–300/350 metres depth in Schnetler & Heilmann-Clausen (2011) and Carlsen & Cuny (2014).

Multiple lines of evidence indicate that deposition of the Lillebælt Clay occurred in offshore, deepshelf to upperbathyal settings (King 2016; Thomsen *et al.* 2012). Molluscan assemblages from Trelde Næs constrain suggested water depths to ~100–300 m (Schnetler & Heilmann-Clausen 2011), an overall assessment of water depth of ca. 500 m (Heilmann-Clausen 2012), whereas otoliths (Schwarzahns & Nielsen 2024; Schwarzahns 2007) and elasmobranch faunas include numerous deepwater taxa (Hansen *et al.* 2013; Carlsen & Cuny 2014), together supporting a lower sublittoral to upper bathyal environment and locally deeper conditions. Recent work from Lillebælt Clay documents a diverse deepsea shark assemblage (e.g., *Apristurus*, *Deania*, *Etmopterus*, *Squaliolus* (Pollerspöck *et al.* 2023), reinforcing the deepwater

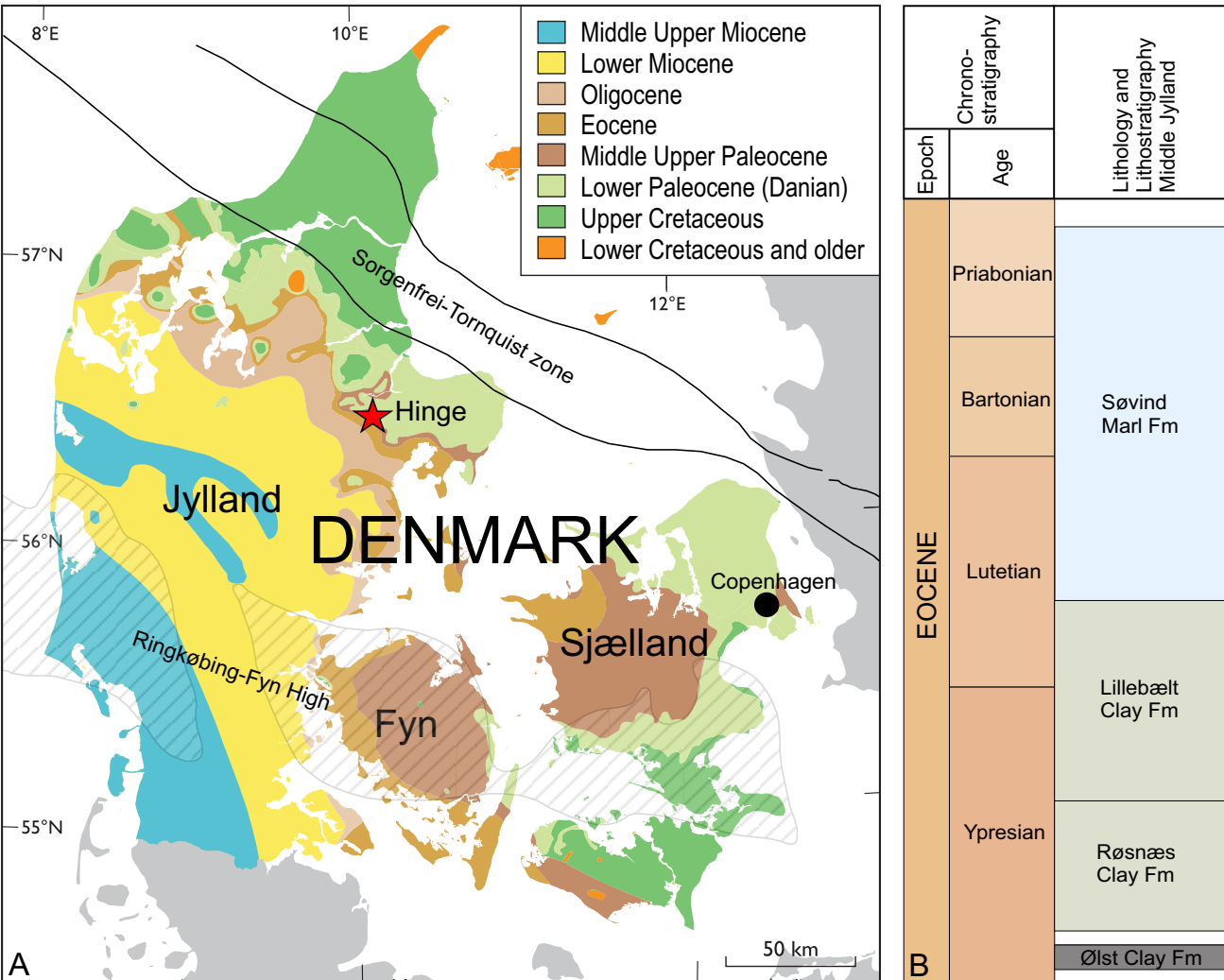


Fig. 1. A: Pre-Quaternary map of Denmark indicating the location of the Hinge claypit in the Eocene deposits of middle Jylland (56.382°N, 10.055°E). Modified after Håkansson & Pedersen (1992). **B:** Schematic representation of the Eocene stratigraphy of Middle Jylland. Modified from Sandersen *et al.* (2014).

character of the Lillebælt Clay at several localities. The Røsnæs Clay Formation is mid-Ypresian in age and the overlying Lillebælt Clay Formation is late Ypresian – early Lutetian (early–middle Eocene) in age (Fig. 1).

The Lillebælt Clay Formation is subdivided into six members, L1 – L6. With L1 being characterized as reddish-brown clay, L2 being grey – green clays. L3 being red – brown clays, L4 green clay with bands of carbonaceous concretions and scattered baryte concretions, L5 is dark grey-green clay with phosphatic concretions, and L6 is brownish grey with carbonate concretions in the lower part (see Heilmann-Clausen *et al.* 1985 for a detailed lithological description). L2 is the most fossiliferous member of the Lillebælt Clay Formation. In Hinge claypit, layers R5 to L2 is the

easiest accessible (Fig. 2A). The lower part of L2 is laterally persistent and contains two closely spaced volcanic ash layers (Fig. 2 D,E, on the picture the two volcanic ash layers are merged into one layer) directly beneath the thickest black sapropel (2–5 cm), which serves as a regionally traceable marker bed. The repeated thin sapropels elsewhere in L2, are widely interpreted to record shortlived episodes of enhanced organic matter flux and reduced bottom-water ventilation superimposed on an otherwise well oxygenated background, consistent with basin-wide dysoxia/anoxia events during the latest Ypresian – earliest Lutetian (Carlsen & Cuny 2014).

