ISSN: 0211-8327 Studia Palaeocheloniologica IV: pp. 205-216

MIOCENE LEATHERBACK TURTLE MATERIAL OF THE GENUS *PSEPHOPHORUS* (TESTUDINES: DERMOCHELYOIDEA) FROM THE GRAM FORMATION (DENMARK)

[Tortugas de cuero miocénicas del género* Psephophorus *(Testudines: Dermochelyoidea) de la Formación Gram (Dinamarca)]

Hans-Volker KARL[1,2], Bent E. K. LINDOW[3] & Thomas TÜTKEN[4]

[1] Thüringisches Landesamt für Denkmalpflege und Archäologie (TLDA). Humboldtstr. 11. D-99423, Weimar, Germany. Email: hvkarl@web.de
[2]c\o Geobiology, Center of Earth Sciences at the University of Göttingen. Goldschmidtstraße 3. DE-37077 Göttingen, Germany
[3] Natural History Museum of Denmark. University of Copenhagen. Øster Voldgade 5-7. DK-1350 Copenhagen K, Denmark. Email: lindow@snm.ku.dk
[4] Emmy Noether-Gruppe "Knochengeochemie". Steinmann Institut für Geologie, Mineralogie und Paläontologie. Arbeitsbereich Mineralogie-Petrologie. Rheinische Friedrich-Wilhelms-Universität Bonn. Poppelsdorfer Schloß. 53115 Bonn, Germany.

(FECHA DE RECEPCIÓN: 2011-01-12)
BIBLID [0211-8327 (2012) Vol. espec. 9; 205-216]

ABSTRACT: Several specimens of fossil leatherback turtle from the upper Miocene (Tortonian) Gram Formation are described and illustrated scientifically for the first time. The specimens are all referred to the taxon *Psephophorus polygonus* and constitute the northernmost occurrence of this taxon in the geological record. Additionally, they indicate that leatherback turtles were a common constituent of the marine fauna of the Late Miocene North Sea Basin.

Key words: Testudines, *Psephophorus*, Miocene, Gram Formation, Denmark.

RESUMEN: Se describen y figuran por primera vez algunos ejemplares de tortugas de cuero fósiles del Mioceno superior (Tortoniense) de la Formación Gram, en

Dinamarca. Son asignados al taxa Psephophorus polygonus, haciéndose constar que son sus registros fósiles más septentrionales. Además, ello indica que las tortugas de cuero fueron habituales en la fauna marina de la Cuenca del Mar del Norte durante el Mioceno superior.

Palabras clave: Testudines, Psephophorus, Mioceno, Formación Gram, Dinamarca.

INTRODUCTION

A number of fossil specimens of leatherback turtle have been recovered from the Upper Miocene Gram Formation since the first discovery in 1904. Although the material has been mentioned and figured in abstracts (e. g. ROSENKRANTZ, 1921; LINDOW, 2004) as well as a number of popular science accounts (ROTH, 1983; BENDIX-ALMGREEN, 1986; DYCK, 1992; ROTH *et al.*, 2005; LINDOW & CUNY, 2008), it has yet to be scientifically described in detail and figured.

The first fossil discovery of turtle remains was made in 1904 and the material was referred to the genus *Psephophorus*. This specimen was split; part of it went to the Zoological Museum in Copenhagen (specimens GM V 2004-728 and 2004-729), while the rest went to the collections of the Natural History Museum in Hamburg (southern Jutland was part of Germany at the time). Unfortunately, the fossil material in Germany was obliterated during "Operation Gomorrah"; the Allied terror bombardment of the Hamburg city centre in July-August 1943 (BENDIX-ALMGREEN, 1986). The next specimen was discovered in 1986 in a rather unexpected place: the loft of the Gram castle (pers. comm. Flemming Roth, April 2003). When exactly this specimen (MSM 1017x1) was originally recovered from the nearby clay pit is unknown, but its colour and appearance is different from those of the 1904 and it clearly represents a separate discovery. The attached sediment clearly shows that it does derive from the Gram Formation. Finally, a single thecal plate of a leatherback turtle (specimen MSM 1607) was recovered from the Gram Claypit in 1995 by a visitor to the museum.

