A new eusuchian (Crocodylia) tooth from the Early or Middle Paleocene, with a description of the Early–Middle Paleocene boundary succession at Gemmas Allé, Copenhagen, Denmark

DANIELA SCHWARZ-WINGS, JESPER MILÀN & PALLE GRAVESEN

Schwarz-Wings, D., Milàn, J. & Gravesen, P., 2014. A new eusuchian (Crocodylia) tooth from the Early or Middle Paleocene, with a description of the Early–Middle Paleocene boundary succession at Gemmas Allé, Copenhagen, Denmark. © 2014 by Bulletin of the Geological Society of Denmark, Vol. 62, pp. 17–26. ISSN 2245-7070. (www.2dgf.dk/publikationer/bulletin). https://doi.org/10.37570/bgsd-2014-62-02

Received 11 April 2014
Accepted in revised form 5 August 2014
Published online 15 August 2014

A recently found crocodylian tooth crown from the basal conglomerate of the Middle Paleocene (Selandian) Lellinge Greensand Formation, differs morphologically from other finds of crocodylian teeth from the Paleocene of southern Scandinavia. The tooth is conical and blunt with a narrow rounded apex, and slightly curved along the axis of its length. The morphology of the tooth suggests it belongs to either the longirostrine eusuchian *Aigialosuchus*, which is known from the Campanian of southern Sweden, or to a member of the Alligatoridae which are the most common crocodylians in northern Europe in the Late Cretaceous. Gavialoid crocodylians, in particular *Thoracosaurus* which is known from the Danian limestome of the Limhamn quarry in southern Sweden and from the Faxe quarry in eastern Denmark, can be excluded because of their deviating tooth morphology. Regardless of its assignment, the tooth is interesting in a stratigraphic context as it demonstrates the existence of at least two crocodylian taxa in Scandinavia during the Early and Middle Paleocene.

Keywords: Crocodylian diversity, Eusuchia, Middle Paleocene, Danian/Selandian boundary, Echinoderm conglomerate, Lellinge Greensand Formation.

Daniela Schwarz-Wings [d.schwarz-wings@mfn-berlin.de], Museum für Naturkunde, Leibniz Institute for Research on Evolution and Biodiversity, Invalidenstrasse 43, DE 10115 Berlin, Germany. Jesper Milàn [jesperm@oesm.dk], Geomuseum Faxe/Østsjællands Museum, Østervej 2, DK-4640 Faxe, Denmark; also Department of Geosciences and Natural Resource Management, University of Copenhagen, Øster Voldgade 10, DK-1350 Copenhagen K, Denmark. Palle Gravesen [palgeolbot@gmail.com], Det Sorte Geomuseum, Skolegade 2B, DK-4874 Gedser, Denmark; also Natural History Museum of Denmark, University of Copenhagen, Øster Voldgade 5–7, DK-1350 Copenhagen K, Denmark.
Corresponding author: Jesper Milàn

The Scandinavian fossil record of Cretaceous and Paleocene Crocodyliformes is extremely scarce, with only a few scattered finds. The Early Cretaceous (Berriasian) of Bornholm and southern Sweden has yielded teeth and skeletal fragments of the non-eusuchian crocodiles *Theriosuchus*, *Bernissartia* and cf. *Goniopholis* (Rees 2000, 2002; Schwarz-Wings *et al.* 2009).

An undesribed jaw fragment preserved in flint of a longirostrine crocodylian with some affinities to *Thoracosaurus* is known from the Maastrichtian chalk of Møns Klint, Denmark (Gravesen & Jakobsen 2012), and fragmentary material of the poorly known eusuchian crocodyliform *Aigialosuchus* is described from the Campanian of southern Sweden (Persson 1959). The eusuchian *Thoracosaurus* is well known from a number of skeletal remains from the Danian of Limhamn quarry in southern Sweden, including a complete skull as well as postcranial material (Lundgren 1890; Troedsson 1923, 1924). Skeletal remains of *Thoracosaurus* sp. comprising a basioccipital, a cervical vertebra, a humerus and a number of isolated teeth, are known from the middle Danian limestone of Faxe quarry, Denmark (Bendix-Almgreen,1972; Bonde *et al.* 2008). From the same quarry, a bite trace *Nihilichnus* in a turtle carapace bears indirect evidence of the presence of a crocodylian (Milàn *et al.* 2011). Finally, an imprint of a 'reptilian' tooth resembling the long slender thoracosaurine teeth is mentioned from the