The stratigraphic interval that yields the coprolites lies within the *Azolla* event, a distinctive regional biohorizon that enables correlation across the Nor-

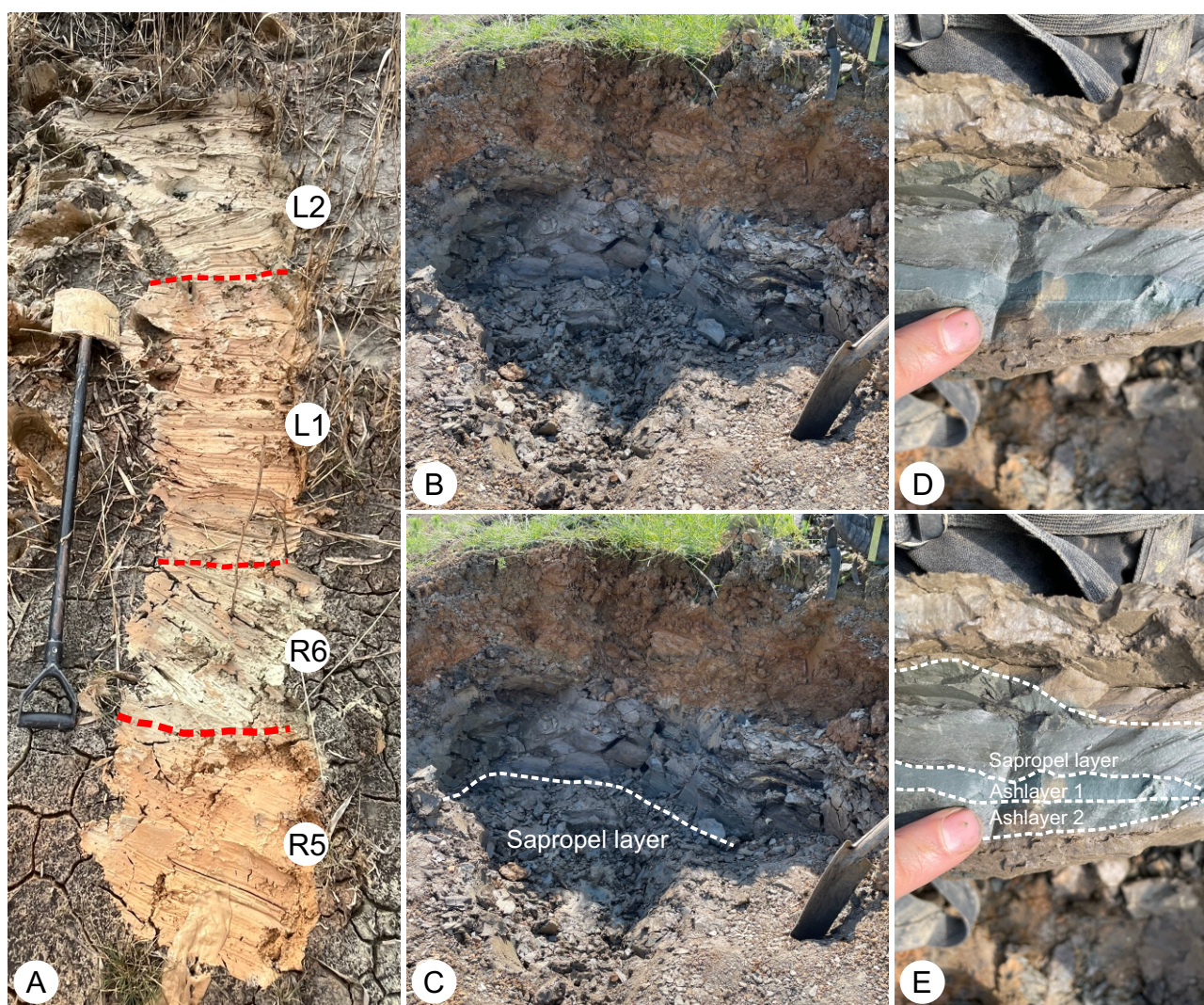


Fig. 2. A: Section through the upper part of the Røsnæs Clay Formation (R5 & R6) and the lower part of the Lillebælt Clay Formation (L1 & L2). The fossils from this study originates from R6 and L2. B: The fossiliferous lower part of L2, from where the majority of the coprolites in this study were retrieved, is laterally persistent and contains a sapropel with two closely spaced volcanic ash layers beneath. C: Same as above with sapropel layer highlighted. D: The ash layers occasionally merge into one at the study site, perhaps due to disturbances caused by earlier bulldozing activity above the locality. E: Same as D, with sapropel and ash layers highlighted.

wegian–Greenland Sea and the North Sea. In Denmark, *Azolla jutlandica* (Collinson *et al.* 2010) occurs in the lower organic-rich part of L2 and its basal range includes the black sapropel bed; magnetobiostratigraphic calibration places the Danish *Azolla* pulse in the upper part of Chron C22n to the lowermost part of C21r (Heilmann-Clausen *et al.* 2010). Arctic coring (ACEX) demonstrates coeval episodic freshening of the Arctic Ocean's surface waters and large scale *Azolla* proliferation (Brinkhuis *et al.* 2006; Heilmann-Clausen *et al.* 2010; Speelman *et al.* 2009). Together, these data provide a robust temporal framework and a paleoceanographic context of enhanced productivity, stratification, and intermittently reduced bottomwater oxygenation for the sapropels that host the coprolites. Regionally, the Lillebælt Clay is part of an epicontinental basin that experienced long-term subsidence following the opening of the North Atlantic, with NAIP volcanism recorded by numerous Palaeogene ash layers and pervasive smectitic clays; this framework explains both the hemipelagic fine-grained lithology and the widespread isochronous marker beds within L2. (Nielsen & Heilmann-Clausen 1988). The exposures of the underlying Røsnæs Clay Formation are not as prominent, and the fossil content not as well studied as that of the Lillebælt Clay.

Material and methods

During a period of 2 years, approximately 2000 kg of material was collected from the Røsnæs clay (R6) and Lillebælt clay (L2) at Hinge claypit. The work was allowed after a written request and approval by the owner. The collected bulk material was divided into smaller pieces (10 cm) and submerged under water in large plastic containers (30 × 45 × 70 cm). Regular manual stirring with a 3-prong cultivator was maintained until most of the material was dispersed. After approximately 4–6 weeks the material was sieved through large custom-built sieves (30 × 50 cm). The top one with a 10 × 10 mm mesh, and the bottom one had a finer 3 × 3 mm mesh. The sieved material was thoroughly rinsed with plenty of water and filtered through double-layered nylon stockings (Denim 20) to retain finer particles. The remaining undispersed material was left submersed under water for another week with regular manual stirring with a 3-prong cultivator and processed when dispersed.