Institutional abbreviations: GM V: Vertebrate palaeontological collection of Geological Museum, University of Copenhagen, Denmark. MSM: Museum Sønderjylland-Naturhistorie og Palæontologi, Gram, Denmark.

GEOLOGICAL SETTING

The deposits of the marine Gram Formation are known from outcrops and boreholes in central, west and south Jutland (figure 1a). The formation is dominated by clay, which was deposited in an open marine setting with a high sedimentation rate and local water depths up to 100 metres (RASMUSSEN, 2005). Dinoflagellate cysts indicate a Serravallian-Tortonian age of the Gram

Formation (PIASECKI, 2005). All the fossil turtle material described below derive from the middle member of the Gram Formation, the Gram Clay proper (*sensu* RASMUSSEN, 2005) and is thus of Tortonian age (figure 1b). During the Tortonian, connection between the North Sea basin and the ocean was limited to a strait between Norway and Scotland (RASMUSSEN, 2005).

Vertebrate fossils are not uncommon in the Gram Formation and include sharks and rays (BENDIX-ALMGREEN, 1983; LINDOW & CUNY, 2008), teleost fish (GAEMERS, 1978), whales (WINGE, 1910; ROTH, 1978; PYENSON & HOCH, 2007; STEEMAN, 2009) and a seabird (HOCH, 2003; ROTH *et al.*, 2005).

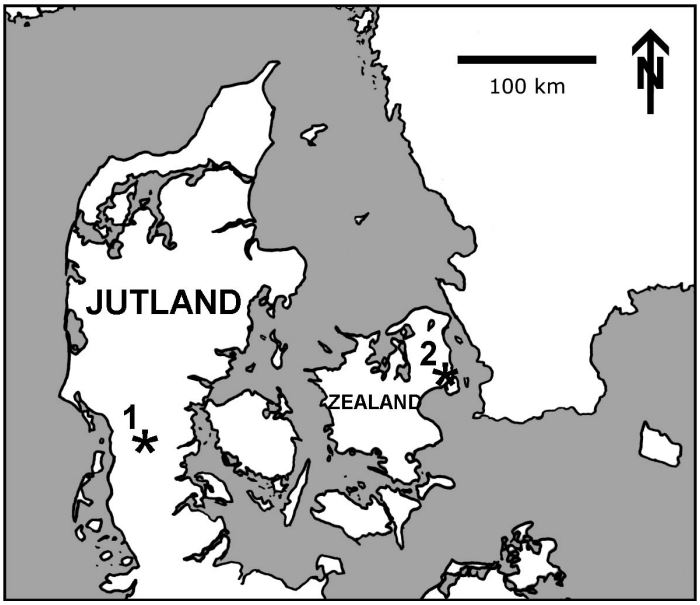

Figure 1. Map of Denmark and surroundings displaying Miocene leatherback turtle fossil sites and depositories. 1: *Gram*: *Gram Claypit and Museum Sønderjylland-Naturhistorie og Palæontologi; 2*: *Copenhagen*: *Geological Museum*.

SYSTEMATIC PALAEONTOLOGY

Order Testudines Linnaeus, 1758

(Chelonii Brongniart, 1800; Latreille, 1800)

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

Family Dermochelyidae Gray, 1825

Genus *Psephophorus* H. v. Meyer, 1846

Psephophorus polygonus H.V. Meyer, 1846

Synonyma:

Psephophorus sp., Rosenkrantz, 1921.

Psephophorus sp. Russell *et al.*, 1982: 41.

Psephophorus sp., Roth, 1983: fig. 15.

Psephophorus sp., Bendix-Almgreen, 1986: 30.

Psephophorus sp., Groessens van Dyck & Schleich[1], 1988: 119.

Psephophorus sp., Dyck, 1992.

Psephophorus polygonus alt. *"Psephophorus" calvertensis*, Lindow, 2004.

Psephophorus sp., Roth *et al.*, 2005: 24-25 & fig. 22.

Psephophorus sp., Lindow & Cuny, 2008: 37.

Localities: Gram Claypit and loft of Gram Castle, Gram, Denmark (fig. 1a).

Horizon: Upper Miocene (Tortonian) Gram Formation (fig. 1a).