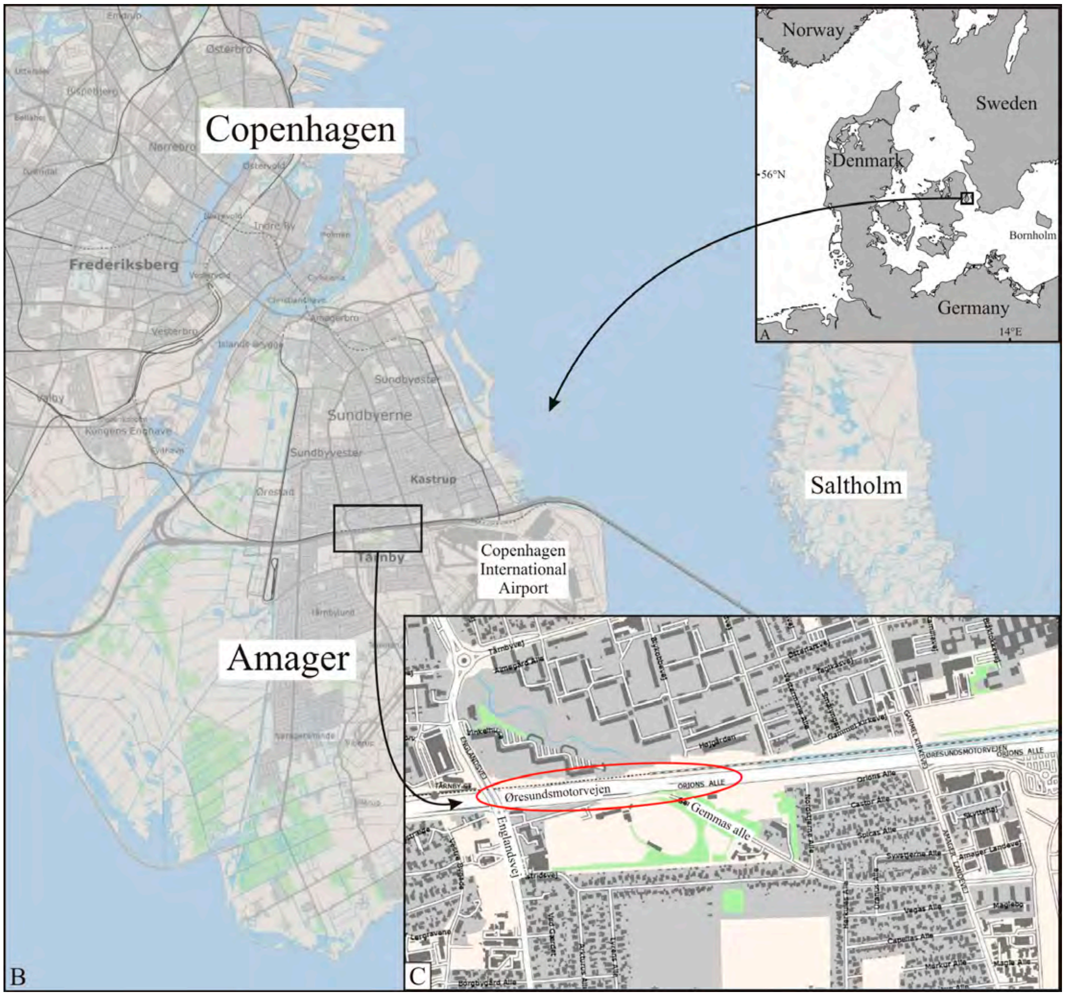

Fig. 1. Location map. **A–B**: The site is located on the island of Amager, part of Copenhagen. **C**: The excavation site (55°37′46″N, 12°36′34″Ø) was open during construction of Øresundsmotorvejen (E20) to Sweden.

lower Selandian *Crania* limestone of Copenhagen (Rosenkrantz 1920a).

In this paper, we describe a newly found crocodylian tooth of a type of eusuchian crocodile hitherto unknown from the Early and Middle Paleocene of Denmark and discuss its implications for the northern European, Paleocene crocodylian diversity. Furthermore, we present the hitherto most detailed description of the now lost locality at Gemmas Allé, Copenhagen, where it was found.

Geological setting

The tooth was discovered in material collected in 1994 from a large road cut at Gemmas Allé on the island of Amager (Fig. 1), when large-scale excavations prior to the coming tunnel and bridge connection between Denmark and Sweden opened a large exposure of the strata at the Danian/Selandian boundary, which in the Danish area is developed as an erosional unconformity (Stouge *et al*. 2000; Clemmensen & Thomsen 2005) marking the boundary between the Lower and Middle Paleocene (Schmitz *et al*. 2011).

The tooth was found in material from the basal conglomerate of the Selandian (Middle Paleocene) Lellinge Greensand Formation (Stouge *et al*. 2000; Clemmensen & Thomsen 2005; Schmitz *et al*. 2011) (Fig. 2A). This characteristic conglomerate occurs at both sides of Øresund, the sound that separates Denmark from Sweden, and contains abundant reworked Danian fossils (Fig. 2D.). In Sweden it occurs in the locality of Klagshamn. In Denmark it could previously been seen in a number of classical, now inaccessible localities in the Copenhagen area, viz., Copenhagen South Harbour, Vestre Gasværk, Sundkrogen and Svanemøllebugten (e.g. Rørdam 1897, 1899; Rosenkrantz 1920a, 1920b, 1924, 1925, 1930, 1938, 1942; Harder 1922; Gry 1935; Milthers 1935; Berthelsen 1962, 1995; Stenestad 1976; Gravesen 1994; Knudsen 1994; Schnetler 2001; Heilmann-Clausen & Surlyk 2006). It may occasionally be exposed during larger construction works. The site at Gemmas Allé was accessible for most of the year 1994 due to the kind understanding of the construction company Per Aarsleff A/S. The section extended for several hundred metres from the road Englandsvej eastwards along Gemmas Allé almost to the buildings of Copenhagen International Airport (Fig. 1B). The site has also been described in literature as the Tårnby Torv locality (e.g. Gravesen 1994). Based on 10 individual sections accurately measured by PG in 1994, a composite log has been made (Fig. 2A).