The material was further reduced by rinsing with cold water while gently massaging the nylon stocking until clear water was leaving the nylon stocking (approximately 15 min). The material was then rinsed with lukewarm water (2 min) before dish soap (approximately 5 ml) was added while gently massaging the nylon stocking (2 min). After soaking for 5

min, cold water was used to remove the excess soap. The material was then transferred to a large (7 × 20 × 30 cm) plastic container and water was added. The floating organic material was given a stir to ensure that no inorganic material (sand and fossils) was attached. The organic material was then slowly decanted out of the plastic container. This process was repeated until most of the organic material was removed. The remaining water was decanted out of the container before the material was dried in an oven at 90 degrees (45 min or until completely dry). The final purified material was sorted using a binocular microscope.

Images were taken using automatic focus stacking. A full frame camera (Canon EOS RP) was mounted on a vertical stand holding a WeMacro focus stacking rail (100 mm). The camera was equipped with a Raynox DCR 150 tube lens system and either a Mitutoyo QV (2.5×/0.14), Mitutoyo M Plan Apo (10×/0.28) or a LAOVA 25 mm F 2.8 Ultra macro 5X objective. Light was provided by custom led lights (4 × 81 Led). Helicon remote was used to control the photo stacking rail and Helicon Focus 7 to render (Method C (pyramid), Smoothing 2) the photos. All figured specimens are stored in the collection of Geomuseum Faxe/Østsjælland's Museum OESM 13424 – OESM 13482.

Systematic ichnology

Vertebrate coprolites

Kylindrocopros igen. nov.

Type ichnospecies. *Kylindrocopros hingeensis* igen. et isp. nov.

Included ichnospecies. Known only from the type ichnospecies.

Etymology. From Greek *kylindros* (rolled book) in allusion to the morphology and Greek *kopros* (dung).

Diagnosis. Phosphatic coprolite with variable lateral profile from ovoid to cylindrical that has a scroll structure with thick layers in terminal view and common vertebrate inclusions.

Distribution. Eocene of Denmark and the United States.

Discussion. There are three named scroll coprolites: (1) *Bibliocoprus beemanensis* from the Carboniferous (Pennsylvanian) of New Mexico in the United States (Hunt *et al.* 2012b); (2) *Tikicopros triassicus* from the Late Triassic of India (Rakshit *et al.* 2019); and (3)

Scrollocoprus tatalensis from the Early Cretaceous of Mongolia (Rummy *et al.* 2021). All three named ichnotaxa are at least twice the size of *Kylindrocopros hingeensis*. *Bibliocoprus beemanensis* differs from *Kylindrocopros hingeensis* in being narrow, elongate, always parallel-sided in lateral view, lacking inclusions and having thin layers in terminal view. *Tikicopros triassicus* differs in being relatively short and wide with thin layers in terminal view. *Scrollocoprus tatalensis* is elongate and narrow in lateral view with a terminal acute apex. *Tikicopros triassicus* and *Scrollocoprus tatalensis* both contain abundant inclusions as do *Kylindrocopros hingeensis* and *Kylindrocopros rakshitae*.

Scroll coprolites have usually been postulated to have been produced by chondrichthyans (Hunt *et al.* 2012b; Stringer & King 2012; Rakshit *et al.* 2019; Dentzien-Dias *et al.* 2021). We concur with this interpretation based on scroll coprolites being produced by a *valvula voluta* that is present in some chondrichthyans (Parker 1885; Owen 1886; McAllister 1987; Hunt & Lucas 2012). Rummy *et al.* (2021) assigned *Scrollocoprus* to a sarcopterygian.

***Kylindrocopros hingeensis* igen. et isp. nov.**

Zoobank id : 69B57E49-A9B5-4886-83D6-B15A721C38CC

Holotype. Østsjællands Museer, OESM 13424 (Fig. 3A).

Paratypes. Lillebælt Clay Formation (Eocene), middle Jylland, Denmark: OESM 13425–13432 (Fig. 3B–I).

Referred specimens. Nanjemoy Formation, Lower Eocene of Virginia, USA: LGP-H-594, NMMNH P-79176, NMMNH P-79632, NMMNH P-79186, NMMNH P-79179, NMMNH P-79632).

Etymology. After the locality of Hinge Claypit, where the specimens were found.

Diagnosis. Coprolite that differs from *Kylindrocopros rakshitae* in the thickness of layers, having three spirals rather than one visible in terminal view. and in being half the length (<15 mm).

Description. The holotype is 9.9 mm long with a maximum width of 2.8 mm. The coprolite is round in cross section and tapers in lateral view. The scroll layers are thick and only three spirals are visible in terminal view. Inclusions are abundant and range in shape from tabular to rounded.



Fig. 3. Holotype and paratype coprolites of *Kylindrocopros hingeensis* igen. et isp. nov. in lateral and anterior views. **A:** Holotype, OESM 13424. **B:** paratype, OESM 13425. **C:** paratype, OESM 13426. **D:** paratype, OESM 13427. **E:** paratype, OESM 13428. **F:** paratype, OESM 13429. **G:** paratype, OESM 13430. **H:** paratype, OESM 13431. **I:** paratype, OESM 13432. All specimens reproduced to same scale.

Type locality. Hinge claypit, middle Jylland, Denmark.

Type horizon. Lillebælt Clay Formation, L2 (Eocene).

Distribution. Eocene of Denmark.

Discussion. *Kylindrocopros hingeensis* is one of the most common coprolites in the Lillebælt Clay Formation. This ichnotaxon represents one of the larger coprolites in the ichnofauna with lengths up to 13.5 mm. *Kylindrocopros* is the only coprolite from the marine Palaeogene with a scroll morphology.

***Kylindrocopros rakshitae* igen. et isp. nov.**

Zoobank id : 8C975CC7-7C90-42E5-8711-F17A38FB092C

Holotype. NMMNH P-79176 (Dentzien-Dias *et al.* 2021, fig. 3A-B).

Paratypes. NMMNH P-79179, NMMNH P-79186 (Dentzien-Dias *et al.* 2021, fig. 3D), NMMNH P-79632 (Dentzien-Dias *et al.* 2020, figs. 3C, F), LGP-H-594 (Dentzien-Dias *et al.* 2021, fig. 3G-H).

Referred specimens. Yazoo Clay, Upper Eocene, Louisiana, USA: unnumbered specimens (Stringer & King 2012, figs 4, 5, 8, table 1),

Etymology. Named in honor of Nibedita Rakshit for her work on coprolite ichnotaxonomy, notably scroll forms.

