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REVISION OF THE PALEOCENE TURTLES (REPTILIA: TESTUDINES) OF DENMARK

[Revisión de las tortugas (Reptilia: Testudines) del Paleoceno de Dinamarca]

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ABSTRACT: Fossil turtles of the Paleocene from Denmark are known over hundred years ago. Especially the marine turtle remains are problematic in their systematic position. However the material was often cited in several papers. In this paper the complete historical sample might become reviewed, described and figured at first time in the history.

Key words: Testudines, Paleocene, København Limestone Formation, Lellinge Greensand Formation.

RESUMEN: Las tortugas fósiles del Paleoceno de Dinamarca se conocen desde hace más de cien años. La posición sistemática de los restos de tortugas marinas es especialmente problemática. El material ha sido citado con frecuencia en varios documentos. En este trabajo se revisa la documentación histórica completa, con muchas descripciones e ilustraciones hasta ahora inéditas.

Palabras clave: Testudines, Paleoceno, Formación Calizas de Copenhague, Formación Areniscas Verdes de Lellinge.

INTRODUCTION

The paper presents new evidence of fossil turtles from Denmark with special emphasis on re-examination of the historic, almost forgotten fossil material in the Geological Museum of Copenhagen. This material from the uppermost Danian and lowermost Selandian was originally mentioned and described by DAMES (1897) (erroneously as upper Cretaceous) and ROSENKRANTZ (1920, 1921, 1923). The soft-shelled turtle remains from the uppermost Danian of Copenhagen are amongst the oldest and northernmost known fossil material of this group from the western Palaearctic (KARL, 1998, 1999).

GEOLOGICAL SETTING

The fossil turtle material described and re-described in this paper derives from two separate, but superimposed lithological units in the Danish Paleocene (see figure 1).

One specimen, an imprint described as belonging to the genus *Trionyx* (but see below), was recovered from the previously-named "lower *Crania*-limestone" (ROSENKRANTZ, 1923). This lithological unit is today referred to the uppermost part of the København Limestone Formation (*sensu* STENESTAD, 1976). The limestone has been described as a weakly stratified micritic limestone with up to 30% lime-sand and lime-silt particles; the upper part is a biosparite with small amounts of glauconite (STENESTAD, 1976). The limestones of the Copenhagen Limestone are uppermost Danian in age; nannofossil analyses at the locality Gemmas Allé assign them to the NP4 Zone; *Chiasmolithus bidens* subzone (D10), while foraminifera indicate the Danian P1c subzone and the *Cerodinium striatum* Zone (STOUGE *et al*., 2000).

The København Limestone Formation (Danian) is unconformably overlain by the Lellinge Greensand (Selandian); a hiatus spanning the Danian-Selandian boundary and representing a regional unconformity separates the two deposits in time (THOMSEN, 1994; STOUGE *et al*., 2000).

The remaining fossil turtle material from the Danish Paleocene; i.e. specimens described by DAMES (1897); mentioned by ROSENKRANTZ (1920, 1921) and a new specimen referred to *Rafetoides* sp. (this paper) all derive from the so-called bottom conglomerate of the Lellinge Greensand Formation (*sensu* STENESTAD, 1976). This formation includes the deposits formerly referred to the "upper *Crania*-limestone" (ROSENKRANTZ, 1920, 1921; STENESTAD, 1976). This is a conglomeratic silty chalk or calcsilitite, whose matrix is mostly composed of calcareous nannofossils, foraminifera and calcite crystals (CLEMMENSEN & THOMSEN, 2005). The conglomerate mainly consists of shell material and sediment particles from eroded older deposits; thus its age is diachronous (STENESTAD, 1976). The bottom conglomerate at Gemmas Allé has been

assigned to nannofossil Zone NP4-5 of MARTINI (1971) (STOUGE *et al.*, 2000) and foraminifer subzone P3a sensu BERGGREN & NORRIS (STOUGE *et al.*, 2000).

STAGE	FORMATION	LOCALITIES	MATERIAL
Selandian (pars)	LELLINGE GREENSAND (Bottom conglomerate)	Larsens Plads Copenhagen South Harbour Gemmas Allé	*Rafetoides henrici* (this study) Cheloniini indet. (DAMES, 1897; ROSENKRANTZ, 1923)
H I A T U S			
Danian (pars)	COPENHAGEN LIMESTONE	Copenhagen South Harbour	*Rafetoides henrici* (ROSENKRANTZ, 1923)

Figure 1. Schematic presentation of the geology and localities of the Paleocene turtle-carrying deposits in the Copenhagen area.

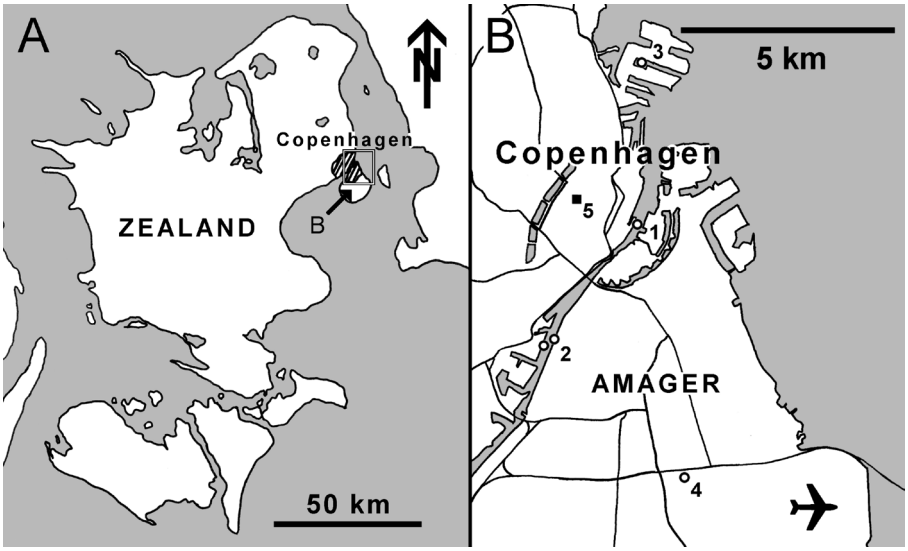

Figure 2. Maps. A = Island of Zealand (eastern Denmark) and surrounding areas showing location of map B. B = Map of Copenhagen and the island of Amager, showing localities mentioned in text: 1: Larsens Plads; 2: Copenhagen South Harbour, excavation I & II; 3: Sundkrogen; 4: Gemmas Allé; 5: Geological Museum, University of Copenhagen (where the specimens are housed today).

