

Two new finds of turtle remains from the Danian and Selandian (Paleocene) deposits of Denmark with evidence of predation by crocodylians and sharks

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Two new fragments of a turtle carapace and a turtle plastron (hypoplastron) have been recovered from glacially transported boulders of Danian and Selandian age. The hypoplastron is identified as *Ctenochelys* cf. *stenoporus*, while the carapace fragment can only be assigned to the family Cheloniidae indet. Both specimens show evidence of predation by crocodylians in the form of rows of circular pits in the bones, and one specimen has rows of elongated scrape traces interpreted as scavenging by sharks. Together with the other, rare finds from the middle Danian of the Faxe Quarry and from late Danian deposits in the Copenhagen area, these new finds add important new knowledge to the sparse fossil record of turtles in Scandinavia, as well as evidence that the genus *Ctenochelys* survived across the K/Pg Boundary.

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Turtle remains are very rare in the Cretaceous and Paleocene chalk, limestone and marl deposits in Denmark and southern Scandinavia, and are restricted to a few incomplete finds which are hard to identify to higher taxonomic levels. Historically, turtles are known from a collection of carapace fragments from the upper Danian København Limestone Formation and the Selandian Lellinge Greensand Formation found in excavations in Copenhagen (Dames 1897; Rosenkrantz 1920, 1921, 1923). A recent revision of this material identified parts of it as *Rafetoides henrici* (Owen & Bell 1849), while the rest belongs to the order Testudines gen. et sp. indet. (Karl & Lindow 2012). Additional material has been found in the middle Danian Faxe Formation of the Faxe quarry and consists of two carapace fragments assignable to Chelonioida indet. (Milàn *et al.* 2011; Adolffsen *et al.* 2017). Three peripheral elements from the carapace of a marine turtle of the family Cheloniidae are known from the upper Maastrichtian limestone of the Møns Klint Formation (Surlyk *et al.* 2013) at Stevns Klint (Karl &

Lindow 2009). This study describes two new finds of turtle fragments in glacially transported boulders from respectively Jyske Rev (the Jutland Bank) and the Gundstrup gravel pit (Fig. 1), identifies them to the highest possible taxonomic level and discusses their taphonomic history.

Material and Methods

The oldest specimen studied consists of a turtle carapace fragment embedded in typical light grey, Danian bryozoan limestone. The specimen was found at the harbour of Esbjerg in a rock pile, which was extracted from the seafloor at Jyske Rev of the North Sea (approximately 57.0°N, 07.7°E; Fig. 1). It is assumed that it was transported from nearby Danian deposits during the last glaciation (Leth 1996; Larsen *et al.* 2009; Jensen *et al.* 2010). The second and youngest specimen consists of an almost complete hypoplastron fragment and a

caudal vertebra, which were found in a boulder (32×16 cm) of Selandian Kerteminde Marl retrieved from glacial deposits in the Gundstrup gravel pit, northern Fyn at 55.56°N, 10.35°E. The Kerteminde Marl Formation is exposed at the nearby coastal cliffs south of Kerteminde on eastern Fyn (Fig. 1). Both specimens are declared Danekræ, national fossil trove (DK-794 and DK-779, respectively) and are stored in the collection of the Natural History Museum of Denmark (NHMD 227324 and 227325).

The plastron fragment NHMD 227325 was compared visually with Late Cretaceous and Paleocene turtles to find overall morphological matches. Subsequently, diagnostic morphological characters used to discriminate between different testudine families and genera were studied (see e.g. Hirayama 1997 and Lehman & Tomlinson 2004). Finally, a simple morphometric analysis was generated to compare selected, critical ratios in the studied plastron with published species.