Referred material: GM V2004-728-Fragment of carapace within clay nodule, with compacted costal bone fragments and associated dermal ossicles (figure 3, plate 2, figures 1-2).

GM V2004-729-Fragment of carapace within clay nodule. Several disassociated dermal ossicles, as well as costal bone fragments, are visible on the underside of the specimen (plate 1, figures 3-4).

MSM 1017x1-fragment of carapace within a clay nodule displaying at least nine or ten layers of dermal ossicles (plate 1, figure 5).

MSM 1607-isolated septagonal carapace ossicle (plate 1, figures 1-2).

Description: All carapace fragments display irregularly-shaped ossicles of varying shape and size. The external surfaces of the ossicles are ornamented by thin lines radiating out from the centre. Two specimens (GM V2004-729 and MSM 1017x1; plate 1: figures 3 and 5) display ossicles set in a small "sunflower pattern", where a central ossicle with scalloped margins is surrounded by a cluster of other ossicles (WOOD *et al.*, 1996). The scalloped ossicle is similar in size to the surrounding ossicles. Ossicle thickness varies between 6 and 11 mm. A thin section through a single ossicle from specimen GM V2004-728, displays three different layers (figure 3); a basal compact layer (1); a middle spongious layer, with an extensive Haversian system (2); and a dorsal cortical

[1] Læderskildpadde *Psephophorus spec.*, Esbjerg, Gram, Otterup, Skærum; Orleanian, Miocene according RUSSELL *et al.* (1982) and GROESSENS VAN DYCK & SCHLEICH (1988), all such informations was transmitted without any reference material.

layer (3). One specimen (GM V2004-728) displays a part of a keel of which approximately 6 cm is preserved. The ridge-bearing ossicles are irregular in shape and longer than wide (plate 2, figures 1-2: k). Wide, flattened costal fragments are present (plate 2, figures 2-3: c).