LOCALITIES

In the following section the various localities within the Copenhagen area which have yielded Paleocene fossil turtle material are discussed (see figure 2). Unfortunately, all are currently inaccessible as the localities were only open during large-scale construction works in the late 19th, as well as early and latest 20th Centuries.

Locality 1: *Larsens Plads, Copenhagen Harbour (lowermost Selandian)*

The sea-turtle material described by DAMES (1897) was collected by Mr. C.E. Aagaard during deepening of the harbour in front of Larsens Plads in 1890 (ROSENKRANTZ, 1920) from "a rather hard, grey-green Limestone with numerous, as of yet not further determined Fossils; *Crania tuberculata* NILSS. is the most common" (DAMES, 1897: 74), which was later referred to "upper *Crania*-limestone" by ROSENKRANTZ (1920) on the basis of its invertebrate fossil content. Thus the material is today referred to the bottom conglomerate of the Lellinge Greensand Formation (lowermost Selandian) Specimen labels from this locality bear the name "Kalkbrænderihavnen".

Locality 2: *Copenhagen South Harbour (lowermost Selandian)*

This collection encompasses all the sea-turtle remains referred to in ROSENKRANTZ (1920, 1921). They were collected in 1918-1920 (according to specimen labels and ROSENKRANTZ, 1923) during the deepening of the Copenhagen South Harbour. They derive from loose blocks of rock derived from the overlying glacial deposits. ROSENKRANTZ (1920, 1921) identified them as deriving from the "upper *Crania*-limestone" and they are thus referable to the bottom conglomerate of the Lellinge Greensand Formation (lowermost Selandian).

Material from two separate excavations are present in the material. Specimens labelled "Excavation I" are dated 1918 and derive from excavations outside the pier "Djævleøen" (ROSENKRANTZ, 1920). Specimens with labels "Excavation II" are dated 1919; they derive from excavations at the south end of the pier at Kalvebodstrand and were collected by ROSENKRANTZ during April and May 1919 (ROSENKRANTZ, 1920).

Locality 3. Sundkrogen/Copenhagen South Harbour (uppermost Danian)

The soft-shell turtle remains (MMH 3887) referred to *Trionyx* by ROSENKRANTZ (1921, 1923) were collected in the spring of 1921 by Alfred Rosenkrantz and Christian Poulsen from loose blocks making up the pier at the "lille Skudehavn" north of Sundkrogen in the Copenhagen Free Harbour; the material contained in the pier derives from the earlier deepening excavations at the South Harbour from 1917-1919 (Locality 2; see above) (ROSENKRANTZ, 1923). The lithology of the sediment around the specimen indicated that it belonged to the "lower *Crania*-limestone" (ROSENKRANTZ, 1923); which today

is referred to the uppermost part of the København Limestone Formation (uppermost Danian).

Locality 4. Gemmas Allé (lowermost Selandian)

One hitherto unpublished specimen of the soft-shell turtle *Rafetoides henrici* (DK 539) derives from the Øresound excavation at Gemmas Allé, Tårnby, on the Island of Amager (southeast Copenhagen). It was collected by Mr. Stig Andersen in January 1995 and derives from the bottom conglomerate of the Lellinge Greensand Formation (lowermost Selandian).

TERMINOLOGY

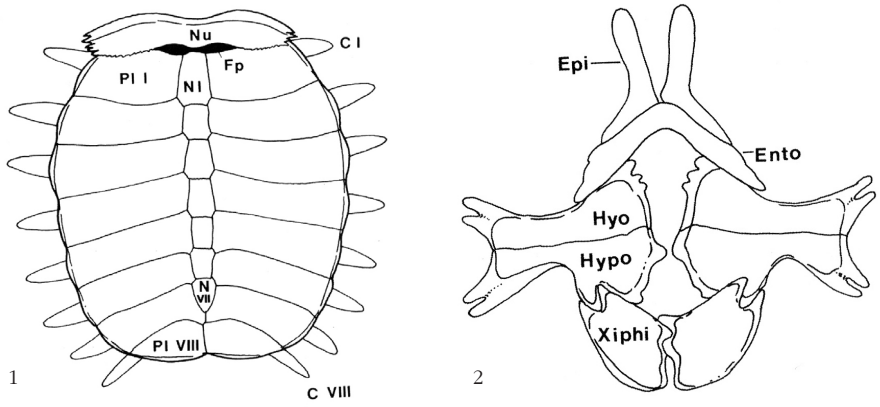

Figure 3-1. Shows the schematic reconstruction of carapace and plastron of trionychine turtles [e. g. Pelodiscus sinensis *(Wiegmann, 1835) according to* KARL *(1998)]. Without scale.*

Carapace plates: nuchal = nu, neurals = n I to n VIII, pleurals = pl I to VIII, peripherals = pe I to pe XI, metaneurals = mn I to II, pygal = py (fig. 3-1-1, fig. 3-2-1).

Carapace scutes: cervical = ce, centrals = c 1 to c 5, laterals = l 1 to l4, caudal = ca (fig. 3-1-1, fig. 3-2-1).