Three morphometric distances (L1, L2 and L3) were measured (Fig. 2) and compared with values obtained from measurements of specimens in the literature, measured directly on the published illustrations when measurements were not stated (Table 1). The



Fig. 1. Map of Denmark with the locations of the specimens indicated. NHMD 227324 was found at Esbjerg Harbour (blue star) in a pile of rocks extracted from Jyske Rev (blue square). NHMD 227325 was found at Gundstrup gravel pit in northern Fyn (red star) and originates from the Kerteminde Marl Formation exposed in the coastal cliffs south of the town Kerteminde (red square).

two morphological ratios $R1 = L1/L3$ and $R2 = L2/L3$ were then plotted against each other. A high R1 value indicates a relatively wide and narrow hypoplastron, while a high R2 value suggests that the suture line that connected the right hypoplastron with the left hypoplastron is relatively short. In contrast to individual distance measures, ratios reflect morphological differences directly. All values were measured at their maximum values as indicated on Fig. 2.

Table 1. Length measurements and morphological ratios of late Cretaceous and Paleocene turtle hypoplastrons

	L1 (cm)	L2 (cm)	L3 (cm)	R1	R2
NHMD 227325	10.5	5.7	13.0	0.8	0.4
<i>L. natatrix</i>	4.0	3.0	5.5	0.7	0.5
<i>C. tenuitesta</i>	5.0	2.9	6.0	0.8	0.5
<i>C. stenoporus</i>	4.4	2.3	5.2	0.8	0.4
<i>C. stenopora</i>	3.5	2.0	4.0	0.9	0.5
<i>G. suyckerbuycki</i>	3.8	4.1	6.5	0.6	0.6
<i>T. latiremis</i>	2.9	1.1	3.0	1.0	0.4
<i>L. niobrarae</i>	2.1	1.3	2.5	0.8	0.5
<i>O. emarginatus</i>	1.0	0.3	0.7	1.4	0.4
<i>D. casieri</i>	0.6	0.25	0.6	1.0	0.4

For L1, L2 and L3, see Fig. 2.

$R1 = L1/L3$; $R2 = L2/L3$.

Sources of the measurements are given in Fig. 5.

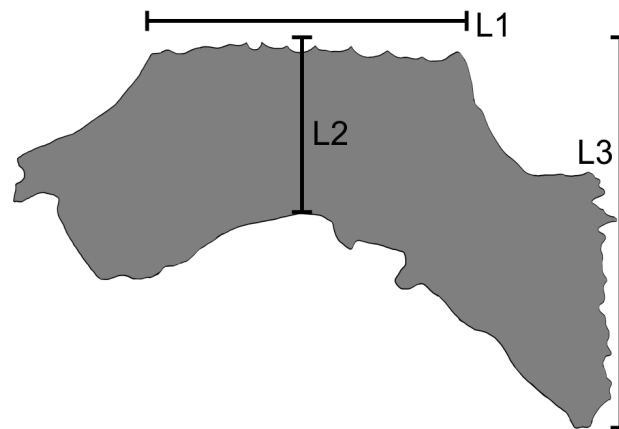


Fig. 2. Sketch of hypoplastron showing the three distances used in the analysis (L1, L2, L3).

Brief notes on the geological framework

The two turtle specimens described were found in erratic Danian and Selandian sedimentary boulders that have been eroded and transported by one or more ice sheets during the Pleistocene and subsequently mixed with Quaternary sediments.

The Danian strata of the Danish Basin are characterised by a variety of limestone types, predominantly bryozoan limestone, coccolith chalk and, in the upper part, relatively coarse skeletal packstones and grainstones. A major regression took place at the end of the Danian at about 61.6 Ma (Vandenberghe *et al.* 2012), resulting in a widespread unconformity (e.g. Thomsen & Heilmann-Clausen 1985; Clemmensen & Thomsen 2005). The succeeding Selandian transgression resulted in a very different sedimentary regime characterised by a considerably higher supply of siliciclastic material. The reasons for this are not clear, but it has been suggested that a tectonic uplift of the Scotland-Shetland Platform played a major role (Clemmensen and Thomsen 2005). Moreover, the significant drop in calcium carbonate sedimentation in the basal Selandian may be explained by the narrowing or closure of the connections to the warmer oceans towards the south, which would have caused less favourable living conditions for the organisms whose skeletons were the main source of calcium carbonate to the sediments (Clemmensen & Thomsen 2005; Heilmann-Clausen 2010).