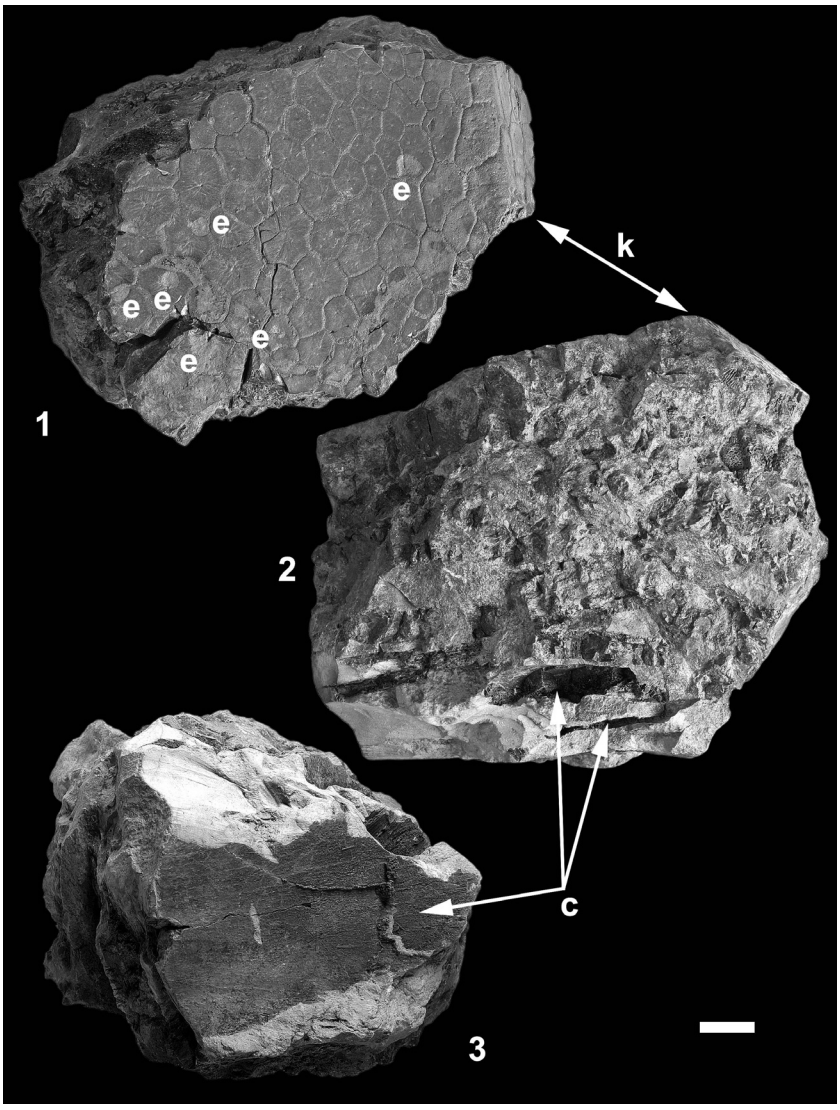

Plate 1. Psephophorus polygonus *from the Gram Formation; fig. 1: MSM 1607, single dermal ossicle, dorsal; fig. 2: visceral; fig. 3: GM V2004-729, Gram clay with epithecal shell remain, dorsal; fig. 4: ventral or lateral; e= marks by adult epibionts; fig. 5: GM 1017x1, Gram clay with epithecal shell remain, dorsal. Scale bar = 1 cm.*