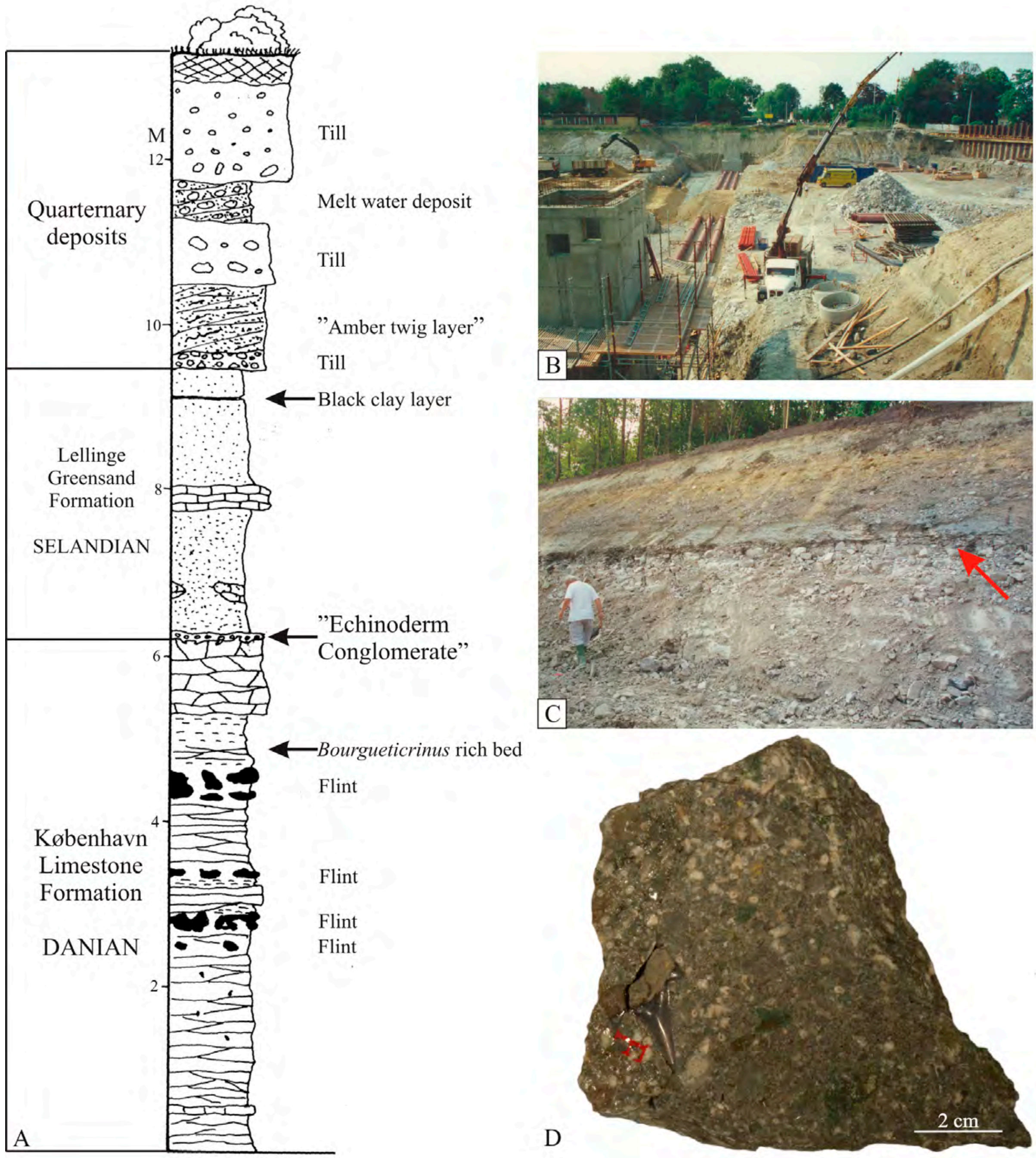

Fig. 2. **A**: Composite log of the section at the Gemmas Allé site, modified after Gravesen (1994). **B**: The western part of the excavation near Englandsvej. **C**: The boundary between the Danian København Limestone Formation and the Selandian Lellinge Greensand Formation. The basal conglomerate of the Lellinge Greensand Formation is indicated by arrow. **D**: Sample of the conglomerate from the Gemmas Allé site. Note the prominent shark tooth beside the red mark. All photos by Sten Lennart Jakobsen.

Upper Danian limestone

The section excavated in 1994 exposed well over 6 m of light grey, fine-grained Danian limestone described as calcarenite, in Danish 'Kalksandskalk', belonging to the top of the København Limestone Formation (København Kalk Formationen of Stenestad 1976). The limestone is partly indurated forming a hard, coherent limestone of the type previously known in Danish and German literature as 'Saltholmskalk', and partly developed as more greyish and softer, marly limestone. The limestone includes a few coherent bands of greyish to black flint as well as scattered, irregular flints nodules. The hard limestone contains only scattered invertebrate macrofossils, most commonly *Echinocorys obliqa*, *Carneithyris lens*, *Crania (Danocrania) tuberculata*, *Lima testis*, *Septifer hauniensis*, several oysters (*Exogyra canaliculata*, "*Pycnodonte*" *vesicularis*), nautiloids (*Cimomia* sp., *Eutrephoceras bellerophon*), *Volutolithes nodifer*, (?) *Scaphella* sp., *Ditrupula schlotheimi*, *Xanthilithes* sp. and trace fossils in the form of burrows of the decapod *Callianassa*.

The softer beds contain a diverse late Danian macro- and mesofauna, which besides many bryozoans comprise species such as *Echinocorys obliqua*, *Cyclaster suecicus*, *Tylocidaris vexillifera* (all index fossils for the later Danian), *Phymosoma* sp., *Stereocidaris*/*Cidaris* spp., ossicles of asteroids (*Recurvaster* sp., *Pycinaster rosenkrantzi*) and stalk ossicles of the crinoid *Bourgueticrinus* cf. *danicus*. The latter characterises a particularly fossiliferous layer near the top of the Danian, just below the indurated limestone beds forming the very top of the Danian at this site. In addition to the species mentioned above the fossiliferous layer also contains *Amussium* sp., *Chlamys palaeocaenica*, *Stegoconcha* sp., *Temnocidaris danica*, ?*Palaeodiadema* sp., *Democrinus* sp., *Nielsenicrinus obsoletus, Isselicrinus paucicirrhus*, comatulids, *Ditrupula schlotheimi*, *Spirorbis hisingeri*, *Crania (Danocrania) tuberculata*, *Argyrotheca scabricula*, "*Scalpellum steenstrupi*" and several species of shark's teeth.

The Danian/Selandian boundary

At Gemmas Allé, the base of the Selandian Lellinge Greensand Formation is developed as a conglomerate. The conglomerate is a greenish, glauconitic and speckled deposit with reworked clasts of light-grey, upper Danian limestone nodules set in a darker, glauconitic matrix and with plentiful reworked late Danian fossils such as *Crania (Danocrania) tuberculata*, *Isocrania posselti*, *Carneithyris lens*, *Echinocorys obliqua*, *Plicatula ravni*, *Graphularia* stems, ossicles of asteroids and crinoids including *Bourgueticrinus,* and frequent often large and dark shark's teeth such as impressive specimens of *Cretalamna appendiculata*, as well as dark coloured vertebrate bone fragments. In its matrix are also seen numerous, shiny, brownish and rounded pellets, possibly fecal pellets from gastropods (Fig. 2D).

In the course of time, the conglomerate has carried widely different names. Apparently the first detailed description was published by the German geologist W. Deecke (1899), based on a glacial erratic boulder from the Rügen area. Rather misleadingly, he named the rock an "Echinodermenbreckzie". Grönwall (1904) changed the name to the more appropriate "Ekinodermkonglomerat" in his study of glacial erratics of the southern Funen area in Denmark. Due to its content of numerous reworked specimens of the brachiopod *Crania* (*Danocrania*) *tuberculata*, it has also been named the "Upper Crania Limestone" e.g. in Rosenkrantz (1920a), or "Forsteningskonglomerat", i.e. fossiliferous conglomerate (Rosenkrantz 1930). Gry (1935) used the widely different name of "Paleocene shelly conglomerate". The rock is widely distributed and well-known as a glacial erratic (German: "Geschiebe") under the name of "Echinodermenkonglomerat" (see e.g. Hucke-Voigt 1967; Gravesen 1993; Schulz 2003; Rohde 2008; Rudolph *et al*. 2010). By dissolution of the rock in acid it is known to yield abundant shark´s teeth such as the impressive fauna described from glacial erratics by Reinecke & Engelhard (1997). Today the unit is generally referred to as the basal conglomerate of the Lellinge Greensand Formation (Clemmensen & Thomsen 2005).

Lower Selandian deposits

The basal conglomerate is followed by a 2–3 m thick sequence of greensand belonging to the lower Selandian Lellinge Greensand Formation, which contains a diverse fauna (e.g. Franke 1927; Ravn 1939; Schnetler 2001; Schwarzhans 2003; Christiansen 2007).

At the Gemmas Allé site, macrofossils were not particularly well-preserved but included typical Lellinge Greensand Formation macrofossils such as *Nucula densistria*, *Dentalium rugiferum*, *Lima testis* and the solitary coral *Trochocyathus calcitrapa.* The greensand beds were partly rather loose and partly forming indurated beds. Distinct cross bedding in the greensand was observed in a part of the exposure at the corner of Gemmas Allé in 1992, between 210 and 225 cm above the base of the Selandian (Claus Heilmann-Clausen, personal communication 2014).