The Danian limestones were deposited in a subtidal shelf palaeoenvironment up to a few hundred metres deep, while the overlying Selandian Kerteminde Marl Formation characterised an offshore, but shallower, inner shelf environment.

Systematic Palaeontology

The taxonomical interpretation of the superfamily Chelonioidea is still debated. Lehman & Tomlinson (2004) regarded the family Cheloniidae as the only family in the superfamily Chelonioidea, whereas Zangerl (1953) subdivided Chelonioidea into Toxochelyidae and Cheloniidae. Karl & Nyhuis (2012) followed the interpretation of Zangerl (1953). Hirayama (1997), on the other hand, subdivided Chelonioidea into the families Cheloniidae and Protostegidae. However, it was recently argued that it is highly implausible that the protostegids are crown chelonoids (Joyce *et al.* 2013). In addition, the position of the various subfamilies within the superfamily Chelonioidea is highly debated. Zangerl (1953) placed Toxochelyinae, Lophochelyinae and Osteopyginae within the family Toxochelyidea, whereas Weems (1988) placed Toxochelyinae and Lophochelyinae within Toxochelyidea, and Osteopyginae within Cheloniidae.

With regard to the overall suprageneric classification, the Converted Clade Names (CCN) suggested by Joyce *et al.* (2004) are used below.

Order Testudines Batch 1788

Suborder Cryptodira Cope 1868

Superfamily Chelonioidea Baur 1893

The superfamily Chelonioidea is the only cryptodiran group that is highly adapted to the marine environment. The fossil record of chelonoids can be traced back into the Early Cretaceous, roughly at 110 Ma. Modern chelonoids form a relatively small group comprising six genera and seven species within two families, Cheloniidae and Dermochelyidae (Hirayama 1997).

Family Cheloniidae Bonaparte 1832

Remarks. The oldest known cheloniid genera, *Toxochelys* and *Ctenochelys*, are documented from Late Cretaceous deposits of North America (Hirayama 1997).

Family Cheloniidae indet.

Figure 3A–F

Material. One specimen, NHMD 227324.

Description. The specimen is a partial pleural plate from a turtle carapace and is approximately 19 cm long and 8 cm wide (Fig. 3). The specimen is broken into four pieces that are held together in an almost anatomically correct position by the sediment (Fig. 3A, C). On the dorsal side of the bone, a shallow groove from the connection between the overlying horny scutes is visible along the midline of the plate and splits into two towards the margin of the plate (Fig. 3C, D). An unidentified flat piece of bone fused to the ventral side of the specimen probably represents a part of the appendicular skeleton.

Remarks. The incomplete specimen NHMD 227324 does not possess morphological characters that allow a more precise determination than Chelonioidea indet.

Occurrence and stratigraphical age. The specimen is from an erratic limestone boulder collected at Jyske Rev off the west coast of Jylland some 40 km west of the town Hanstholm (approximately 57.0°N, 07.7°E). Due to substantial silicification we did not observe identifiable calcareous nannoplankton specimens in the matrix, but the texture and overall nature of the bryozoan limestone demonstrate that it is Danian rather than Maastrichtian in age. Hence, the fossiliferous bryozoan limestone originates either from one of the Danian outcrops situated in the belt extending from the town of Hanstholm on the northern west coast

of Jylland across northern and central-east Jylland to eastern Sjælland (e.g. Thomsen 1995), or alternatively from Danian deposits that are exposed on the seafloor near the Jyske Rev area (Leth 1996, 2003).