Diagnosis. As for ichnogenus.

Description. The holotype is 17 mm long with a maximum width of 8.5 mm. The coprolite is round in cross section and tapers in lateral view. The scroll layers are thick and only one spiral is visible in terminal view. Inclusions occur in the holotype and referred specimens and include fish vertebrae and other debris (Stringer & King 2012, fig. 8; Dentzien-Dias *et al.* 2021).

***Kathemacopros* igen. nov.**

Type ichnospecies. *Kathemacopros duffini* igen. et isp. nov.

Included ichnospecies. Known only from the type ichnospecies.

Etymology. From Greek *kathhema* (necklace) as the coprolite resembles a string of beads and Greek *kopros* (dung).

Diagnosis. Cylindrical phosphatic coprolite that is separated by deep furrows into a series of segments that are often disc shaped or triangular in lateral view and includes multiple bone inclusions.

Distribution. Eocene of Denmark.

Discussion. This is a highly distinctive coprolite that exhibits similarities to the larger segmented morphotype of Dentzien-Dias *et al.* (2021, fig. 6) but it differs in the depth of the sulci between the segments, in having more irregularly shaped segments and in exhibiting more acute terminations. An incomplete coprolite from the Late Cretaceous of India is also similar in morphology (Hunt *et al.* 2012a, fig. 2W). Segmented coprolites are common in felids and hyenas from the later Cenozoic, although of much larger size, than the herein described specimens (Hunt & Lucas 2012).

***Kathemacopros duffini* igen. et isp. nov.**

Zoobank id : 6A8A3C96-15D8-46A4-B74E-E937D7D18305

Holotype. Østsjællandss Museer, OESM 13433 (Fig. 4A).

Paratypes. OESM 13434–3447 (Fig. 4B–O).

Etymology. In honor of Christopher J. Duffin for his great contributions to the science of coprology.

Diagnosis. As for ichnogenus.

Description. The holotype is 14 mm long with a maximum width of 4 mm. The coprolite is round in cross section and cylindrical but not straight with rounded terminations. The coprolite is divided by lateral sulci that divide the body into segments. There are abundant rounded bony inclusions.

Type locality. Hinge claypit, middle Jylland, Denmark.

Type horizon. Lillebælt Clay Formation, L2 (Eocene).

Distribution. As for ichnogenus.

***Osteocopros* igen. nov.**

Type ichnospecies. *Osteocopros frandseni* igen. et isp. nov.

Included ichnospecies. Known only from the type ichnospecies.

Etymology. From Greek *osteon* (bone) in reference to

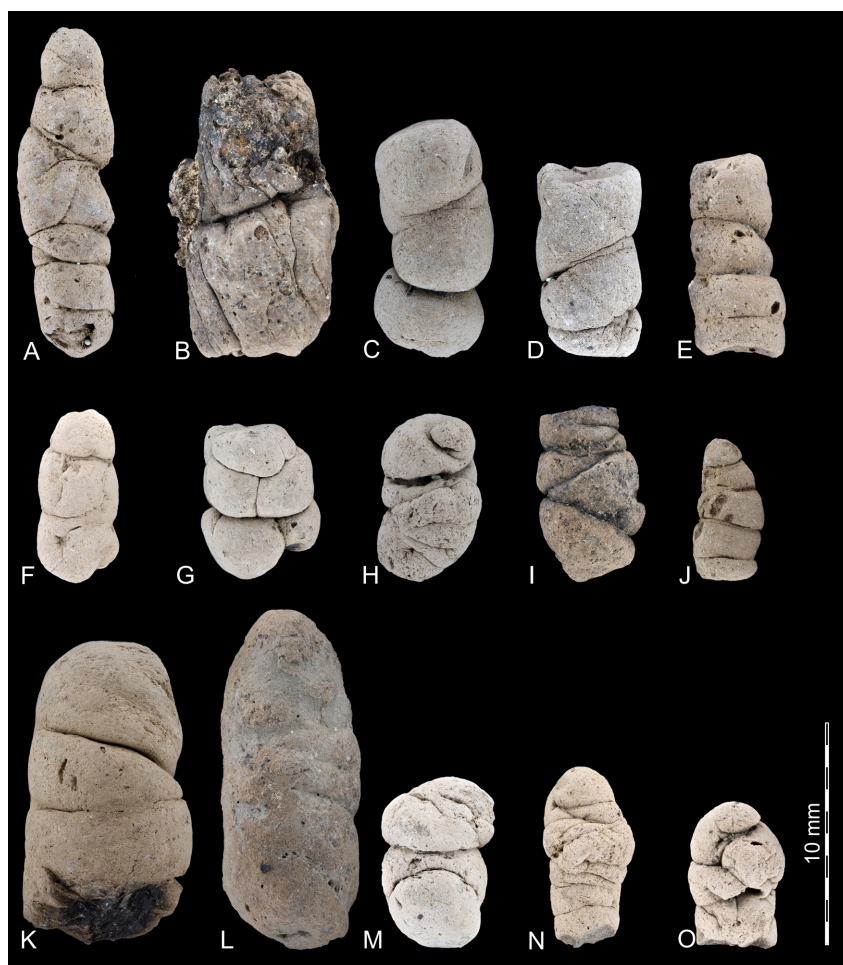


Fig. 4. Holotype and paratype coprolites of *Kathemacopros duffini* igen. et isp. nov. in lateral view. **A:** holotype, OESM 13433. **B:** paratype, OESM 13424. **C:** paratype, OESM 13435. **D:** paratype, OESM 13436. **E:** paratype, OESM 13437. **F:** paratype, OESM 13438. **G:** paratype, OESM 13439. **H:** paratype, OESM 13440. **I:** paratype, OESM 13441. **J:** paratype, OESM 13442. **K:** OESM 13443, OESM 13444. **M:** OESM 13445 **N:** OESM 13446. **O:** OESM 13447. All specimens reproduced to same scale.

the large number of bony inclusions and Greek *kopros* (dung).

Diagnosis. Large cylindrical phosphatic coprolite with very irregular surface texture and a high proportion of bony inclusions.

Distribution. Eocene of Denmark.

***Osteocopros frandseni* igen. et isp. nov.**
 Zoobank id : 4F113C1E-EE27-4917-BF5E-743E5554F536

Holotype. Østsjællanders Museer OESM 13449, (Fig. 5A).

Paratype. OESM 13450 (Fig. 5B).

Etymology. Named in honor of George Frandsen, founder and curator of the Poozeum in Williams, Arizona, USA, a museum which houses the world's largest collection of coprolites, and who has also published on coprolites.

Diagnosis. As for ichnogenus.