In one of the measured sections the greensand also included a few centimetres of a black clay or marl, similar to the typical 'sorte ler' (black clay) which has previously been found and described from the lower Selandian deposits of the Copenhagen area, e.g. at the classical site of Vestre Gasværk (Rosenkrantz 1930; Milthers 1935). At Gemmas Allé, the macrofossils in the black clay layer are crushed due to Pleistocene glacial deformation because this incompetent layer acted as a kind of lubricant during dislocation of the Selandian and Pleistocene strata in the top part of the sequence. Similar glacial deformation was also evident at the Vestre Gasværk locality. Though mostly crushed, the early Selandian species in the black clay at Gemmas Allé were readily identifiable and showed a very diverse early Selandian invertebrate fauna (table 3 in Schnetler 2001).

Quaternary deposits

The Pleistocene strata comprise three different Late Weichselian tills and at least two horizons of meltwater deposits, the lower one (above the lowermost Weichselian till) being developed as a typical 'amber-and-twigs-layer' (Danish 'rav-pindelag'). These are meltwater sands or gravels with abundant Baltic amber plus various plant remains, probably of both Late Tertiary (Neogene) and Pleistocene age. Amber-and-twigs-layers have been found in several localities in the Greater Copenhagen area as for example Valby Bakke, Vestre Gasværk, Frihavnen and Ordrup as well as the recent excavation at Nørreport Station in Central Copenhagen (see e.g. Milthers 1935; Berthelsen 1995; Ørestadsselskabet I/S 2001).

Description of the tooth

The tooth was found in a bulk sample collected in 1994 by Palle Gravesen and Sten Lennart Jakobsen, Natural History Museum of Denmark. However, it was first discovered in 2013 by the amateur geologist Mogens Madsen, Fredericia, by acid dissolution of the collected material. The tooth is declared Danekræ (DK-734) and is stored in the collection of the Natural History Museum of Denmark (MGUH-30862).

The preserved tooth crown has a basoapical height of 20.4 mm and a basal maximum width of 14.5 mm (Fig. 3). A large, basoapically oriented crack in the enamel divides the tooth crown on the lingual side and continues also labially. Two other cracks are visible around the tooth, disturbing also the mesial

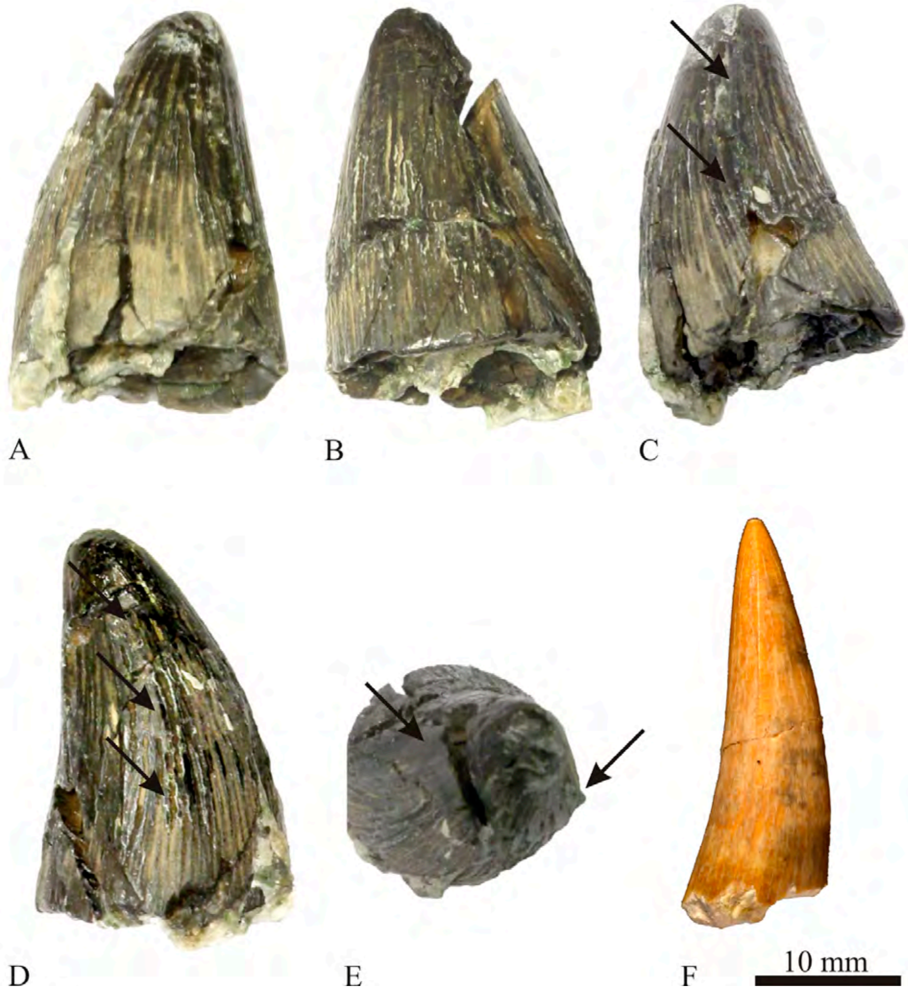

Fig. 3. Isolated crocodylian tooth from the basal conglomerate of the Lellinge Greensand Formation (Middle Paleocene) (MGUH-30862), **A**: Lingual view. **B**: Labial view. **C**: Mesial view. **D**: Distal view. **E**: In apical aspect. The weak carina (cutting edge) is visible in the mesial, distal and apical views, indicated by arrows. **F**: Thoracosaurid tooth from the Middle Danian of Faxe Quarry for comparison. Photos **A**–**E** by Heinrich Mallison. Photo **F** by Sten Lennart Jakobsen.

and distal carina. The cracks expose the underlying dentine.

The tooth crown is conical and blunt in habitus. The base of the tooth crown is circular, and the apex is narrowly rounded. The tooth crown is only very slightly labiolingually compressed and very slightly curved along the axis of its length. The lingual side of the tooth crown is slightly less convex than the labial side. Visible, but weak, carinae are present both on the medial and the distal side. The carinae start directly dorsally to the base of the tooth crown and fade ventrally towards its apex. The carinae are smooth and separated from the rest of the striated enamel only by their greater height and overall smoothness. The apex of the tooth crown is slightly worn, with the outermost layer of the enamel chipped off.

Both on the labial and on the lingual sides the enamel is strongly striated. This striation is produced by a pattern of deep grooves or flutes in the enamel. The numerous grooves extend straight from the base of the tooth crown until its apical part. Due to the tapering of the tooth crown, some of the grooves become wedged into the surrounding ones ending between them, but none of them swerve laterally to reach the carinae. The striae end lingually at the dorsal fifth of the tooth crown, but labially extend slightly higher, into the dorsal sixth of the crown.