Genus *Ctenochelys* Zangerl 1953

Remarks. Zangerl (1953) remarked that *Ctenochelys* and *Lophochelys* are difficult to distinguish from each other. Hirayama (1997) went one step further and was of the opinion that the species of the genus *Lophochelys* erected by Zangerl (1953), including the original type

species *Lophochelys natatrix* Zangerl, were based on poorly preserved juvenile specimens of *Ctenochelys* or *Toxochelys*, indicating that the identification of *Lophochelys* is dubious.

Ctenochelys cf. *stenoporus* (Hay 1905)

Figure 4

Material. One hypoplastron and one caudal vertebra, NHMD 227325.

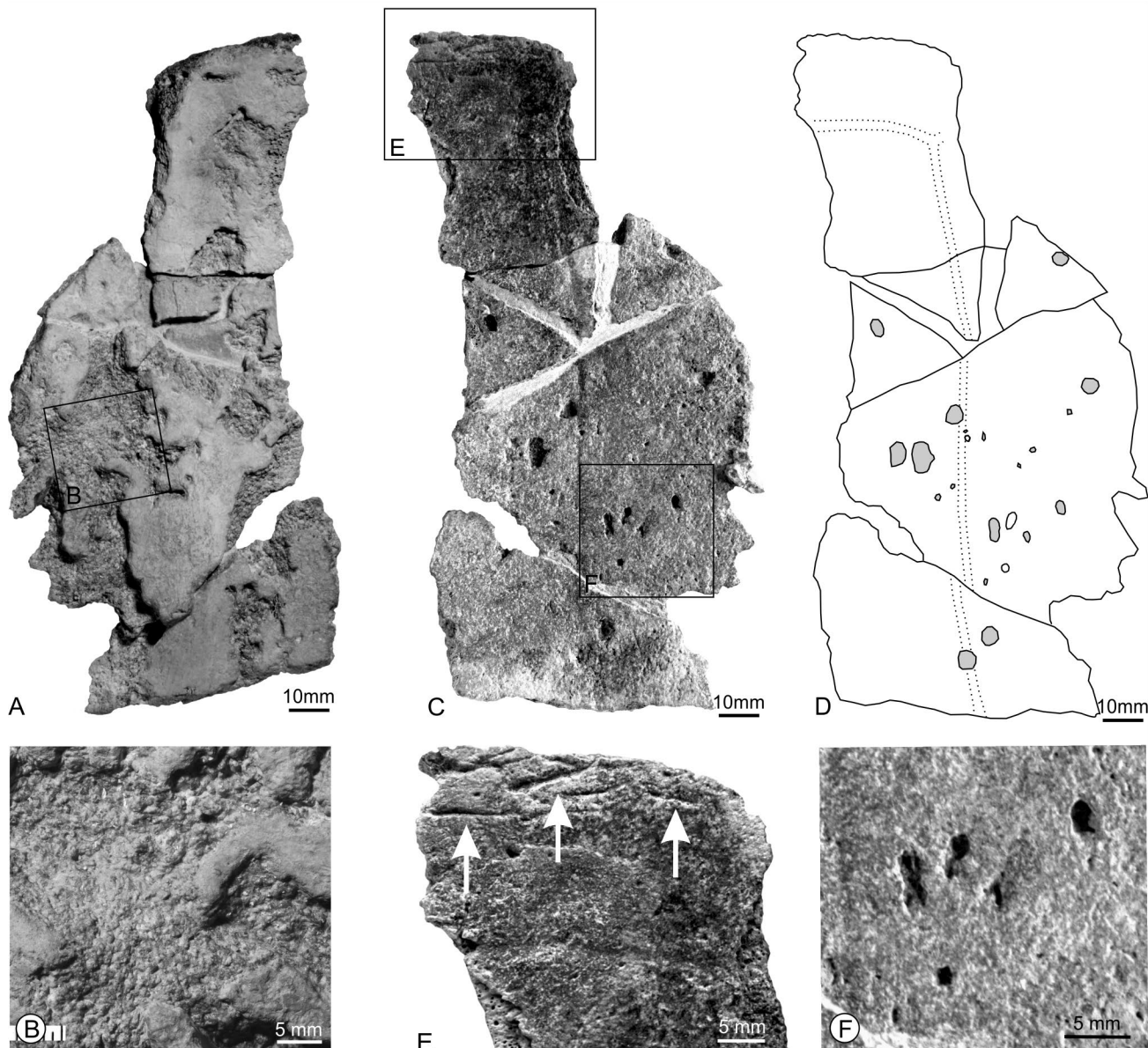


Fig. 3. Carapace fragment (NHMD 227324) with traces of bites. **A:** Ventral surface of the fragment, showing areas of bioerosion and pathologies. **B:** Close-up of the exposed parts of the spongy bone in the eroded areas. **C:** Dorsal side of the six fragments held together by sediment. **D:** Sketch of the dorsal surface showing rows of circular bite traces. The shallow groove from the contact between the overlying horny scutes is indicated. **E:** Close-up of elongated scratch traces interpreted as scavenging by sharks. **F:** Close-up of circular bite traces interpreted as predation by crocodilians.

Synonymy.

cf. 1875 *Toxochelys serrifer* n. sp. - Cope, p. 299, (Hay 1905, p. 178, figs. 1–3).

cf. 1905 *Ctenochelys stenoporus* n. sp. - Hay, pp. 180–181, figs. 8–11.

cf. 1905 *Toxochelys procax* Cope - Hay, pp. 181–182, figs. 13–14.

cf. 1908 *Toxochelys elkader* Hay - Hay, pp. 174–176, figs. 221–223.

cf. 1953 *Lophochelys natatrix* n. sp. - Zangerl, pp. 218–220, figs. 91–93.

cf. 1953 *Lophochelys venatrix* n. sp. - Zangerl, pp. 224–226, figs. 95–97.