Description. The holotype is 9 mm long with a maximum width of 3.5 mm. The coprolite is round in cross section and cylindrical with rounded terminations. The surface texture is very irregular. The coprolite contains abundant bony inclusions. They are dominantly equant in shape, but some are linear and all probably all pertain to bony fish, including one identifiable vertebra.

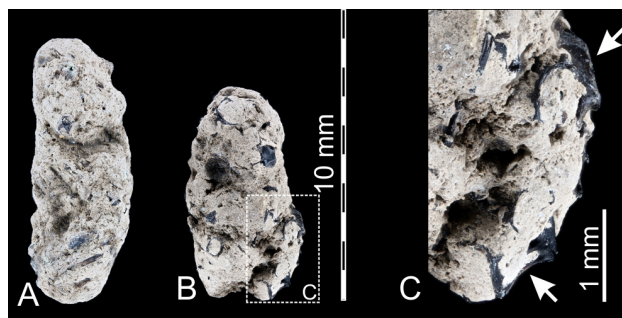


Fig. 5. Holotype and paratype of *Osteocopros frandseni* igen. et isp. nov. **A:** Holotype OESM 13449. **B:** Paratype OESM 13450, **C:** Close up of inclusions in B.

Type locality. Hinge claypit, middle Jylland, Denmark.

Type horizon. Lillebælt Clay Formation, L2 (Eocene).

Distribution. As for ichnogenus.

Discussion. These coprolites include a large density of vertebrate inclusions. Spiral coprolites such as *Kylin-drocopros hingeensis* igen. et isp. nov. and *Liassocopros* and *Sauropros* from the marine Early Jurassic of England, often contain significant quantities of inclusions, but they are usually less common in non-spiral forms (Hunt *et al.* 2012a, figs. 1H, I-J). Coprolites of borophagine canids and hyenas in the later Cenozoic also yield large volumes of bony inclusions (Hunt & Lucas, 2021). Other putative Palaeogene coprolites with many inclusions probably represent regurgitalites (e.g., Hunt & Lucas 2016, fig. 4E). The Danish coprolites most likely represent a carnivorous teleost.

***Commacopros* igen. nov.**

Type ichnospecies. *Commacopros dentziendiasae* igen. et isp. nov.

Included ichnospecies. Known only from the type ichnospecies.

Etymology. From Greek *komma* (punctuation mark) in reference to morphology of the coprolite in lateral view and Greek *kopros* (dung).

Diagnosis. Reniform coprolite with rounded cross section and ends with one narrower tip folded over.

Distribution. Eocene of Denmark.

***Commacopros dentziendiasae* igen. et isp. nov.**

Zoobank id : 170C9B0F-988A-42E4-916E-2913FD2B4A89

Holotype. Østsjællanders Museer, OESM 13451 (Fig. 6A).

Paratypes. OESM 13452–13454 (Fig. 6B–D).

Etymology. Named for Paula Dentzien-Dias for her significant contributions to the study of vertebrate coprolites.

Diagnosis. As for ichnogenus.

Description. The holotype is 1.2 mm long cm long with a maximum diameter of 0.55 mm. The coprolite is curved in lateral view with rounded ends. One end is broadly rounded and the other is narrower and the tip is folded over, round in cross section and cylindrical with rounded terminations. Some of the paratypes are approximately half the size of the holotype (Fig. 7C-D).

Type locality. Hinge claypit, middle Jylland, Denmark.

Type horizon. Lillebælt Clay Formation, L2 (Eocene).

Distribution. As for ichnogenus.

Discussion. Larger reniform coprolites are most common in the late Triassic and Late Cretaceous. These coprolites represent *Alocopros triassicus* and *A. indicus* (Hunt & Lucas 2025). However, the terminations in these coprolites are equal in size and the lateral margins preserve longitudinal furrows and thus they differ from *Commacopros dentziendiasae* igen. et isp. nov. The Danish coprolites may represent a carnivorous teleost.

***Kranocopros* igen. nov.**

Type ichnospecies. *Kranocopros lucasi* igen. et isp. nov.

Included ichnospecies. Known only from the type ichnospecies.

Etymology. From Greek *kranos* (helmet) in allusion to



Fig. 6. Holotype and paratypes of *Commacopros dentziendiasae* igen. et isp. nov., in lateral view. A: Holotype OESM 13451. B: Paratype, OESM 13452. C: paratype, OESM 13453. D: paratype OESM 13454. All specimens reproduced to same scale.

the shape of termination of the coprolite and Greek *kopros* (dung).

Diagnosis. Elongate coprolite with rounded cross section that is composed of a tightly folded sigmoidal cylinder with a folded tip with an acute rounded tip.

Distribution. Eocene of Denmark.

***Kranocopros lucasi* igen. et isp. nov.**

Zoobank id : 658E72DE-E331-4974-BCC7-B4E1C-D53C3EC

Holotype. Østsjællanders Museer, OESM 13458 (Fig. 7D).

Paratypes. OESM 13455–13457 (Fig. 7A–C).

Etymology. Named in honour of Spencer G. Lucas of the New Mexico Museum of Natural History and Science for his substantial contributions to the study of coprolites.

Diagnosis. As for ichnogenus.

Description. The holotype is a broken fragment of a coprolite that is 8.5 mm long with a maximum diameter of 3.8 mm. It may represent about 50% of the length of the complete coprolite. The coprolite is subrounded in cross section and in lateral view it is evident that it is composed of a tightly sigmoidally folded cylinder which is reminiscent of an intestinal tract. The tip is acute but rounded termination and folded over relative to the long axis of the coprolite.

Type locality. Hinge claypit, middle Jylland, Denmark.

Type horizon. Lillebælt Clay Formation, L2 (Eocene).

Distribution. As for ichnogenus.

Discussion. This is a very distinctive form of coprolite in that it is comprised of a tightly coiled fecal tube within a fusiform mass. The tube is rounded in cross section and uniform in diameter. These coprolites lack the spiral morphology of chondrichthyan coprolites and thus may represent a carnivorous teleost.

***Hingecopros* igen. nov.**

Type ichnospecies. *Hingecopros lillebaeltensis* igen. et isp. nov.

Included ichnospecies. Known only from the type ichnospecies.

Etymology. From the name of the Hinge Quarry and Greek *kopros* (dung).

Diagnosis. Elongate coprolite with spindle shape in lateral view which is a sigmoidal mass composed of an irregularly coiled mass with varying diameters.

Distribution. Eocene of Denmark.