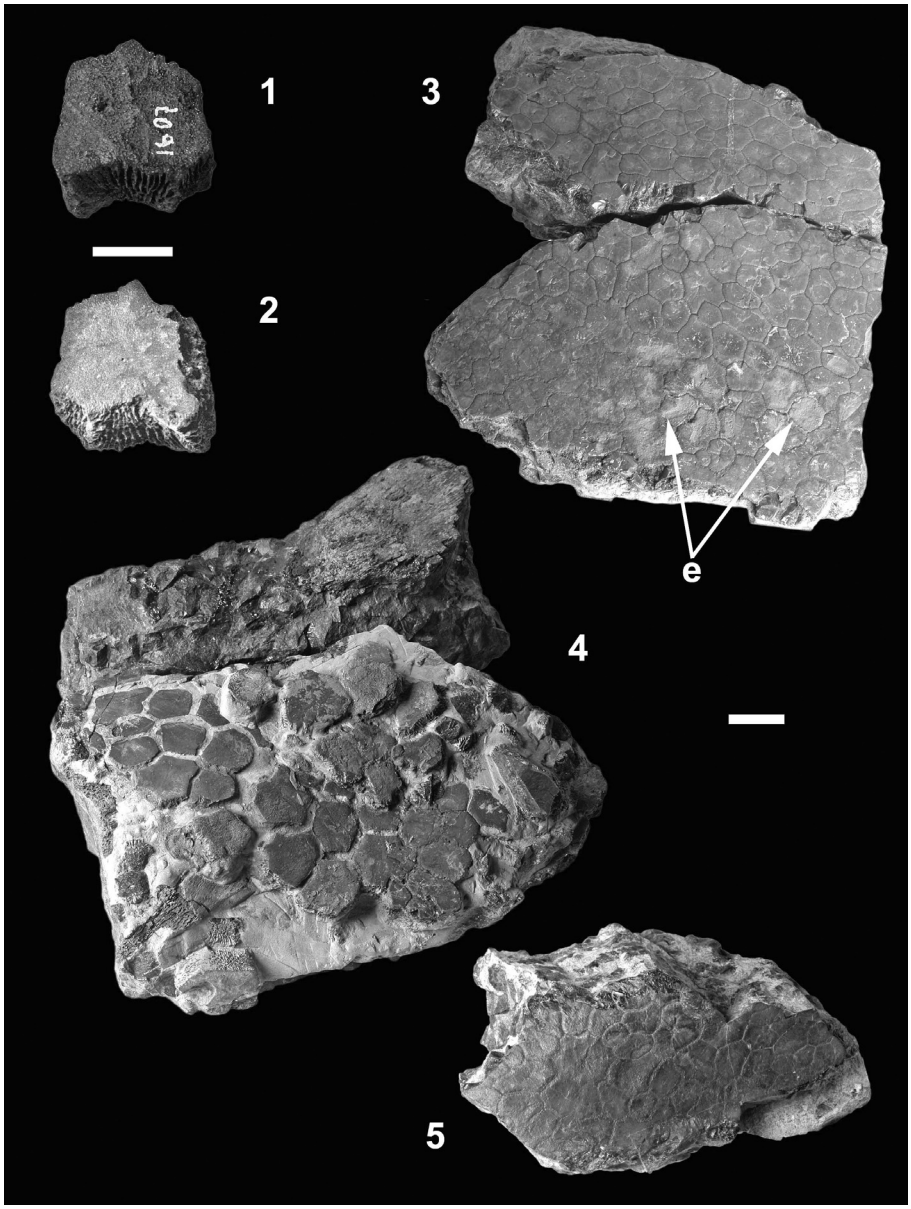

Plate 2. Psephophorus polygonus, *from Gram Formation; fig. 1: GM V2004-728, Gram clay with epithecal shell remain, dorsal; fig. 2: cross section with many layers of dermal ossicles; fig. 3= visceral with costal remains, k= keel, c= costa, e= marks by juvenile epibionts. Scale bar = 1 cm.*

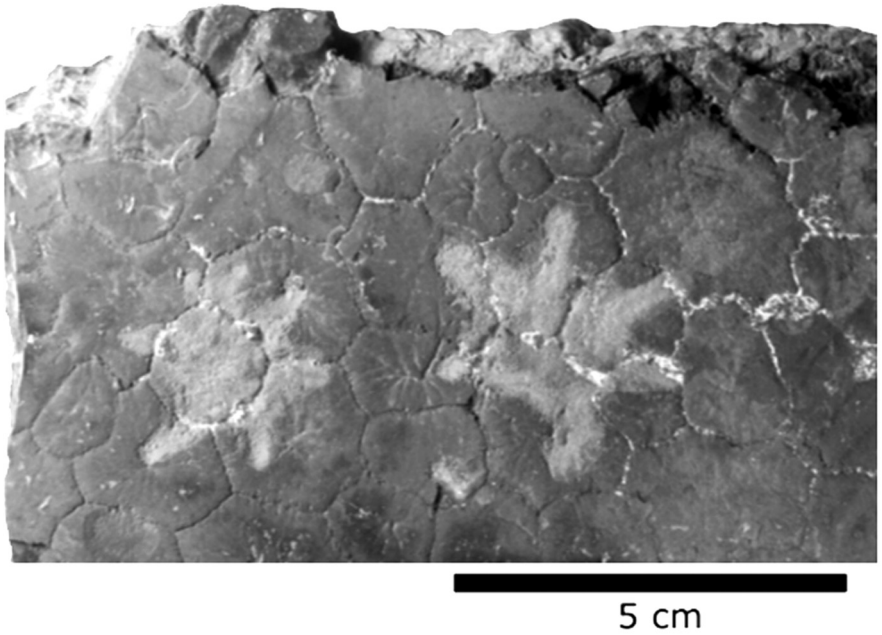

Figure 2. Two marks of epibionts on specimen GM V2004-729 probably made by barnacles (Arthropoda: Balanidae). See also plate 1, figure 3.

Pathologic and taphonomic remarks: The carapace surface of specimen GM V2004-728 displays six irregularly rounded or ovoid shallow depressions. These depressions measure between 4 and 11 mm in width and clearly transgress the sutural boundaries between individual ossicles. In the depressions, the carapace surface appears "etched" with a roughened surface (figure 2). Two larger, roughly six-pointed star-shaped marks are present on the carapace surface of specimen GM V2004-729 (figure 2; plate 1, figure 3: e). They measure approximately 30 mm and 35 mm in diameter, respectively. These structures are interpreted as scars from epibionts, which were attached to the carapace and irritated the tissue. The larger marks on specimen GM V2004-729 are tentatively interpreted as being those of barnacles (Arthropoda: Balanidae LEACH, 1817).

Specimen MSM 1017x1 displays several layers of more-or-less consecutive layers of dermal ossicles in lateral view. This feature has also been observed in extant *Dermochelys*, where it is due to post-mortem collapse and folding as well as sliding of the carapace (WOOD *et al.*, 1996).