Plastron plates: epiplastrals = epi, entoplastron = ento, hyoplastron = hyo, hypoplastron = hypo, xiphiplastron = xiphi (fig. 3-1-2, fig. 3-2-2).

Plastron scutes: gulars = gu, humeral = hu, pectorals = pec, abdominals = ab, femorals = fe, annals = an (fig. 3-1-2, fig. 3-2-2).

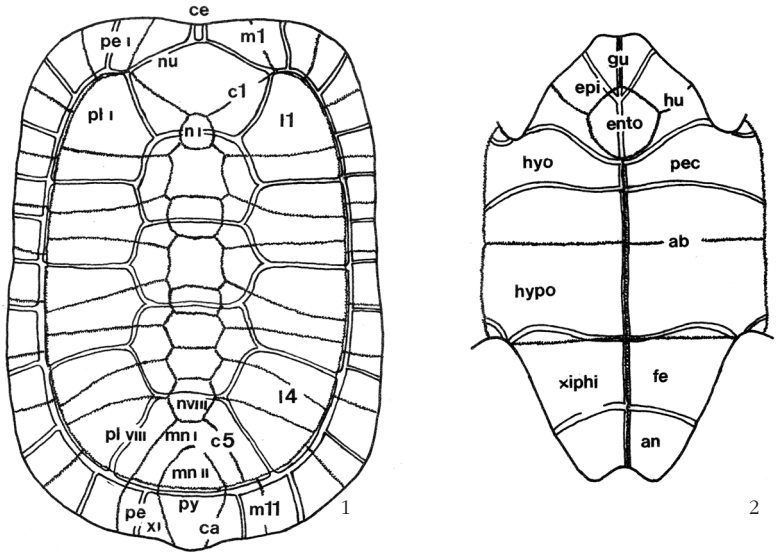

Figure 3-2. Shows the schematic reconstruction of carapace and plastron of a turtle (e. g. Testudo *according to* KARL, *2007). Without scale.*

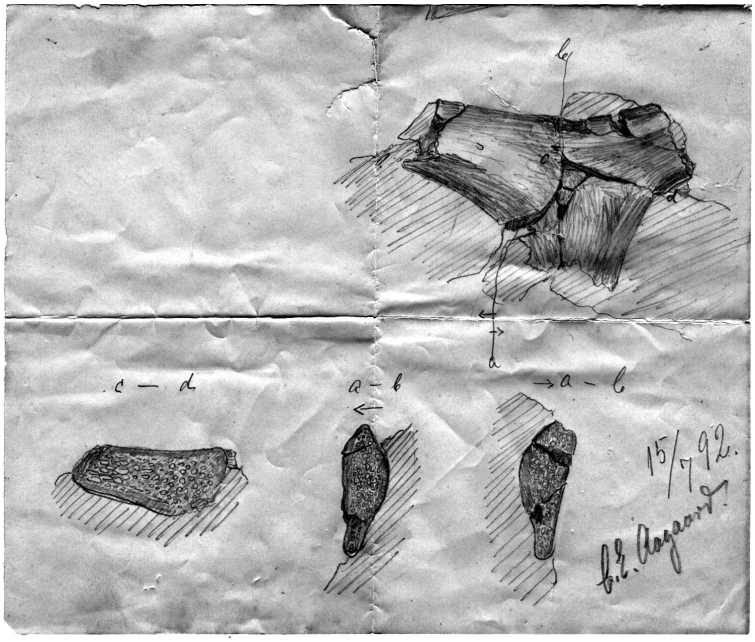

Figure 4. MMH 1938.57, Testudines, gen. et spec. indet. from the Paleocene of Copenhagen, Scapular remain. Original graphite sketch by C. E. Aagaard dated 15.7.92.

SYSTEMATIC PALAEONTOLOGY

Order Testudines Linnaeus, 1758

(Chelonii Brongniart, 1800; Latreille, 1800)

Infraorder Cryptodira Duméril & Bibron, 1835 [non Cope, 1871]

Superfamily Trionychoidea Fitzinger, 1826

Family Trionychidae Fitzinger, 1826

Subfamily Trionychinae Fitzinger, 1826

Tribe Trionychini Fitzinger, 1826

Subtribe Rafetoidina Karl, 1998

Genus *Rafetoides* Karl, 1998

***Rafetoides* cf. *henrici* (Owen, 1849)**

Synonyma:

- *Trionyx* sp., Rosenkrantz, 1923: 4.
- *Trionyx* sp., Russell *et al.*, 1982: 39 (KBN=København Kalk Formation).
- *Trionyx* sp., Karl, 1999: 40.

Localities: Sundkrogen/Copenhagen South Harbour (3) and Gemmas Allé (4).

Horizon: Paleocene: Danian (København Limestone Formation) and Selandian (Lelllinge Greensand Formation).

Remarks: The new material from 1995 is of great importance.

Description: Both known fossil remains shown the characters of the British materials from the London clay described by OWEN (1849). The only other species of that genus is *Rafetoides austriacus* (Peters, 1858) from the Eocene to middle Oligocene of central and southeast Europe. The discus surface in the latter displays taller structural elements in the ornament, contrary to the type species *Rafetoides henrici* from the same age of northwest Europe.

REFERED MATERIALS

MGUH 3887 [24] Imprint of the dorsal surface of a pleural plate with a single shell imprint *(Crania)*, furthermore a silicon cast of the imprint. Original of ROSENKRANTZ, 1923, see pl. 1, figs. 1-2.

DK 539 [25] Pleural fragment from Gemmas Allé, Tårnby, on the Island of Amager, see pl. 1, fig. 3.

Fam. indet.

(?Superfamily Chelonioidea Baur, 1893, ?Family Cheloniidae Gray, 1825)

Synonyma:

- *Allopleuron* sp., DAMES, 1897: 73.
- *?Allopleuron* sp., RUSSELL *et al.*, 1982: 40 (LLL = Lellinge Formation).
- *Allopleuron* sp., GROESSENS VAN DYCK & SCHLEICH, 1988: 138.