Discussion. Both *Kranocopros* and *Hingecopros* consist of a sigmoidal structure in a fusiform coprolite. *Kranocopros* is comprised of a regularly sized tubular body with smooth surfaces that is folded. In contrast *Hingecopros* is formed from an irregularly shaped and sized body which is strongly wrinkled. Thus, we consider the two ichnogenera as distinct.

***Hingecopros lillebaeltensis* igen. et isp. nov.**

Zoobank id : F34353B5-83DA-41EA-A8DD-DE-533D6ED0B7

Holotype. Østsjællanders Museer, OESM 13459 (Fig. 8A).

Paratypes. OESM 13460–13465 (Fig. 8B–G).



Fig. 7. Holotype and paratypes of *Kranocopros lucasi* igen. et isp. nov. **A:** Paratype OESM 13455. **B:** Paratype OESM 13456. **C:** Paratype OESM 13457. **D:** Holotype OESM 13458. All specimens reproduced to same scale.

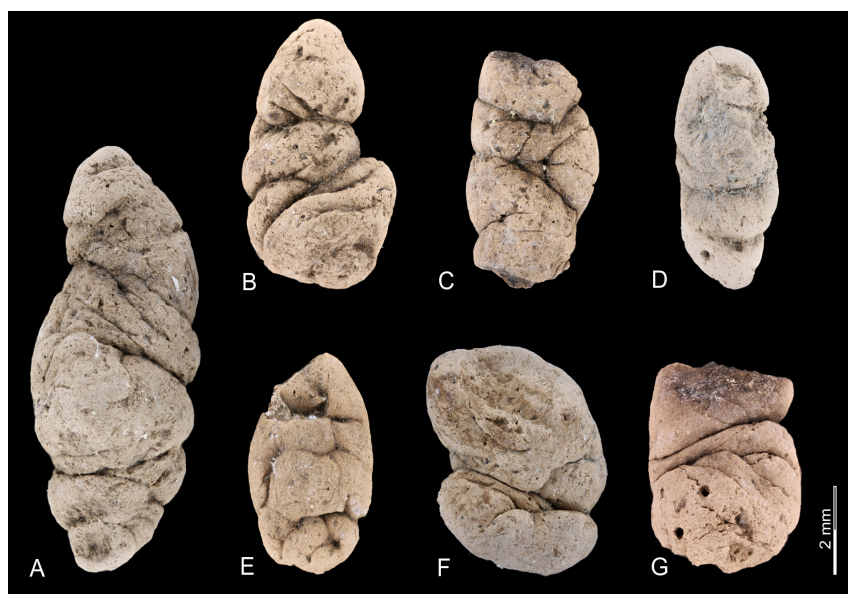


Fig. 8. A: Holotype of *Hingecopros lillebaeltensis* igen. et isp. nov. OESM 13459. B–G: Paratypes of *Hingecopros lillebaeltensis* igen. et isp. nov. B: OESM 13460. C: OESM 13461. D: OESM 13462. E: OESM 13463. F: OESM 13464. G: OESM 13465. All specimens reproduced to same scale.

Etymology. Named for the Lillebælt Clay Formation from which the holotype originates.

Diagnosis. As for ichnogenus.

Description. The holotype is a complete coprolite that is 9.8 mm long with a maximum diameter of 4.2 mm. The coprolite is spindle-shaped in lateral view and is composed of an elongate, irregular, sigmoidal mass. The coprolite contains a large number of small bony inclusions up to 0.2 mm in diameter

Type locality. Hinge claypit, middle Jylland, Denmark.

Type horizon. Lillebælt Clay Formation, L2 (Eocene).

Distribution. As for ichnogenus.

Discussion. This ichnotaxon is reminiscent of the sinuous morphotype of Dentzien-Dias *et al.* (2021, fig. 5) but it differs in being smaller (length 9.8 mm versus 1.5 cm), being more flattened in lateral view and having a more irregular diameter to the coil. These coprolites may represent a carnivorous teleost.

Morphotype A

Referred specimen OESM 13448, (Fig. 9)

Locality. Hinge claypit, middle Jylland, Denmark.

Horizon. Lillebælt Clay Formation, L2 (Eocene).

Discussion. Coprolites with similar morphology to OESM 13448, being elongate, cylindrical coprolites from the Paleogene, but of much larger size, have often been referred to crocodilians based on actualist

studies of modern crocodile feces (e.g., Lucas *et al.* 2012, Milan 2012., Milàn & Hedegard 2010). Halaçlar *et al.* (2023) named *Crococopros naduongensis* for such coprolites from the late Eocene of Vietnam. The holotype and referred specimens include a range of morphologies that derive from nonmarine strata in Vietnam and China. The Lillebælt Clay ichnofauna Formation contains one small elongate coprolite that could fit within this morphoseris but because of its small size (length of 14 mm) and marine origin we do not assign it to this ichnotaxon.

Morphotype B

Referred specimens. OESM 13466–13469 (Fig. 10A–D).

Locality. Hinge claypit, middle Jylland, Denmark.

Horizon. Lillebælt Clay Formation, L2 (Eocene).

Discussion. Coprolites of this morphotype are cylindrical and often curved with a circular cross section



Fig. 9. A single coprolite of Morphotype A (OESM 13448).



Fig. 10. Coprolites of Morphotype B in lateral view. A: OESM 13466. B: OESM 13467. C: OESM 13468. D: OESM 13469. All specimens reproduced to same scale.

and rounded terminations. They have rough surface textures and abundant small inclusions. They are approximately 4-6 mm in length.

Morphotype C

Referred specimens. OESM 13470 – 13475 (Fig. 11A–F).

Locality. Hinge claypit, middle Jylland, Denmark.

Horizon. Lillebælt Clay Formation, L2 (Eocene).

Discussion. Several coprolites consist of a cylindrical element which is folded (OESM 13470), braided (OESM 13472) or coiled (OESM 13471). These coprolites have a rough external texture and varying numbers of inclusions.

Morphotype D

Referred specimens. OESM 13476 (Fig.12A).

Locality. Hinge claypit, middle Jylland, Denmark.

Horizon. Røsnæs Clay Formation, R6 (Eocene).

Discussion. Microcoprolites of this morphotype are cylinders with rounded poles. Most range in length from 0.6 mm to 0.9 mm in length with diameters of 0.25 to 0.4 mm. They vary from straight to slightly curved in lateral view. Their most characteristic feature is a series of even-spaced lateral grooves.

Morphotype E

Referred specimens. OESM 13477 (Fig.12B).

Locality. Hinge claypit, middle Jylland, Denmark.

Horizon. Røsnæs Clay Formation, R6 (Eocene).