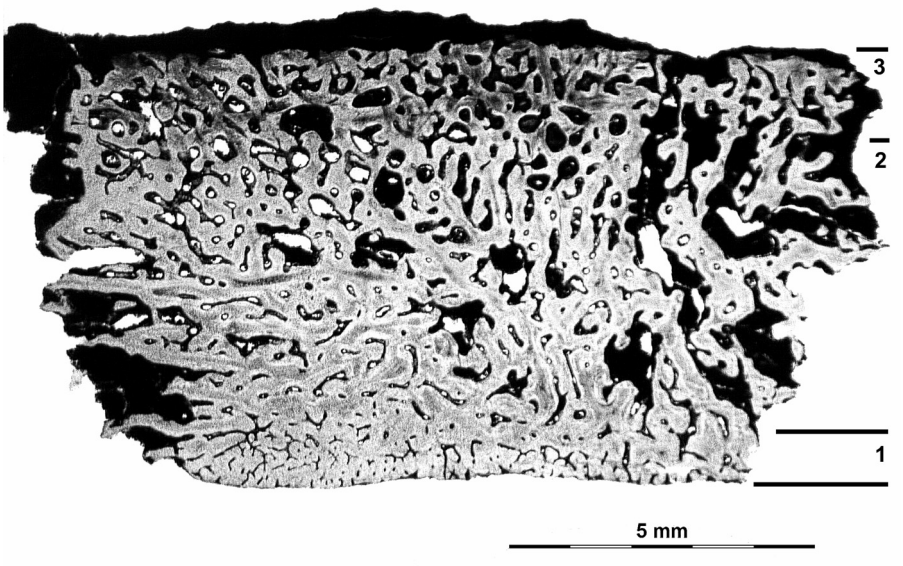

Figure 3. Thin section of a single ossicle from GM V2004-728; see also plate 2; figure 2.1: basal compact layer; 2: middle spongious layer (Haversian system there is most extensive) and 3: dorsal cortical layer.

Mineralogical and geochemical analysis: X-Ray structural analysis of a costal fragment (from specimen GM V2004-728) indicate that it is almost exclusively preserved as carbonate hydroxyapatite $Ca_5(PO_4CO_3)_3(OH)$, likely with FeS, Ca or silicate present in small quantities.

The bone compacta of a rib fragment of specimen GM V2004-708 was analyzed in triplicate for its phosphate oxygen isotope analysis ($\delta^{18}O_p$) according to the method described in TÜTKEN *et al.* (2006). The turtle bone has an $\delta^{18}O_p$ value of 22.7‰, which is well within the range of modern leatherbak turtle bones that have an average value of 22.4 ± 0.6‰ (COULSON *et al.*, 2008). This suggests that the $\delta^{18}O_p$ value has probably not been significantly diagenetically altered. Under this assumption the oxygen isotope composition of the ambient water ($\delta^{18}O_{H2O}$) was calculated using the $\delta^{18}O_p$-$\delta^{18}O_{H2O}$-calibration for marine turtles of COULSON *et al.* (2008). The reconstructed $\delta^{18}O_{H2O}$ value of 1.4‰ is somewhat higher than modern seawater values of around 0‰. This indicates that this *Psephophorus* tutle has lived in slightly ^{18}O-enriched seawater and/or was altered by a diagenetic fluid with such a high, seawater-like $\delta^{18}O_{H2O}$ value.

Plate 3.

DISCUSSION

An overview of currently recognised fossil leatherback turtle taxa is given by WOOD *et al.* (1986) and updated in KARL & LINDOW (2010). Only two taxa of leatherback turtles are recognised from the Miocene: *Psephophorus polygonus* and *"Psephophorus" calvertensis* (WOOD *et al.*, 1996). *P. polygonus* was present in the North Sea region 10 million years ago. Isotope studies of molluscs indicate that water temperatures in the North Sea Basin at that time appear to have been similar to present interglacial values, although within a large range (BUCHARDT, 1978a,b). This is mirrored by the assemblages of fossil molluscs and elasmobranchs from the Gram Formation, whose recent relatives present a bewildering array of genera spanning arctic to subtropical climates (SCHNETLER, 2005; LINDOW & CUNY, 2008).