Localities: Larsens Plads (1) and Copenhagen South Harbour (2).

Horizon: Paleocene, Selandien (Lellinge Greensand Formation).

Remarks: According to RUSSELL *et al.*, 1982 and GROESSENS VAN DYCK & SCHLEICH (1988) "*Allopleuron*" is present, based on the brief remarks by DAMES (1897). However, none of the highly fragmentary shell remains of the original collection is anatomically comparable to the genus *Allopleuron* Baur, 1888 and the taxon must therefore be removed from the checklist of Danish fossil turtles.

Description: The cheloniid material from the Danish Palaeocene is too poorly preserved for a detailed determination. The thickness and surface structure of the single plates may be comparable to a true turtle. Smooth plate types comparable to proximate parts of pleurals are MMH 1938.57, GM V2008-27a-b, GM V2008-29, GM V2008-32a-b, GM V2008-33a-b, GM V2008-34, peripherals: GM V2008-38, and pygal: GM V2008-31.

REFERED MATERIALS

GM V2008-27a.b [1] Imprint of proximate pleural fragment (visceral) (a) and silicon cast from Copenhagen South Harbour (b), leg. A. Rosenkrantz, 1919, see pl. 2, figs. 3-4;

MMH 1938.57 [2] Pleural fragment in dorsal aspect (extremely smooth), original specimen of Dames (1897), see pl. 5, fig. 4;

GM V2008-28a-b [3] Imprint of proximate pleural fragment (dorsal) (a) and silicon cast from Copenhagen South Harbour (b), leg. Rosenkrantz, 1919, see pl. 2, figs. 1-2;

GM V2008-29 [4] Pleural fragment in dorsal (a) and visceral aspect (b), leg. A. Rosenkrantz, 1919, see pl. 5, fig. 2;

GM V2008-30 [5] Bone fragment (?turtle), leg. A. Rosenkrantz, 1919, see pl. 4, fig. 2;

GM V2008-31 [6] Pygal plate (dorsal), leg. A. Rosenkrantz, 1919, see pl. 4, fig. 1;

GM V2008-32a-b [7] Imprint of proximate pleural fragment (dorsal) (a) and silicon cast from Copenhagen South Harbour (b), leg. A. Rosenkrantz, 1919, see pl. 2, figs. 5-6;

GM V2008-33a [8] Dorsal pleural fragment in sediment matrix, pleural fragment in visceral aspect, sediment with imprint of GM 2008-33a, cast of the imprint of b, leg. A. Rosenkrantz, 1919, see pl. 3, figs. 1-4; **[23]** four slides possibly derived from this specimen, not figured here.

GM V2008-34 [9] Pleural fragment in dorsal aspect, leg. A. Rosenkrantz, 1919, see pl. 4, fig. 7;

GM V2008-35 [10] Several bone fragments (?turtles), leg. A. Rosenkrantz, 1919, see pl. 5, fig. 11;

GM V2008-36 [11] Plate fragment in internal aspect, leg. A. Rosenkrantz, 1919, see pl. 4, fig. 6;

GM V2008-37 [12] ?Skull fragment, leg. A. Rosenkrantz, 1919, see pl. 4, fig. 4;

GM V2008-38 [13] Peripheral plate in visceral aspect, leg. A. Rosenkrantz, 1920, see pl. 4, fig. 5;

MMH 1938.57 [14] Scapular, fragment of the area of articulation, original specimen of Dames (1897), see fig. 4 and pl. 4, fig. 3;

MMH 1938.57 [15] Pleural fragment in visceral aspect, original specimen of Dames (1897), see pl. 5, fig. 9;

GM V2008-39 [16] Median pleural fragment, leg. A. Rosenkrantz, 1919, see pl. 5, figs. 3, 7;

MMH 1938.57 [17] Several fragments of turtle shell plates (neural), original specimens of Dames (1897), see pl. 5, fig. 12;

GM V2008-40a-b [18] Imprint of pleural fragment (a) and reptile tooth (?crocodile), leg. A. Rosenkrantz, 1919, see pl. 5, fig. 10;

MMH 1938.57 [19] Marginal fragment of plastron fragment, original specimen of Dames (1897), see pl. 5, fig. 1a-b;

GM V2008-41a-c [20] Bone fragments (a: ?free rib end, b: ?fish fragment, c: shell plate fragment), leg. A. Rosenkrantz, 1920, see pl. 5, fig. 6;

GM V2008-42 [21] Pleural fragment in medial aspect, leg. A. Rosenkrantz, 1919, see pl. 5, fig. 8;

MMH 1938.57 [22] Peripheral fragments with two slides, original specimens of Dames (1897), see pl. 5, fig. 5.

THE PALAEOGEOGRAPHIC AND PALAEOCLIMATIC IMPORTANCE OF THE DANISH TURTLES

Remains of fossil soft-shelled turtles (Trionychinae) are numerous from many Cenozoic deposits in Europe. None-the-less the highest concentration of finds is in the Neogene; from the Palaeogene widespread reconstruction of areas of distribution are only possible for the Eocene and Oligocene (KARL, 1999). On the contrary, in mainland Europe there are only few records from