Discussion. This morphotype is represented by mi-

crocoprolites that are cylinders with rounded ends. They range in length from 0.7 mm to 0.9 mm in length with diameters of 0.3 to 0.4 mm. They vary from straight to slightly curved in lateral view. They differ from Morphotype C and E in lacking lateral striations or abundant bony inclusions.

Morphotype F

Locality. Hinge claypit, middle Jylland, Denmark.

Horizon. Røsnæs Clay Formation, R6 (Eocene).

Referred specimen. OESM 13478 (Fig.12C).

Discussion. This morphotype is represented by abundant microcoprolites with lengths ranging from 0.6 mm to 0.9 mm. They are cylindrical in morphology with rounded terminations and are straight to slightly curved in lateral view. They differ from Morphotype C and E in containing abundant bony inclusions.

Invertebrate coprolites

Ichnofamily Lumbricariidae Schweigert, 2001

Funiculocopros igen. nov.

Type ichnospecies. *Funiculocopros sinuosus* igen. et isp. nov.

Included ichnospecies. Known only from the type ichnospecies.

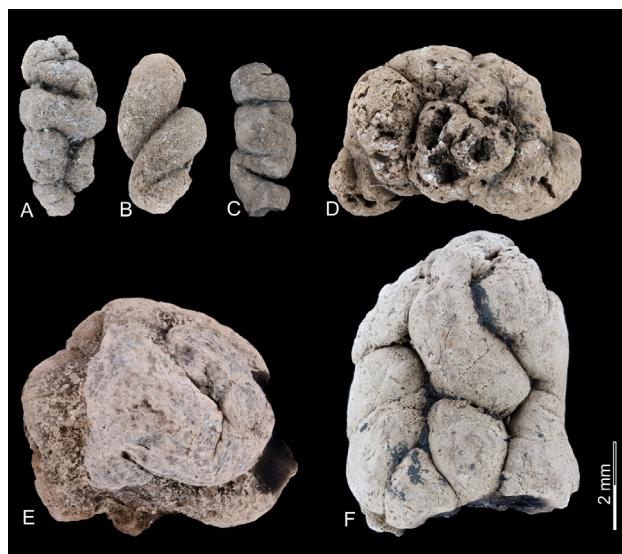


Fig. 11. Coprolites of Morphotype C in lateral view. A: OESM 13470. B: OESM 13471. C: OESM 13472., D: OESM 13473. E: OESM 134474. F: OESM 13475. All specimens reproduced to same scale.

Etymology. From Latin *funiculus* (rope) in allusion to the morphology and Greek *kopros* (dung).

Diagnosis. Phosphatic microcoprolite that is an elongate continuous string with a rounded ovoid cross section that forms regular loops about 2 mm long whose main segments are sub-parallel.

Distribution. Eocene of Denmark.

Discussion. This ichnogenus is closest in morphology



Fig. 12. Microscopic coprolites from Rønæs Clay Formation, layer R6. **A:** Morphotype D. OESM 13476. **B:** Morphotype E. OESM 13477. **C:** Morphotype F. OESM 13478. All specimens reproduced to same scale.

to the invertebrate bromalite *Anfractuocoprolithus aphelusspecimen* from the Cambrian and Ordovician (Bischoff 1994; Knaust 2020; Voldman *et al.* in press). *Funiculocopros sinuosus* differs in having a more flattened cross section and in forming regular loops with long straight sections rather than being tightly-coiled and irregular (Bischoff 1994, pl. 1; Knaust 2020, fig. 6H). Knaust (2020) considered that the morphology of *Anfractuocoprolithus aphelusspecimen* suggested that it is cololite rather than a coprolite. Cololites preserved in the absence of a body are eviscerolites which are uncommon and preserve the morphology of part of the intestinal tract (Hunt & Lucas 2012, 2021). The elongate folded morphology indicates an extruded, hence coprolitic, origin. Knaust (2020) notes that some molluscs (notably species of Pectinidae) produce feces consisting of cylindrical rods that are entangled (Arakawa 1965). It is also possible that this ichnotaxon pertains to a previously unrecognized form of vertebrate coprolite.

***Funiculocopros sinuosus* igen. et isp. nov.**
Zoobank id : 802395FC-A2A1-4D6A-A4FA-1F97E86F0055

Holotype. Østsjællands Museer OESM 13479 (Fig. 13A).

Paratypes. OESM 13480–13482 (Fig. 13B–F).

Etymology. From Latin *sinuosus* (winding) in reference to the coiling of the ichnospecies.

Diagnosis. As for ichnogenus.

Description. The holotype is 2.9 mm long with a maximum width of 2 mm. The coprolite consists of four flattened and rounded strands about 0.4–0.5 mm in width that are straight to sinuous with tight bends at the ends of the specimen. is laterally flattened. OESM 13479 is 2.2 mm long and 1.1 mm in maximum width with elongate segments subparallel. Eight additional specimens are tentatively assigned to this ichnotaxon as it consists of coiled segments that are only partially arranged in a sub-parallel arrangement.

Type locality. Hinge claypit, middle Jylland, Denmark.

Type horizon. Lillebælt Clay Formation, L2 (Eocene).

Distribution. As for ichnogenus.

Discussion. The Lumbricariidae are currently only known from the Paleozoic and Mesozoic and this is thus the youngest occurrence of the ichnofamily (Knaust 2020, fig. 12).

Discussion

There are three other large samples of marine vertebrate coprolites from the Eocene. The middle Eocene Fürstenau Formation of Germany preserves a coprofauna dominated by heteropolar coprolites and lacking any scroll forms (Diedrich & Felker 2012). This pertains to the *Crassocopros* ichnofacies of Hunt *et al.* (2018). Scroll coprolites are rare in the post-Cretaceous and yet the coprofauna described herein as well as those from the early Eocene Potapaco Member of the Nanjemoy Formation, Virginia, USA (Dentzien-Dias *et al.* 2021) and the upper Eocene Yazoo Clay, Louisiana, USA (Stringer & King 2012) all contain a significant proportion of scroll coprolites. Most non-spiral coprolites from these units are attributed to teleost fishes. We name this distinctive and recurrent association of scroll coprolites as the *Kylindrocopros* ichnofacies which is currently only known from the Eocene of eastern North America and Western Europe.

The Lillebælt Clay ichnoassemblage is most similar to that from the Nanjemoy Formation. *Kylindrocopros*

isp. occurs in both ichnofaunas and *Kathemacopros partitus* and *Hingecopros lillebælti* *igen. et isp. nov.* show similarities to the segmented and sinuous morphotypes respectively of Dentzien-Dias *et al.* (2021). This similarity could be based on age, environment or both.