cf. 1953 *Ctenochelys tenuitesta* n. sp. - Zangerl, pp. 227–237, figs. 99–106.

cf. 1997 *Ctenochelys stenoporus* (Hay) - Hirayama, pp. 226–227, fig. 1 (includes synonymy).

Description. The specimen is a hypoplastron preserved in a boulder of marl. Associated with the hypoplastron is a single caudal vertebra (Fig. 4). The hypoplastron is 19 cm long and roughly 6 cm wide throughout, making it much longer than wide. The suture that connected the hypoplastron to the hyoplastron is

serrated, as is the medial edge. The lateral edge is missing. The morphology of the specimen shows that this possessed a large fontanelle in the midline of the plastron (Fig. 4B).

Discussion. Because of the incomplete nature of many of the holotypes of previously erected *Ctenochelys* species, all known *Ctenochelys* species were synonymised by Hirayama (1997), resulting in a single species, *C. stenoporus*. Moreover, Hirayama (1997) regarded *Lophochelys natatrix* as a synonym of *Ctenochelys stenoporus* and *Lophochelys niobrarae* as a synonym of *Toxochelys latiremis*. This interpretation is followed here.

In the morphometric plot (Fig. 5), NHMD 227325 is situated very close to *Ctenochelys stenoporus* (including its junior synonyms *C. tenuitesta* and *Lophochelys natatrix*) and *L. niobrarae*, which indicates that these four taxa have a similar shape of the hypoplastron. This is in support of the taxonomical interpretation by Hirayama (1997) and suggests that NHMD 227325 belongs to *Ctenochelys stenoporus* or a closely related descendant of this species. Because of the incomplete material and the ensuing uncertainty, however, we have chosen to use open nomenclature, and specimen