Discussion and systematic assignment

The rounded cross section of the basis of the tooth crown together with the presence of weak, unserrated carinae and the striation of the enamel demonstrate that the isolated tooth belongs to a crocodyliform (Fig. 3). Secondary criteria for this assignment is the size of the tooth crown and its Middle Paleocene age (Selandian basal conglomerate), which excludes the marine reptiles such as sauropterygians or mosasaurs. Morphologically, the tooth can be characterised as rather generalistic, showing no specific dietary adaptations and lacking unambiguous features that would allow a closer taxonomic assignment. Determination of the tooth is also hampered by the overall rareness of Paleocene crocodylians in Europe (Efimov & Yarkov 1993; Buscalioni *et al*. 2003; Delfino *et al*. 2005; Buscalioni & Vullo 2008; Martin & Delfino 2010). Non-eusuchian crocodyliforms are not known from Europe after the Maastrichtian, and all known crocodyliforms of the Paleocene of Europe belong to Eusuchia (Buscalioni *et al*. 2003; Martin & Delfino 2010).

The sparse Scandinavian fossil record of Paleocene crocodylians comprises *Thoracosaurus* from the Danian limestone of the Limhamn quarry in southern Sweden (Lundgren 1890; Troedsson 1923, 1924), and skeletal fragments and loose teeth of possible thoracosaurid affinities from the Danian of the Faxe quarry, Denmark (Bendix-Almgreen 1972; Bonde *et al*. 2008). However, crocodylian bite traces, *Nihilichnu*s, in a turtle carapace fragment from the Faxe quarry (Milàn *et al.* 2011) suggest the presence of a crocodylian with more robust jaws than the extreme long, narrow and delicate jaws of *Thoracosaurs* which are unsuited for a chelonivorous diet.

Comparisons of the described tooth with non-eusuchian mesoeucrocodylians from the latest Cretaceous of Europe yield no similarities, and a taxonomic assignment to dyrosaurids (Buffetaut & Lauverjat 1978), *Doratodon* (Buffetaut 1979, 1980; Company *et al*. 2005), *Ischyrochampsa* (Vasse 1995), or *Theriosuchus* (Martin *et al*. 2010) can be excluded by differences in tooth morphology. The overall morphological similarity of the tooth from Gemmas Allé to those of the thalattosuchian *Machimosaurus* (Krebs 1967, 1968; Buffetaut 1982) is a convergence, because the youngest occurrence of *Machimosaurus* extends only as far as to the Early Cretaceous (Valanginian, Cornée & Buffetaut 1997). The stratigraphic age of the described specimen also strongly suggests its affiliation with the Eusuchia.

Among Late Cretaceous and Early Paleocene eusuchian crocodylians of Europe, *Thoracosaurus* is the only better known taxon from Scandinavia. The teeth of *Thoracosaurus scanicus* (= *Th. macrorhynchus*, Brochu 2004) from the Danian in Limhamn quarry (Troedsson 1924) differ from the described specimen by their more slender and acute, conical shape and differences in the striation pattern (Fig. 3F). *Thoracosaurus* teeth have a different ratio between crown height and basal width (between 1.9 and 3.3 in *Th. macrorhynchus* (Koken 1888; Troedsson 1924; Laurent *et al*. 2000; Brochu 2004) as compared to 1.4 in the specimen from Gemmas All*é*. The described tooth differs in its stouter morphology also from the teeth of other contemporary gavialoid crocodylians (Brochu 2004; Delfino *et al*. 2005) and it cannot be assigned to this group. Isolated crocodylian teeth from the Danian limestone at Limburg, Holland, are all referred to *Thoracosaurus* (Jagt *et al*. 2013); however one of them shows a much broader, stouter conical shape than typical *Thoracosaurus* teeth (Jagt *et al*. 2013, fig 19a).

Asiatosuchus should also be considered as a potential candidate for the bearer of the tooth. *Asiatosuchus* is primarily known from Asia (Mook 1940; Angielczyk & Gingerich 1998), but it has also been identified from the Paleocene of Russia (Efimov & Yarkov 1993) and from the Eocene locality of Messel in Germany (Berg 1966; Rossmann & Blume 1999). The teeth of *Asiatosuchus* generally have tooth crowns similar in shape to the tooth from Gemmas All*é*. However, they differ from the latter by the lateral expansion of the enamel striae onto the distinct carinae, which gives them a serrated appearance (Berg 1966; Angielczyk & Gingerich 1998) that is clearly absent in the specimen from Gemmas Allé.

Turning to late Cretaceous forms, the only other Scandinavian crocodylian is *Aigialosuchus villandensis.* This species was erected on the basis of fragmentary remains of the rostrum and preorbital region from the Campanian deposits at Blaksudden, Ivö, Sweden (Persson 1959). *Aigialosuchus* is a problematic taxon in need of revision (Martin & Delfino 2010). As pointed out by Martin & Delfino (2010), the contribution of the nasal to the posterior margin of the external naris in *Aigialosaurus* makes incorporation of this taxon into Gavialoidea unlikely. Its anatomical affinities could even place *Aigialosaurus* within the tomistomime Crocodyloidea, although the taxon then would be much older than the latter clade (Piras *et al.* 2007). Until a thorough taxonomic revision of this material is carried out, the systematic position of *Aigialosaurus* within the Crocodylomorpha will remain unclear. Although stratigraphically younger, the isolated tooth from Gemmas All*é* resembles in many aspects the description and figures of *Aigialosuchus villandensis* as "short, stout and slightly recurved; ... densely striated in an apico-basal direction and exhibit only slight indications of anterior and posterior carinal crests" (Persson 1959: p. 473). However, without a personal examination of the remains of *Aigialosaurus* by the first author, and considering the limited quality of the figures and data in Persson (1959), no certain assignment of the tooth from Gemmas All*é* to this taxon can be made at this point.

Among the late Cretaceous eusuchians from Europe, the alligatoroid *Acynodon* can be excluded because of its peculiar tooth morphology. Teeth of *Acynodon* are either slender and possessing a distinct carina, or slightly bulbous with striations which are replaced by a pattern of pustules on the enamel (Buscalioni *et al*. 1997; Martin 2007; Delfino *et al*. 2008b). The teeth of *Arenysuchus* from the Maastrichtian of Spain (Puértolas *et al*. 2011) are morphologically very similar to the tooth from Gemmas Allé. They differ mainly by their general lack of a striation pattern and a slightly lower crown height.

Overall morphological similarities to the described tooth are also present in other alligatoroid teeth from the late Cretaceous of Europe. *Allodaposuchus* teeth from southern Europe (Buscalioni *et al*. 2001; Delfino *et al*. 2008a; Martin 2010) seem to display a weaker pattern of striation, but stronger carinae than in the described tooth. *Musturzabalsuchus* from Spain (Buscalioni *et al*. 1997; Company *et al*. 2005) seems to possess teeth of both similar habit and striation in the posterior part of the dentary. However, the description and the figures are too poor to allow a certain assignment without personal examination of the material. Finally, from southern France, *Massaliasuchus* seems to possess rather identical teeth in the posterior part of maxilla and dentary (Martin & Buffetaut 2008). However, the description and illustrations of this material are of insufficient quality for a detailed comparison.