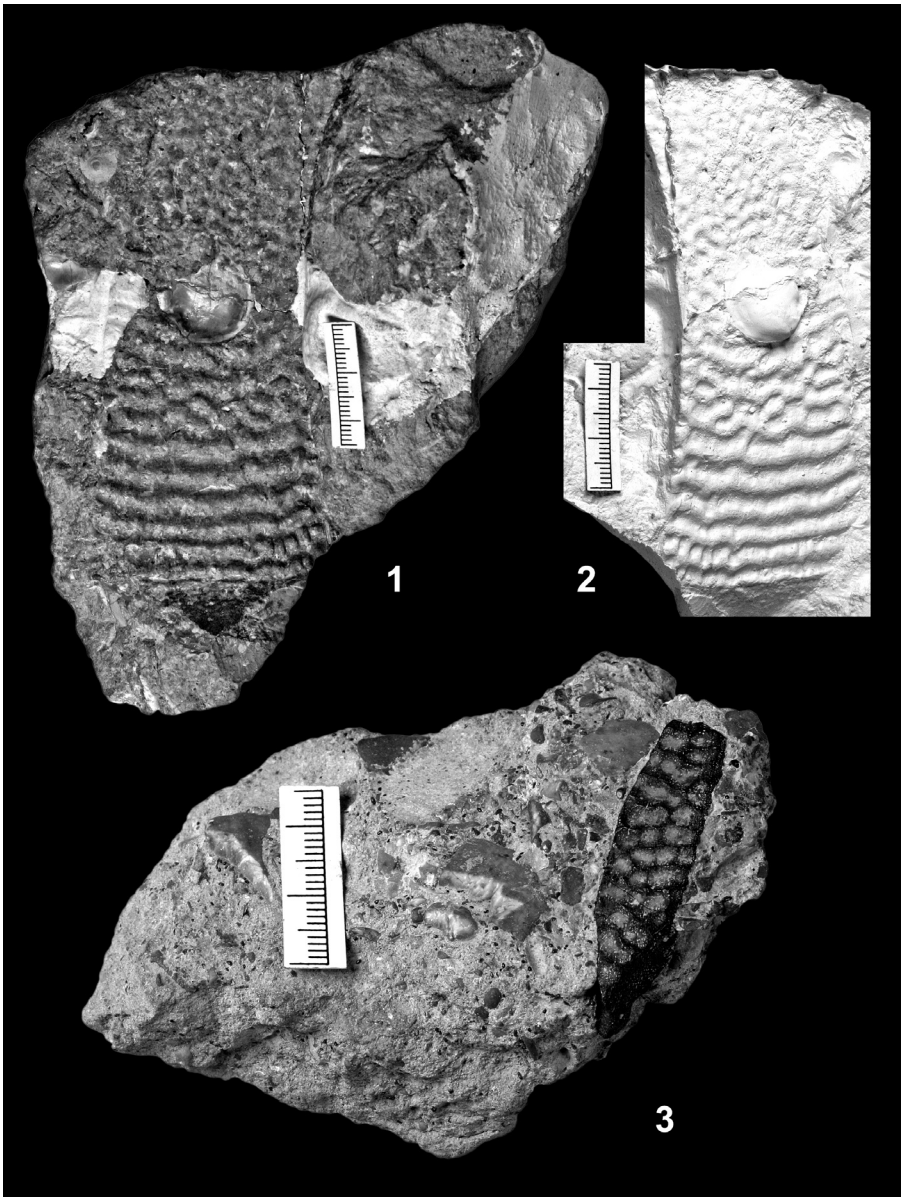

Plate 1. Rafetoides *cf.* henrici *(Owen, 1849) from the Paleocene of Sundkrogen/Copenhagen South Harbour (locality 3): 1: MGUH 3887 Imprint of the dorsal surface of a pleural plate with a single shell imprint (Crania); 2: silicon cast of 1; 3: DK 539 Pleural fragment from Gemmas Allé, Tårnby, on the Island of Amager (locality 4); scale bar 3 cm.*