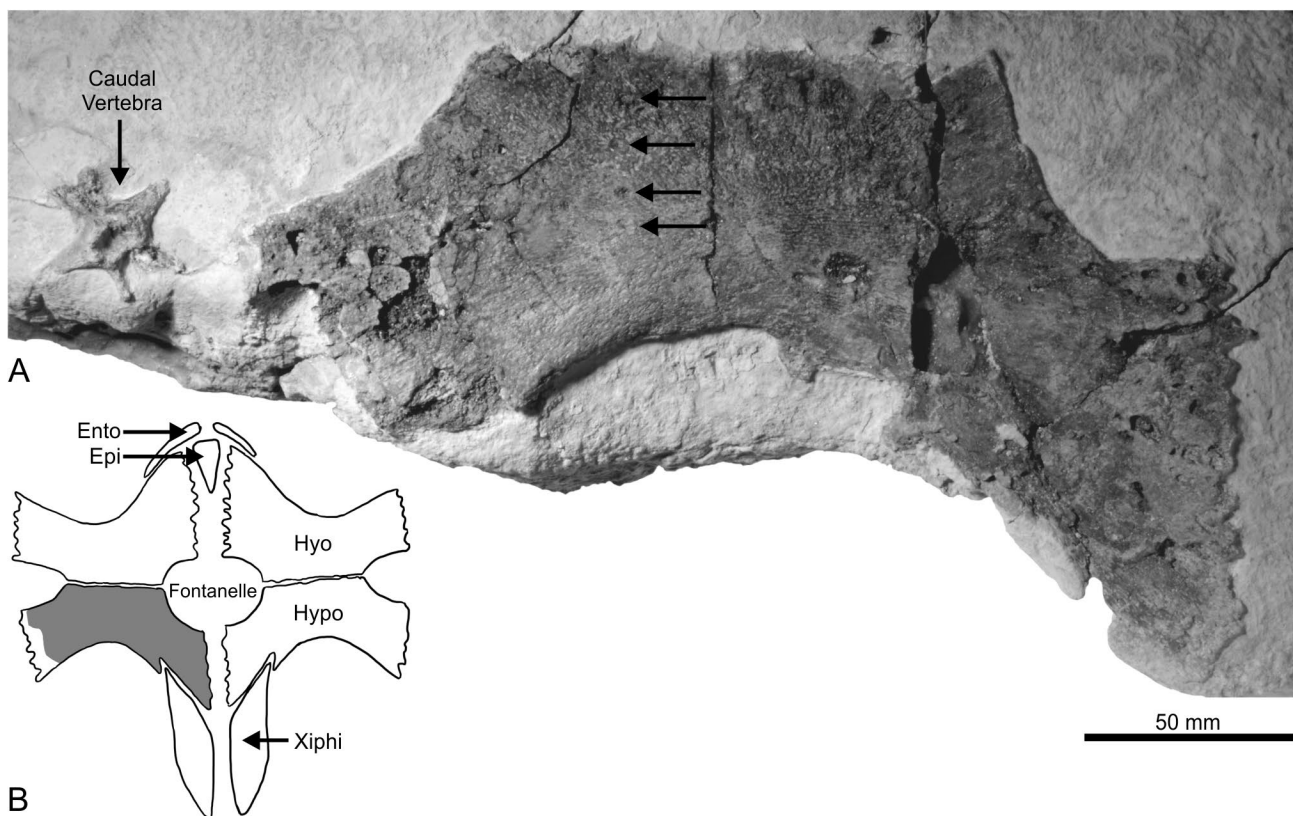


Fig. 4. A: Hypoplastron (NHMD 227325) partly embedded in Kerteminde Marl. A row of four circular bite traces is indicated by arrows. B: Sketch of turtle plastron with names of the individual skeletal elements indicated. Ento: entoplastron, Epi: Epiplastron, Hyo: Hyoplastron, Hypo: Hypoplastron, Xiphi: Xiphiplastron. The central fontanelle is formed by recession of the margins of the paired Hyo- and Hypoplastrons.