Because of the overall morphological similarity to some alligatoroid taxa, and because the alligatoroids are the most frequent crocodylians in the Upper Cretaceous deposits of Europe (Martin & Delfino 2010), we consider an assignment of the tooth from Gemmas Allé to the Alligatoroidea as the most plausible. However, the assignment is clearly uncertain.

Conclusion

The morphology and stratigraphic age (earliest Middle Paleocene) of the tooth from Gemmas Allé indicate that the specimen belongs to a eusuchian crocodyliform with a rather generalistic dentition. A more precise taxonomic assignment is extremely difficult as it is not known whether the striation pattern of the enamel is diagnostic or should be regarded as an acccidential variation. Two possibilities appear for a taxonomic assignment: 1), the tooth belongs to *Aigialosuchus*, a longirostrine eusuchian of uncertain systematic affinity, or 2), the tooth belongs to a member of the Alligatoroidea. The Alligatoroidea are the most common crocodylians in the Upper Cretaceous deposits of Europe. They form a highly diverse group including both more generalistic forms (*Allodaposuchus* or *Massaliasuchus*) and more specialized forms (*Acynodon)*. Gavialoid crocodylians and in particular *Thoracosaurus*, can be excluded because of their deviating tooth morphology.

Regardless of its assignments, the tooth from Gemmas Allé is interesting in a stratigraphic context, as it constitutes one of the few Danian/Selandian records of crocodylians in Europe in general and in Scandinavia in particular. Together with body and trace fossil evidence from the Faxe quarry, the tooth demonstrates the existence of at least one other crocodylian taxon than *Thoracosaurus* in the Early and Middle Paleocene of Scandinavia. It clearly demonstrates that this part of the Paleocene of Northern Europe must have accommodated a more diverse crocodylian fauna than hitherto known.

Acknowledgements

We are grateful to Sten Lennart Jakobsen for help with photos of the now lost locality. Mogens Madsen is thanked for his work with dissolving the conglomerate and finding the tooth. Heinrich Mallison, Museum Für Naturkunde, Berlin, kindly provided detailed photos of the tooth. Inken Mueller-Töwe, Naturstyrelsen, provided location maps. Finn Surlyk provided useful discussion of the stratigraphy. The critical and constructive reviews by Claus Heilmann-Clausen and Erik Thomsen greatly helped to improve the manuscript.

References

Angielczyk, K.D. & Gingerich, P.D. 1998: New specimen of cf. *Asiatosuchus* (Crocodyloidea) from the Middle Eocene Drazinda Formation of the Sulaiman Range, Punjab (Pakistan). Contributions from the Museum of Paleontology, The University of Michigan 30, 163–189.

Bendix-Almgreen, S.E. 1972: Kæmpeøgler i Danmark?. VARV 1972(3), 66–73.

Berg, D.E. 1966: Die Krokodile, insbesondere *Asiatosuchus* und aff. *Sebecus*?, aus dem Eozän von Messel bei Darmstadt/ Hessen. Abhandlungen des Hessischen Landesamtes für Bodenforschung 52, 1–105.

Berthelsen, O. 1962: Cheilostome Bryozoa in the Danian Deposits of East Denmark. Danmarks Geologiske Undersøgelse, II. Række 83, 290 pp.

Berthelsen, O. 1995: Fra det nordlige Sokkelund. Noget om geologi, teglværker, grusgravning og tørveskæring i Søllerød, Lyngby-Taarbæk, Gentofte og Gladsaxe kommuner. 71 pp, Danmarks og Grønlands Geologiske Undersøgelse, Miljø- og Energiministeriet.

Bonde, N., Andersen, S., Hald, N. & Jakobsen, S.L. 2008: Danekræ - Danmarks bedste fossiler, 226 pp. Copenhagen: Gyldendal.

Brochu, C.A. 2004: A new Late Cretaceous gavialoid crocodylian from eastern North America and the phylogenetic relationships of thoracosaurs. Journal of Vertebrate Paleontology 24, 610–633.

Buffetaut, E. 1979: Revision der Crocodylia (Reptilia) aus den Gosau-Schichten (Ober-Kreide) von Österreich. Beiträge zur Paläontologie von Österreich 6, 89–105.

Buffetaut, E. 1980: Crocodilians from the continental Upper Cretaceous of Europe: New finds and interpretations. Mesozoic Vertebrate Life 1, 5–14.

Buffetaut, E. 1982: Le crocodilien *Machimosaurus* von Meyer (Mesosuchia, Teleosauridae) dans le Kimmeridgien de l'Ain. Bulletin trimestre de la Société Géologique de la Normandie et Amis du Muséum du Havre LXIX, 17–26.

Buffetaut, E. & Lauverjat, J. 1978: Un Crocodilien d'un type particulier dans le Cénomanien de Nazarè. Comptes Rendus Sommaire des Seances de la Societe geologique de France 1978, 79–82.

Buscalioni, A.D. & Vullo, R. 2008: Three steps in the Cretaceous evolution of crocodylomorpha: example from Barremian to Maastrichtian diversity in the Iberian Peninsula, and what about mid-Cretaceous gap? In: Mazin, J.-M., Pouech, J., Hantzpergue, P. & Lacombe, V. (eds), Mid-Mesozoic Life and Environments. Documents des Laboratoires de Géologie de Lyon 164, 29–32.

Buscalioni, A.D., Ortega, F. & Vasse, D. 1997: New crocodiles (Eusuchia: Alligatoroidea) from the Upper Cretaceous of southern Europe. Comptes Rendu de l'Academie des Sciences, Paris, Sciences de la Terre et des Planètes 325, 525–530.

Buscalioni, A.D., Ortega, F., Weishampel, D.B. & Jianu, C.M. 2001: A revision of the crocodyliform *Allodaposuchus precedens* from the Upper Cretaceous of the Hateg Basin, Romania. Its relevance in the phylogeny of Eusuchia. Journal of Vertebrate Paleontology 21, 74–86.

Buscalioni, A.D., Pérez-Moreno, B.P. & Sanz, J.L. 2003: Pattern of biotic replacement in modern crocodiles during the Late Cretaceous. Coloquios de Paleontología 1, 77–93.

Christiansen, N. 2007: The Fauna of the Lellinge Greensand in the Hedeland area. Unpublished M.Sc. thesis, University of Copenhagen, 101 pp.