A third lineage, leading to recent *Dermochelys coriacea* must also have been present in the Miocene, as *Psephophorus* is certainly not the ancestor of *Dermochelys* (WOOD *et al.*, 1996). Analysis of mitochondrial DNA sequences from recent leatherback turtles *Dermochelys coriacea* indicated that the species may be less than 900 ky old (DUTTON *et al.*, 1999). The oldest true fossil remains referred to *Dermochelys* are two dermal ossicles from the Pliocene/ early Pleistocene Lee Creek Mine deposits of North Carolina, USA (KÖHLER, 1996). *Dermochelys* is, amongst others, characterised by having much thinner dermal ossicles than *Psephophorus polygonus*. The extant *Dermochelys coriacea* maintains its body temperature at about 25 ºC to 26 ºC, and is also reported to possess counter-current heat exchangers to prevent overheating, as well as very good insulation (extensive sub-cutaneous fat) which allows it to venture from tropical seas (where it breeds) into temperate seas, where it feeds. These adaptations allow large reptiles like the leatherbacks to maintain a constant and relatively high body temperature (gigantothermy) and high metabolic rates (ALBRIGHT *et al.*, 2003). Because the first 'thin shelled' dermochelyids appeared in the Pliocene-earliest Pleistocene (Lee Creek Mine), the evolution of homothermic adaptations is suggested as being linked to the cooling of the oceans. The world climate in the Pliocene is generally described as becoming increasingly colder to finally reach a point where cold conditions prevailed and glaciation started in the latest Pliocene-earliest Pleistocene. See overview in KÖHLER (1997).

The leatherback turtle material from the Gram Formation furnish three new pieces of information. Firstly, they are type specimens of the base fauna of the Gram Formation. Secondly, they constitute the northernmost fossil evidence of the genus *Psephophorus* worldwide. Thirdly, the fact that three different specimens are known from the Gram Formation, indicates that leatherback turtles of the genus *Psephophorus* must be considered a common part of marine fauna of the Tortonian North Sea.

ACKNOWLEDGEMENTS

Dr. Klaus Wemmer from Geocenter of University Göttingen, Department Isotope Geology made the X-Ray Structure Analysis. Flemming Roth, former director of Museum Sønderjylland-Naturhistorie og Palæontologi, as well as Gilles Cuny of the Natural History Museum in Copenhagen are both thanked for allowing the authors to study and analyse material in their care. This research was made possible by a SYNTHESYS grant (DK-TAF-4140) to Hans-Volker Karl.

BIBLIOGRAPHY

ALBRIGHT, L. B.; WOODBURNE, M. O.; CASE, J. A. & CHANEY, D. S. (2003): A leatherback sea turtle from the Eocene of Antarctica: Implications for antiquity of gigantothermy in Dermochelyidae. *Journal of Vertebrate Paleontology*, **23**: 945-949.

BENDIX-ALMGREEN, S. E. (1983): *Carcharodon megalodon* from the Upper Miocene of Denmark, with comments on elasmobranch tooth enameloid: Coronoïn. *Bulletin of the Geological Society of Denmark*, **32**: 1-32.

BENDIX-ALMGREEN, S. E. (1986): Skaller, skeletter og årmillioners 1er. *In*: CHRISTENSEN, H. V. (Ed.): Midtsønderjyllands Museum på Gram Slot, 76-86. Naturhistorie og geologi. *Grafisk afdeling*. Amtsgården, Aabenraa, Denmark, pp. 22-33.

BUCHARDT, B. (1978a): Oxygen isotope paleotemperatures from the Tertiary period in the North Sea area. *Nature*, **275**: 121-123.

BUCHARDT, B. (1978b): Oxygen isotope paleotemperatures from the Tertiary North Sea and a 30 million years climatic periodicity. *Danish Meteorological Institute Climatological Papers*, **4**: 243-248.

COULSON, A.; KOHN, M.; SHIRLEY, M.; JOYCE, W. & BARRICK, R. (2008): Phosphate oxygen isotopes from marine turtle bones: Ecologic and palaeoclimate applications. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **264**: 78-84.

DUTTON, P. H.; BOWEN, B. W.; OWENS, D. W.; BARRAGAN, A. & DAVIS, S. K. (1999): Global phylogeography of the leatherback turtle (*Dermochelys coriacea*). *Journal of Zoology*, **248**: 397-409.

DYCK, K.-P. (1992): Die Meeresschildkröte *Psephophorus*-ein "Danekræ" aus dem Jahre 1904. *Aufschluss*, **43**: 103-104.