NHMD 227325 is referred to *Ctenochelys cf. stenoporus*. Weems (2014, fig. 12) described a Danian cheloniid specimen which was interpreted as *?Lophochelys* sp. Superficially, it resembles NHMD 227325, but the R2 ratio is much larger in *?Lophochelys* than in the studied specimen (1.16 versus 0.4).

Occurrence and stratigraphical age. The specimen was found in an erratic boulder of the Kerteminde Marl Formation retrieved from the Gundstrup gravel pit, Fyn, Denmark (approximately 55.56°N, 10.35°E). The presence of the calcareous nannofossils *Neochiastozygus perfectus*, common *Prinsius dimorphosus* and rare reworked Cretaceous nannofossils (Schnetler & Nielsen 2018) in the marly matrix reveal a basal Selandian age of the turtle specimen (Thomsen 1995, Clemmensen & Thomsen 2005, Schnetler & Nielsen 2018).

Discussion

Identification of the specimens

Fossil turtle remains from the Late Paleocene are relatively rare, and the general lack of described material from this period has resulted in a scant and incomplete phylogeny of the family Cheloniidae (Weems 1988). Most fossils belonging to Cheloniidae have been found in North America. However, considering the relative proximity of North America and Europe during the

Paleocene, it is not unlikely that the range extended further east than previously assumed.

With very few exceptions, the cheloniids discussed here, including *Ctenochelys stenoporus*, have been recorded from the Cretaceous only (Zangerl 1953; Hirayama 1997). This leads to three obvious interpretations with regard to the specimen NHMD 227325 (*Ctenochelys cf. stenoporus*): 1) *Ctenochelys* existed through a longer time interval than previously assumed and survived the Cretaceous/Paleogene boundary; 2) the specimen is not a *Ctenochelys* but belongs to a closely related descendant not previously described, and 3) the specimen is reworked from the Cretaceous. The last interpretation, however, seems unlikely because all other macrofossils documented from the marl blocks at Gundstrup - including several Danekræ - are of lower middle Paleocene (lower Selandian) age.

Predation traces

Both specimens studied display predation traces consisting of circular pits arranged in rows. NHMD 227324 has several rounded pits with diameters between 3–6 mm present on the surface, some arranged in smaller groups or rows. The pits are u-shaped in cross section (Fig. 3D, F). In addition to the circular pits, one end of the carapace plate bears groups of elongated scratch traces up to 11 mm in length, 2 mm in width and 1 mm deep. The traces are V-shaped in cross section (Fig. 3E). NHMD 227325 has a row of small, 3–4 mm wide, circular pits with a U-shaped