Clemmensen, A. & Thomsen, E. 2005: Palaeoenvironmental changes across the Danian–Selandian boundary in the North Sea Basin. Palaeogeography, Palaeoclimatology, Palaeoecology 219, 351–394.

Company, J., Superbiola, X.P., Ruiz-Omeñaca, J.I. & Buscalioni, A.D. 2005: A new species of Doratodon (Crocodyliformes: Ziphosuchia) from the Late Cretaceous of Spain. Journal of Vertebrate Paleontology 25, 343–353.

Cornée, J.-J. & Buffetaut, E. 1997: Découverte d'un Téléosauridé (Crocodylia Mesosuchia) dans le Valanginien supérieur du massif d'Allauch (sud-est de la France). Comptes Rendu de l'Academie des Sciences, Paris, Sèrie D 288, 1151–1154.

Deecke, W. 1899: Ueber eine als Diluvialesgeschiebe vorkommende Paleocäne Echinodermenbrecchie. Mitteilungen des Naturwissenschaftlichen Vereins für Vorpommern und Rügen 31, 67–76.

Delfino, M., Piras, P. & Smith, T. 2005: Anatomy and phylogeny of the gavialoid crocodylian Eosuchus lerichei from the Paleocene of Europe. Acta Palaeontologica Polonica 50, 565–580.

Delfino, M., Codrea, V., Folie, A., Dica, P., Godefroid, P. & Smith, T. 2008a: A complete skull of Allodaposuchus precedens Nopsca, 1928 (Eusuchia) and a reassessment of the morphology of the taxon based on the Romanian remains. Journal of Vertebrate Paleontology 28, 111–122.

Delfino, M., Martin, J.E. & Buffetaut, E. 2008b: A new species of *Acynodon* (Crocodylia) from the Upper Cretaceous (Santonian–Campanian) of Villaggio del Pescatore, Italy. Palaeontology 51, 1091–1106.

Efimov, M.B. & Yarkov, A.A. 1993: A Paleocene crocodile from the lower Volga Basin. Paleontological Journal 27, 114–118.
Franke, A. 1927: Die Foraminiferen und Ostracoden des Palaeocäns von Rugaard in Jütland und Sundkrogen bei Kopenhagen. Danmarks Geologiske Undersøgelse, II. Række 46, 49 pp.
Gravesen, P. 1993. Fossiliensammeln in Südskandinavien. 248 pp. Weinstadt: Goldschneck-Verlag.
Gravesen, P. 1994: Udgravningerne til Øresundsforbindelsen ved Tårnby på Amager 1994 – en kort beskrivelse. Lapidomanen 1994, 5pp.
Gravesen, P., & Jakobsen, S.L. 2012: Skrivekridtets Fossiler. 154 pp. Copenhagen: Gyldendal.
Grönwall, K.A. 1904: Forsteningsførende Blokke fra Langeland, Sydfyn og Ærø samt bemærkninger om de ældre Tertiærdannelser i det baltiske område. Danmarks Geologiske Undersøgelse, II. Række 15, 62 pp.
Gry, H. 1935: Petrology of the Paleocene sedimentary rocks of Denmark. Danmarks Geologiske Undersøgelse, II. Række 61, 171 pp.
Harder, P. 1922: Om Grænsen mellem Saltholmskalk og Lellinge Grønsand og nogle Bemærkninger om Inddelingen af Danmarks ældre Tertiær. Danmarks Geologiske Undersøgelse, II. Række 38, 108 pp.
Heilmann-Clausen, C., & Surlyk, F. 2006: Koralrev og Lerhav. In: Sand-Jensen, K. & Larsen, G. (eds), Naturen i Danmark, Geologien, 181–226. Copenhagen: Gyldendal.
Hucke-Voigt, K. 1967: Einführung in die Geschiebeforschung. (Sedimentärgeschiebe). Herausgegeben und erweitert von E. Voigt, 132 pp. Oldenzaal: Nederlandse Geologische Stichting.
Jagt, J.W.M., van Bakel, B.W.M., Cremers, G., Deckens, M.J.M., Dortangs, R.W., van Es, M., Fraaije, R.H.B., Kisters, P.J.M., van Knippenberg, P.H.M., Lemmens, H., Nieuwenhuis, E., Severijns, J. & Stroucken, J.W. 2013: Het Vroeg Paleoceen (Danien) van zuidelijk Limburg en aangrenzend gebied – nieuwe fauna´s en nieuwe inzichten. Afzettingen WTKG 34, 198–230.
Koken, E. 1888: *Thoracosaurus macrorhynchus* Bl. aus der Tuffkreide von Maastricht. Zeitschrift der Deutschen Geologischen Gesellschaft 40, 754–773.
Krebs, B. 1967: Der Jura-Krokodilier *Machimosaurus* H. v. Meyer. Paläontologische Zeitschrift 41, 46–59.
Krebs, B. 1968: Le crocodilien *Machimosaurus*. Memória dos Servicos Geológicos de Portugal (N.S.) 14, 21–53.
Laurent, Y., Buffetaut, E., & Le Loeuff, J. 2000: Un crane de thoracosaurine (Crocodylia, Crocodylidae) dans le Maastrichtien superieur du sud de la France. Oryctos 3, 19–27.
Lundgren, B. 1890: Ein Gavial aus dem Senon von Annetorp bei Malmö. Neues Jahrbuch für Mineralogie, Geologie und Paläontologie 2, 275.
Martin, J.E. 2007: New material of the Late Cretaceous globidontan *Acynodon iberoccitanus* (Crocodylia) from southern France. Journal of Vertebrate Paleontology 27, 362–372.
Martin, J.E. 2010: *Allodaposuchus* Nopsca, 1928 (Crocodylia, Eusuchia), from the Late Cretaceous of southern France and its relationships to Alligatoroidea. Journal of Vertebrate Paleontology 30, 756–767.
Martin, J.E. & Buffetaut, E. 2008: *Crocodilus affuvelensis* Matheron, 1969 from the Late Cretaceous of southern France: a reassessment. Zoological Journal of the Linnean Society 152, 567–580.
Martin, J.E. & Delfino, M. 2010: Recent advances in the comprehension of the biogeography of Cretaceous European eusuchians. Palaeogeography, Palaeoclimatology, Palaeoecology 293, 406–418.
Martin, J.E., Rabi, M. & Csiki, Z. 2010: Survival of *Theriosuchus* (Mesoeucrocodylia: Atoposauridae) in a Late Cretaceous archipelago: a new species from the Maastrichtian of Romania. Naturwissenschaften 97, 845–854.
Milàn, J., Lindow, B.E.K. & Lauridsen, B.W. 2011: Bite traces in a turtle carapace fragment from the middle Danian (Lower Paleocene) bryozoan limestone, Faxe, Denmark. Bulletin of the Geological Society of Denmark 59, 61–67.
Milthers, V. 1935: Nordøstsjællands Geologi. 2. edition. Danmarks Geologiske Undersøgelse, V. Række 3, 192 pp.
Mook, C.C. 1940: A new fossil crocodilian from Mongolia. American Museum Novitates 1097, 1–3.
Ørestadsselskabet I/S 2001: Metro. Gangtunnel ved Nørreport. Geologi. Datering af sand. Ravpindelag. Report by Cowi Consult, 5 pp. + appendices.
Persson, P.O. 1959: Reptiles from the Senonian (U. Cret.) of Scania (S. Sweden). Arkiv för Mineralogi och Geologi 2, 431–478.
Piras, P., Delfino, M., Favero, L.D. & Kotsakis, T. 2007: Phylogenetic position of the crocodylian *Megadontosuchus arduini* and tomistomine palaeobiogeography. Acta Palaeontologica Polonica 52, 315–328.
Puértolas, E., Canudo, J.I. & Cruzado-Caballero, P. 2011: A New Crocodylian from the Late Maastrichtian of Spain: Implications for the initial radiation of Crocodyloids. PLOS One 6, 1–12.
Ravn, J.P.J. 1939: Études sur les mollusques du Paléocène de Copenhague. Det Kongelige Danske Videnskabernes Selskab Biologiske Skrifter 1(1), 106 pp.
Rees, J. 2000: An Early Cretaceous scincomorph lizard dentary from Bornholm, Denmark. Bulletin of the Geological Society of Denmark 48, 105–109.
Rees, J. 2002: Shark fauna and depositional environment of the earliest Cretaceous Vitabäck Clays at Eriksdal, southern Sweden. Transactions of the Royal Society of Edinburgh, Earth Sciences 93, 59–71.
Reinecke, T. & Engelhard, P. 1997: The Selachian Fauna from Geschiebe of the Lower Selandian Basal Conglomerate in the Danish Subbasin. Erratica, Monographien zur Geschiebekunde 2, 32 pp.
Rohde, A. 2008: Auf Fossiliensuche an der Ostsee. 272 pp. Neumünster: Wachholtz Verlag.