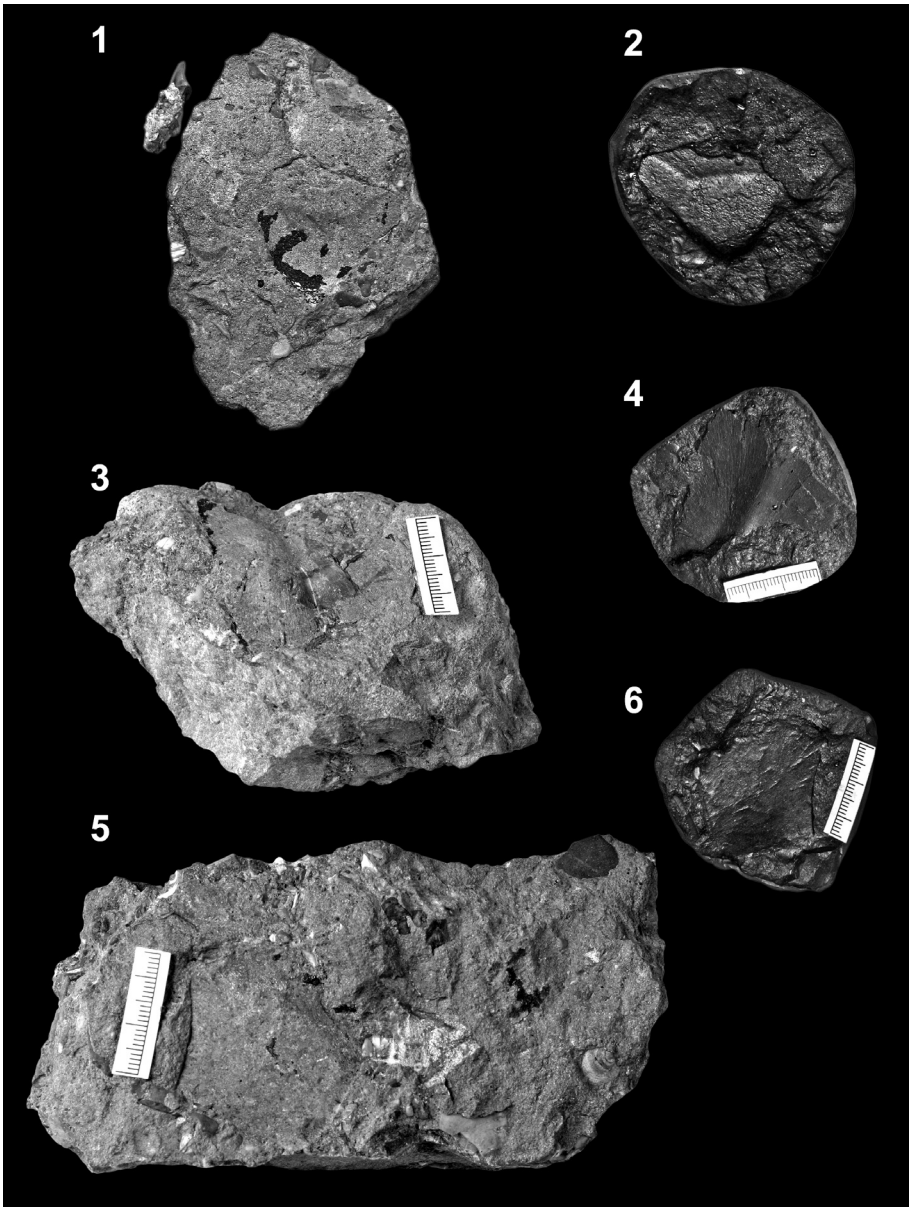

Plate 2. Testudines, gen. et spec. indet from the Paleocene of Copenhagen: 1: GM V2008-28a-b Imprint of proximate pleural fragment (dorsal) (a) and 2: silicon cast from Copenhagen South Harbour (b); 3= GM V2008-27a.b Imprint of proximate pleural fragment (visceral) (a) and 4: silicon cast from Copenhagen South Harbour (b); 5: GM V2008-32a-b Imprint of proximate pleural fragment (dorsal) (a) and 6: silicon cast from Copenhagen South Harbour (b); scale bar = 3 cm.

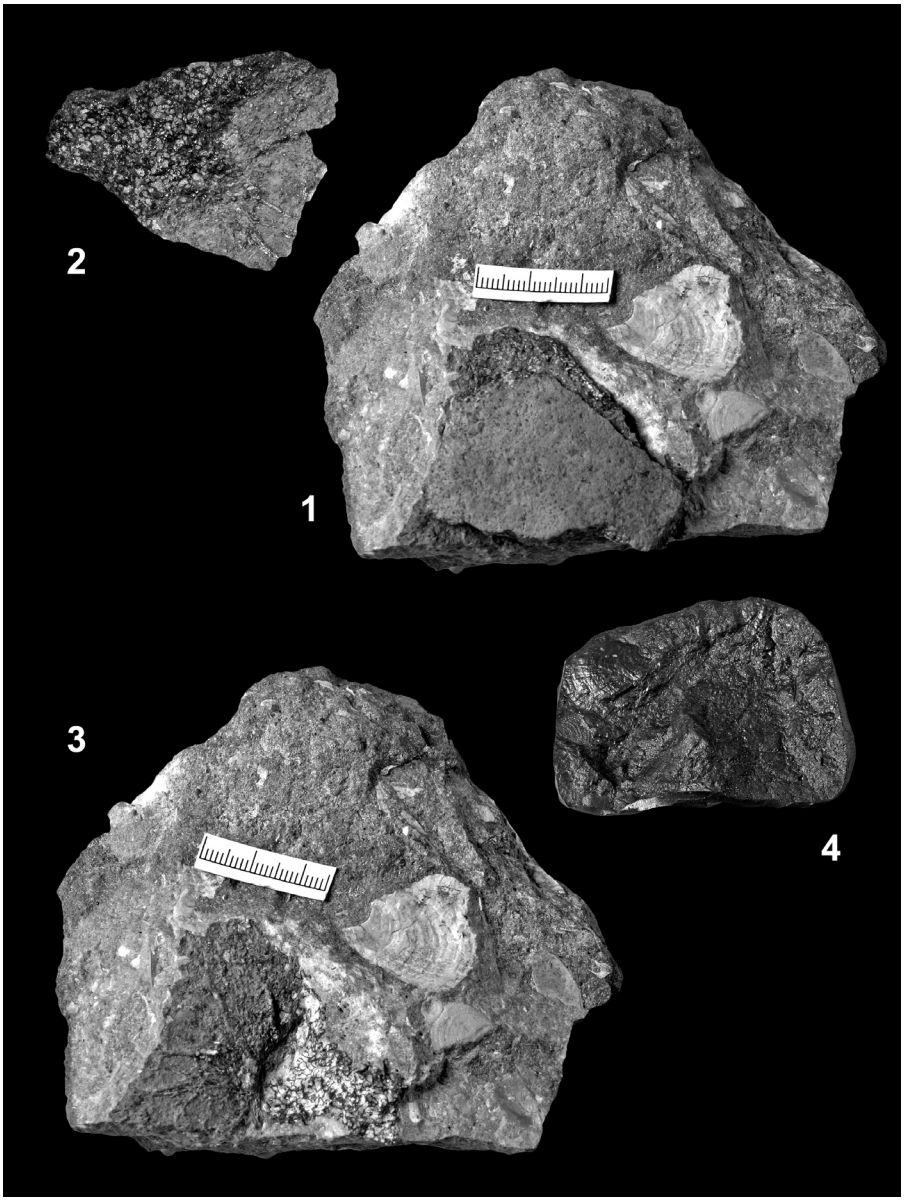

Plate 3. Testudines, gen. et spec. indet from the Paleocene of Copenhagen: 1: GM V2008-33a Dorsal pleural fragment in sediment matrix; 2: GM V2008-33a Visceral view of pleural fragment; 3: GM V2008-33b Sediment matrix with visceral imprint of GM 2008-33a; 4: GM V2008-33c Cast of the imprint of b; scale bar = 3 cm.