Funiculocopros sinuosus is interpreted to represent an invertebrate coprolite, possibly derived from a mollusc. It is unusual for an ichnofauna to include both vertebrate and invertebrate coprolites. Voldman *et al.* (2024, in press) described small phosphatic coprolites from the Ordovician of Argentina that are dominated by invertebrate specimens but include two that may represent vertebrates. Probable invertebrate coprolites such as *Lumbricaria* are common in the Solnhofen Lagerstätte that also contains vertebrate coprolites that are largely undescribed.

The Lillebælt clay fauna

The Lillebælt Clay Formation has preserved a rich fauna of vertebrates and invertebrates, and excessive collections of material exists in museums and private

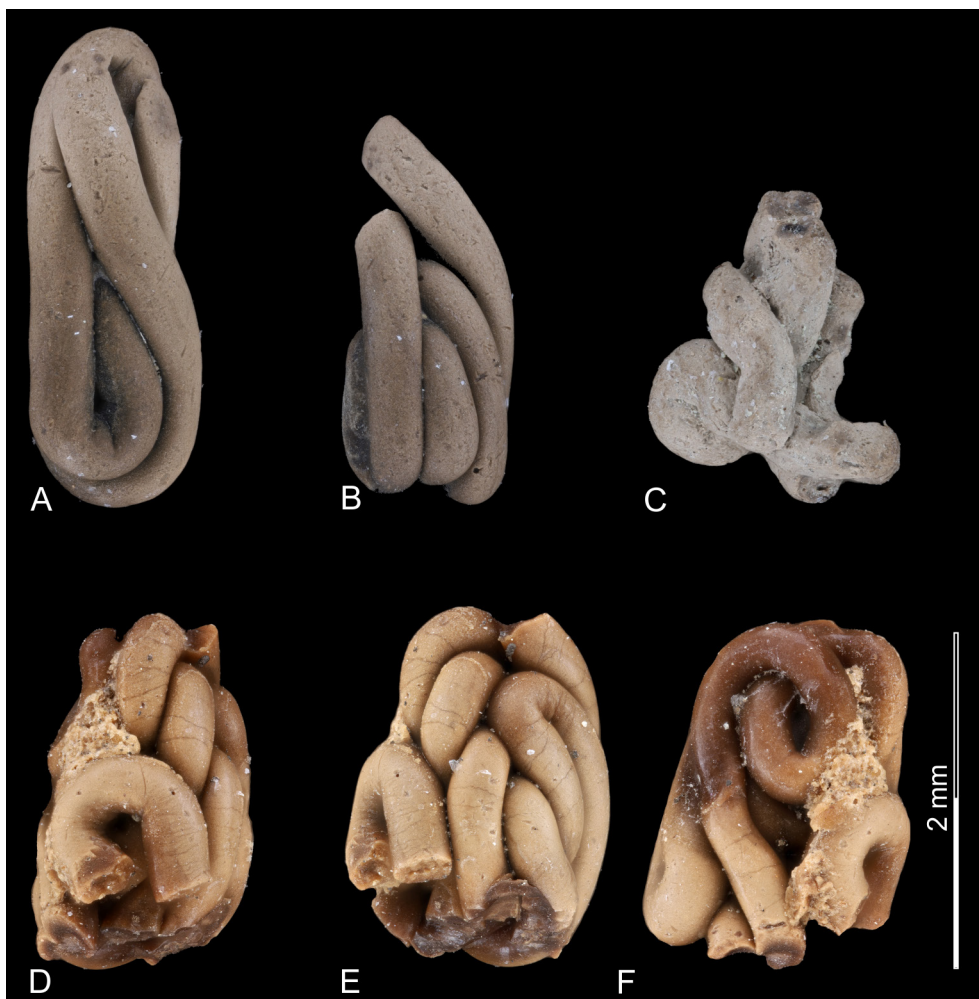


Fig. 13. Holotype and paratypes of *Funiculocopros sinuosus* *igen. et isp. nov.* in lateral view. A: holotype OESM 13479. B: paratype OESM 13480. C: paratype OESM 13481. D–F: OESM 13482 viewed from three angles, each rotated 45 degrees, showing the complex coiling of the specimen. All specimens reproduced to same scale.

collections. Chondrichthyans are particularly abundant, both as teeth but also as preserved vertebrates documenting more than 30 taxa (Carlsen & Cuny 2014., Hansen *et al.* 2013., Pollerspöck *et al.* 2023., Rudebeck & Riehmman 2022). Remains of bony fish are commonly found both as isolated teeth (Carlsen & Cuny 2014) or isolated bones (Heilmann-Clausen *et al.* 1985) or as voids from dissolved otoliths (Schwarzahns & Nielsen 2024). Three-dimensionally preserved skeletal remains of fish are often encountered in concretionary nodules (Bonde *et al.* 2008, Carnevale *et al.* 2024), and abundant undescribed material exists at the collection of the Natural History Museum of Denmark, as well as in private collections. Other vertebrates from the Lillebælt clay include bird remains (Lindow 2008), and undescribed remains of snakes from the collection of the Natural History Museum of Denmark. The formation further contains a rich and diverse invertebrate fauna which has been sporadically documented (Bonde 1968., Bonde *et al.* 2008; Collins & Jakobsen 2003; Schnetler & Heilmann-Clausen 2011; Jakobsen & Andersen 2025), as well as abundant trace fossils (Nielsen *et al.* 2015).

All the vertebrate coprolites described herein pertain to fish. *Kylindrocopros hingeensis* was produced by an organism with a scroll valve and thus probably represents a chondrichthyan (Hunt *et al.* 2012b; Stringer & King, 2012; Rakshit *et al.* 2019; Dentzien-Dias *et al.* 2021). The remaining twelve ichnotaxa and morphotypes pertain to non-elasmobranchs. This is unusual as there is often a bias in favor of the preservation of chondrichthyan coprolites (Hunt *et al.* 2015).

Conclusions

The diverse coprofauna recovered from the Eocene Lillebælt Clay Formation at the Hinge claypit is very significant for a number of reasons including:

- The sample size is very large and contains a wide diversity of vertebrate and invertebrate coprolites from the Danish Eocene.
- It is a rare example of a diverse ichnofauna of small vertebrate coprolites.
- Morphologically and ichnotaxonomically, the fauna from the Hinge clay pit is among the most diverse worldwide and further represents an unusual association of micro- and macrocoprolites as well as being a rare case of co-occurring vertebrate and invertebrate coprolites.
- The presence of the coprolite ichnogenus *Funiculocopros sinuosus* igen. et isp. nov. is the first occurrence of the ichnofamily Lumbricariidae after the Mesozoic.
- The vertebrate coprolites were produced by fish.

- The coprofauna represents the newly recognized *Kylindrocopros* ichnofacies.

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