Rørdam, K. 1897: Kridtformationen i Sjælland i Terrænet mellem København og Køge, og paa Saltholm. Avec Résumé en francais. Danmarks Geologiske Undersøgelse, II. Række 6, 152 pp.

Rørdam, K. 1899: Beskrivelse til Kaartbladene Kjøbenhavn og Roskilde i 1:100 000. Danmarks Geologiske Undersøgelse, I. Række 6, 107 pp. + plates.

Rosenkrantz, A. 1920a: Craniakalk fra Kjøbenhavns Sydhavn. Danmarks Geologiske Undersøgelse, II. Række 36, 79 pp.

Rosenkrantz, A. 1920b: En ny københavnsk Lokalitet for forsteningsførende Paleocæn. Meddelelser fra Dansk Geologisk Forening 5, 1–10.

Rosenkrantz, A. 1924: De københavnske Grønsandslag og deres Placering i den danske Lagrække. Meddelelser fra Dansk Geologisk Forening 6, 1–39.

Rosenkrantz, A. 1925. Undergrundens tektoniske Forhold i København og nærmeste Omegn. Meddelelser fra Dansk Geologisk Forening 6, 1–18.

Rosenkrantz, A. 1930: Den paleocæne Lagserie ved Vestre Gasværk. Meddelelser fra Dansk Geologisk Forening 7, 371–390.

Rosenkrantz, A. 1937: Bemærkninger om det østsjællandske Daniens Stratigrafi og Tektonik. Meddelelser fra Dansk Geologisk Forening 9, 199–212.

Rosenkrantz, A. 1942: Om de strukturelle Forhold i den prækvartære Undergrund i Østsjælland. Meddelelser fra Dansk Geologisk Forening 10, 152–158.

Rossmann, T. & Blume, M. 1999: Die Krokodil-Fauna der Fossillagerstätte Grube Messel: Ein aktueller Überblick. Natur und Museum 129, 261–270.

Rudolph, F., Bilz, W., & Pittermann, D. 2010: Fossilien an Nord- und Ostsee. 283 pp. Wiebelsheim: Quelle & Meyer.

Schmitz, B., Pujalte, V., Molina, E., Monechi, S. Orue-Etxebarria, X., Speijer, R.P., Alegrat, L., Apellaniniz, E., Arenillas, I., Aubry, M.-P., Baceta, J.-I., Berggren, W.A., Bernaola, G., Caballero, F., Clemmensen, A., Dinarés-Turell, J., Dupais, C., Heilmann-Clausen, C., Orús, A.H., Knox, R., Martin, R.M., Ortiz, S., Payros, A., Petrizzo, M.R., Salis, K., Sprong, J., Steurbbaut, E., & Thomsen, E. 2011: The Global Stratotype Sections and Points for the bases of the Selandian (Middle Paleocene) and Thanetian (Upper Paleocene) stages at Zumaia, Spain. Episodes 34, 220–243.

Schnetler, K.I. 2001: The Selandian (Paleocene) mollusc fauna from Copenhagen, Denmark: the Poul Harder 1920 collection. Danmarks og Grønlands Geologiske Undersøgelse (GEUS), Bulletin 37, 73 pp.

Schulz, W. 2003: Geologischer Führer für den norddeutschen Geschiebesammler. Cw Verlagsgruppe, Schwerin, 507 pp.

Schwarz-Wings, D., Rees, J. & Lindgren, J. 2009: Lower Cretaceous Mesoeucrocodylians from Scandinavia (Denmark and Sweden). Cretaceous Research 30, 1345–1355.

Schwarzhans, W. 2003: Fish otoliths from the Paleocene of Denmark. Geological Survey of Denmark and Greenland Bulletin 2, 94 pp.

Stenestad, E. 1976: Københavnsområdets geologi især baseret på citybaneundersøgelserne. Danmarks Geologiske Undersøgelse, III. Række 45, 149 pp.

Stouge, S., Hjortkjær, B.F., Rasmussen, J.A., Roncaglia, L. & Sheldon, E. 2000: Micro- and nannofossil biostratigraphy across the Danian/Selandian Stage boundary at Gemmas Allé, Copenhagen, Denmark. GFF 122, 161–162.

Troedsson, G.T. 1923: Om krokodilfyndan i Skånes yngsta Krita. GFF 45, 549–567.

Troedsson, G.T. 1924: On crocodilian remains from the Danian of Sweden. Lunds Universitets Årsskrift 2, 20, 1–75.

Vasse, D. 1995: *Ischyrochampsa meridionalis* n. g. n. sp., un crocodilien d'affinité gondwanienne dans le Crétacé supérieur du Sud de la France. Neues Jahrbuch für Geologie und Mineralogie, Monatshefte 1995, 501–512.