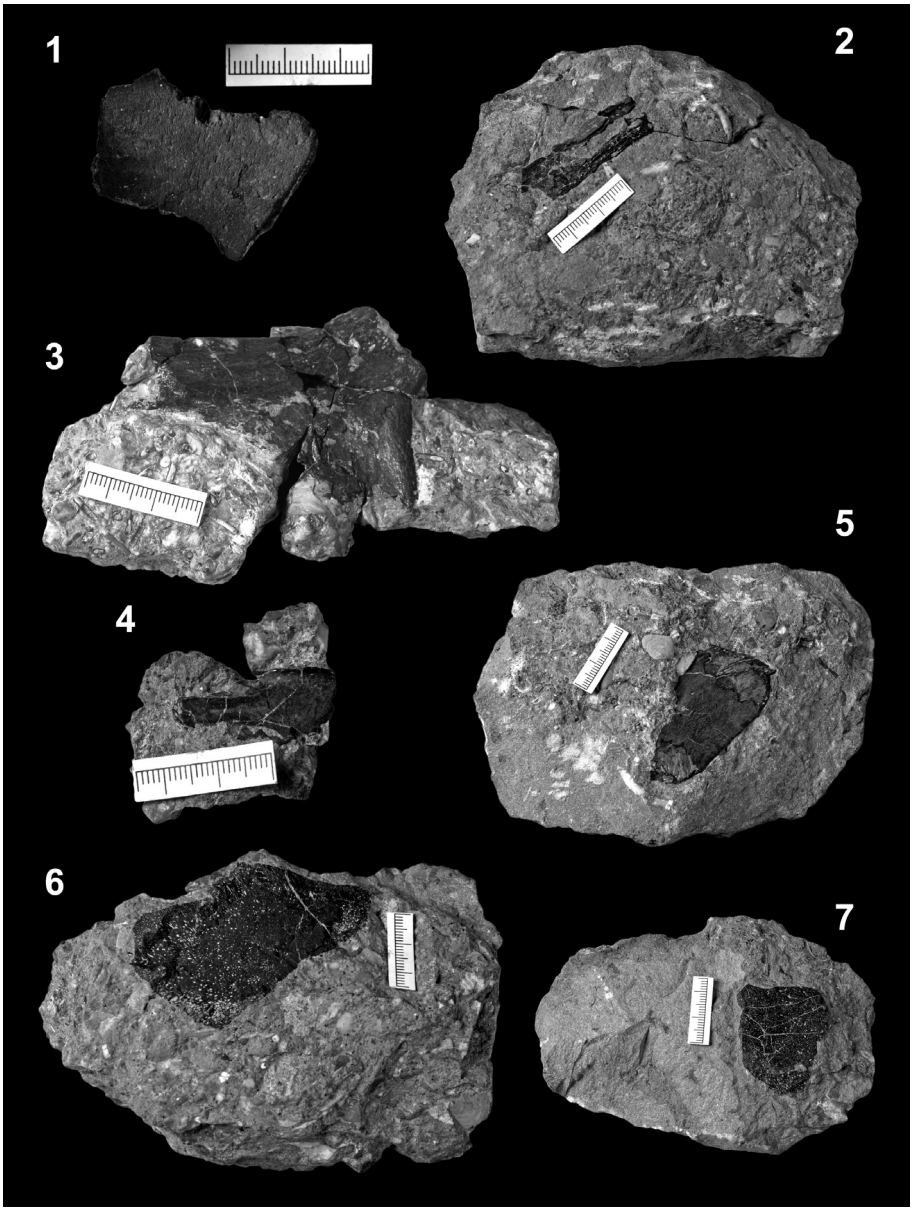

Plate 4. Testudines, gen. et spec. indet from the Paleocene of Copenhagen: 1: GM V2008-31 Pygal plate (dorsal); 2: GM V2008-30 Bone fragment (?turtle); 3: MMH 1938.57 Scapular fragment from the area of articulation, 4: GM V2008-37 ?Skull fragment; 5: GM V2008-38 Peripheral plate in visceral aspect; 6: GM V2008-36 Plate fragment in internal aspect; 7: GM V2008-34 Pleural fragment in dorsal aspect; scale bar = 3 cm.

the oldest epoch of the Palaeogene, the Paleocene, concentrated in France (the Paris Basin) and Belgium (Brussels Basin) (KARL, 1999). ROSENKRANTZ (1921, 1923) referred the impression of a shell fragment from the uppermost København Limestone Formation to the group. Later, a rib plate was recovered during excavations at for the Øresund tunnel at Tårnby in January 1995.

According to the current hypothesis of KARL (1999) the oldest Paleocene populations of trionychine turtles are derived from immigration of North American forms *(Aspideretoides)*. This immigration happened in the Upper Cretaceous across the Thule or Geer routes, a land bridge between northern Europe and North America (Greenland) which existed before the opening of the North Atlantic.

The Danish fossils described here, especially the shell fragment (N.º 5A), holds a key position. This is both the oldest known material of this group in Europe and the most northerly remains known from the epoch. It is therefore likely that we are dealing with the earliest representatives of the group in the entire western Palaearctic.

According to ROTHAUSEN (1994) the oceans and shallow seas were emptied of marine reptiles after the Cretaceous/Tertiary border event. The few surviving testudines and squamates played only a marginal role in colonising the empty ecological niches, a process which took a relatively long time. At first the surviving taxa of cheloniids, such as the Cretaceous survivors *Chelonia* and *Puppigerus*, were mainly see-grass eaters, and soon also meat-eaters *(Caretta)*. Especially *Puppigerus* with its short, stout extremities widened into paddles and lightly elongated phalanges, but a normal carapace, is not especially well-adapted to a marine life. It was probably a typical inhabitant of shallow waters. MOODY (1993) records no marine turtles for the Paleocene of northwest Europe and DE LAPPARENT DE BROIN (2001) gave a survey of European fossil turtles generally.