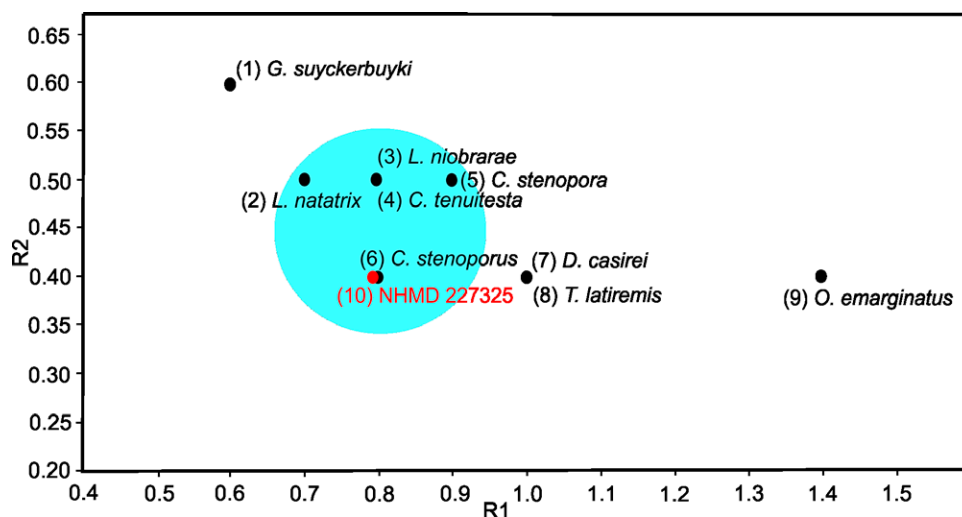


Fig. 5. Graphical representation of the calculated morphological ratios ($R1 = L1/L3$, $R2 = L2/L3$, see Methods). The specimens are named by their original species designations. (1) *Glyptochelone suyckerbuyki* (Lehman & Tomlinson 2004, fig. 6, bottom left); (2) *Lophochelys natatrix* (Zangerl 1980, fig. 3e); (3) *Lophochelys niobrarae* (Zangerl 1953, fig. 94); (4) *Ctenochelys tenuitesta* (Zangerl 1980, fig. 3f); (5) *Ctenochelys stenopora* (Zangerl 1953, fig. 111); (6) *Ctenochelys stenoporus* (Hirayama 1997, fig. 1B); (7) *Dollochelys casirei* (Zangerl 1980, fig. 3d); (8) *Toxochelys latiremis* (Zangerl 1953, fig. 73); (9) *Osteopygis emarginatus* (Zangerl 1980, fig. 3a). The light blue shaded area indicates the field of *C. stenoporus sensu stricto*.

cross section present in the middle part of the plastron (Fig. 4A). The distance between the pits is 9–11 mm.

In both specimens, the uniform arrangement of the pits, as well as the uniformity of their size and shape, suggest that they are bite traces. Identical traces are present in a turtle specimen found in the middle Danian limestone of the Faxø quarry (Milàn *et al.* 2011), which were interpreted as crocodylian bite traces. The uniformity of the pits suggests they are from a predator with more or less homodont uniform dentition such as a crocodylian, which frequently preys on turtles (Milàn *et al.* 2010); this also fits well with the geological age of the specimens. Crocodylians are known from several isolated finds from both the Cretaceous and Paleocene chalk and limestones, and in the Danian at least two crocodylomorphs co-existed, the longirostrine *Thoracosaurus* (Troedsson 1924; Adolfsson *et al.* 2017) and a more robust, possible alligatorid (Schwarz-Wings *et al.* 2014). Furthermore, specimen NHMD 227324 (Fig. 3) has preserved elongated scrapes which are fairly similar to scrapes seen in the specimens described from the Faxø quarry (Milàn *et al.* 2011). These are interpreted as traces from scavenging by sharks which were abundant during the Paleocene (Adolfsson & Ward 2015). Bite traces on the fossil bone surface indicate a factual interaction between animals, whether antagonistic, scavenging or predator–prey interaction, which can provide direct evidence of the feeding behaviour of extinct carnivores, as well as information on the trophic structure of the palaeocommunity (Botfalvai *et al.* 2014). In this case it demonstrates that the Paleocene turtles in Denmark coexisted with crocodylian predators that either actively hunted turtles, or at least scavenged them.

Dissolution pits

The dissolved areas on the ventral surface of NHMD 227324 are very similar to dissolution pits described by Botfalvai *et al.* (2014) in carapace fragments of Cretaceous turtles. The pits on NHMD 227324 are interpreted as pathologies, although post-mortem bioerosion by invertebrates or microbial activity cannot be fully excluded.

Conclusions

The two new turtle fragments add important new information about the Paleocene turtle fauna of Denmark. Despite the very limited material, a hypoplastron and a carapace fragment, the morphological and morphometrical analysis allows us to identify the hypoplastron NHMD 227325 as *Ctenochelys* cf. *stenop-*

rus. This is the first evidence of the genus *Ctenochelys* surviving the K/Pg boundary mass extinction event. The carapace fragment NHMD 227324 can be assigned to the family Cheloniidae indet. only. Both specimens show evidence of crocodylian predation or scavenging, and the carapace fragment further show evidence of scavenging by sharks.

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