Following ROTHAUSEN (1967) the marine reptiles of the Mesozoic generally must have depended on subtropical to tropical waters. As a model for a similar climatic dependence he makes an analogy between the recent leatherback turtle *Dermochelys* and the Tertiary genus *Psephophorus*, whose northern distribution border remains a little south of the 20 ºC yearly isotherm of the Palaeogene. It is not known whether this is due to a physiologically related temperature limit or if the food was strongly temperature dependent. Nowadays *Dermochelys* is an occasional guest even in northerly waters (Great Britain, Ireland, the Baltic). The soft-shelled turtles also display a distributional center in the tropics and subtropics of Africa, Asia, Australasia and North America. Furthermore, *Apalone spinifera* reaches southern Canada while *Pelodiscus maacki* reaches the Amur-Ussuri region and can live in temperate regions with marked seasonal differences. The closest relatives

of the European species of *Rafetoides* are the Upper Cretaceous genera *Aspideretoides* and *Apalone* of North America. Therefore the Paleocene turtles of Denmark do not unequivocally support a warm climate, as they might also indicate a global cooling at the K/T-boundary.

DISCUSSION

Due to their fragmentary condition, the Paleocene turtle remains from Copenhagen cannot be determined to the level of family, genus or species. If that was sea turtles, a relationship to representatives of the western European genus *Puppigerus* is likely, but the question remains open until more complete material is recovered. Placement of parts of the material in the genus *Allopleuron sensu* Dames (1897) is not supported. The only remains which can be referred with certainty belong to the soft-shell turtles, namely *Rafetoides* cf. *henrici* (Owen, 1849).

ACKNOWLEDGEMENTS

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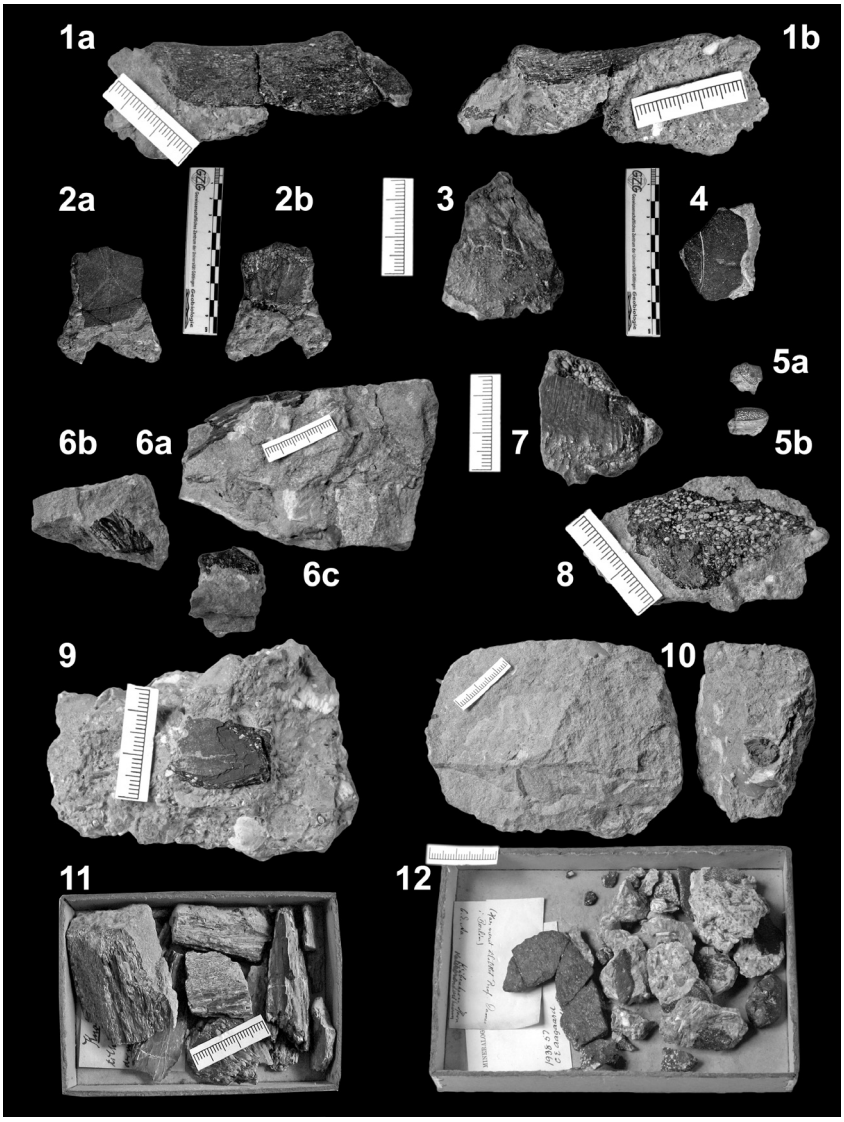

Plate 5. Testudines, gen. et spec. indet from the Paleocene of Copenhagen: 1a-b: ***MMH 1938.57*** *?Plastron fragment (margin); 2:* ***GM V2008-29*** *Pleural fragment in dorsal (a) and visceral aspect (b); 3:* ***GM V2008-39*** *Pleural fragment (median); 7: other side of* ***GM V2008-39****, 4:* ***MMH 1938.57*** *Pleural fragment in dorsal aspect (extremely smooth); 5:* ***MMH 1938.57*** *Peripheral fragments; 6:* ***GM V2008-41a-c*** *Bone fragments (a: ?Free rib end, b: ?Fish fragment, c: Shell plate fragment); 8:* ***GM V2008-42*** *Pleural fragment in medial aspect; 9:* ***MMH 1938.57*** *Pleural fragment in visceral aspect; 10:* ***GM V2008-40a-b*** *Imprint of pleural fragment (a) and reptile tooth (?crocodile), 11:* ***GM V2008-35*** *Several bone fragments, ?turtles; 12:* ***MMH 1938.57*** *Several fragments of turtle shell plates (neurals); scale bar = 3 cm.*

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