GAEMERS, P. A. M. (1978): A biozonation based on gadidae otoliths for the northwest European younger Cenozoic, with description of some new species and genera. *Mededelingen van de Werkgroup Tertiaire en Kwartaire Geologie*, **15**: 141-161.

GROESSENS VAN DYCK, M. & SCHLEICH, H. H. (1988): Zur Verbreitung tertiärer und quartärer Reptilien und Amphibien Europas-Belgien, Dänemark, Niederlande, Schweden. *Studia Geologica Salmanticensia*. Vol. Esp. **3**: 113-147.

HIRAYAMA, R. (1994): Phylogenetic systematics of chelonioid sea turtles. *The Island Arc*, **3**: 270-284.

HOCH, E. (2003): The first bird from the Danish Miocene. *In*: BARRETT, P. (Ed.): 51st *Symposium of Vertebrate Palaeontology and Comparative Anatomy. Abstracts*, pp. 20-21.

KARL, H.-V. & LINDOW, B. E. K. (2010): Eocene leatherback turtle material of the genus *Egyptemys* (Testudines: Dermochelyoidea) from Denmark. *Studia Geologica Salmanticensa*, **46**: 55-63.

KÖHLER, R. (1996): Chapter 3: *Turtles*, pp. 41-331, figs. 21-85, pls. 1-6. Unpupl. Diss. Univ. Otago, New Zealand.

LINDOW, B. E. K. (2004): Remains of fossil leatherback turtle (Testudinata: Dermochelyidae) from the Late Miocene Gram Formation of Denmark. *In*: EVANS, M. & FORREST, R. (Eds.): *52nd Symposium of Vertebrate Palaeontology and Comparative Anatomy. Abstracts*, p. 35.

LINDOW, B. E. K. & CUNY, G. (2008): Danmarks største fossiler. *Naturens Verden*, **91 (5)**: 32-40.

MAYER, H. von (1846): Letter on various fossils. *Neues Jahrbuch Mineralogie Geologie Paläontologie*, **1846**: 462-476.

PIASECKI, S. (2005): Dinoflagellate cysts of the Middle-Upper Miocene Gram Formation, Denmark. *Palaeontos*, **7**: 29-45.

PYENSON, N. & HOCH, E. (2007): Tortonian pontoporiid odontocetes from the eastern North Sea. *Journal of Vertebrate Paleontology*, **27**: 757-762.

RASMUSSEN, E. S. (2005): The geology of the upper Middle-Upper Miocene Gram Formation in the Danish area. *Palaeontos*, **7**: 5-18.

ROSENKRANTZ, A. (1921): Meddelelse om tertiære Skildpadder fra Danmark. *Meddelelser fra Dansk Geologisk Forening*, **6**: 2-3.

ROTHAUSEN, K. (1958): Marine Vertebraten (Odontaspidae, Lamnidae, Sparidae, Dermochelyidae, Squalodontidae) im oberoligozänen Meeressand von Süchteln und Düsseldorf. *Fortschritte der Geologie in Rheinland und Westfalen*, **1**: 363-384.

ROTH, F. (1978): *Mesocetus argillarius* sp.n. (Cetacea, Mysticeti) from Upper Miocene of Denmark, with Remarks on the Lower Jaw and the Echolocation System in Whale Phylogeny. *Zoologica Scripta*, **7**: 63-79.

ROTH, F. (1983): Livet i "Gram-havet". *Nordslesvigske Museer*, **10**: 10-28.

ROTH, F.; HOCH, E.; & ABRAHAMSSON, M. (2005): Gram lerets fossiler. *Naturens Verden*, **88 (4)**: 16-25.

RUSSELL, D. E. *et al.* (1982): Tetrapods of the Northwest European Tertiary Basin. *Geologisches Jahrbuch Reihe* A, **60**: 5-74.

SCHNETLER, K. I. (2005): The Mollusca from the stratotype of the Gram Formation (Late Miocene, Denmark). *Palaeontos*, **7**: 62-190.

SEELEY, H. G. (1880): Note on *Psephophorus polygonus* v. Meyer, a new Type of Chelonian reptile allied to the Leathery Turtle. *Quarterly Journal of the Geological Society of London*, **36**: 406-413.

STEEMAN, M. E. (2009): A new baleen whale from the Late Miocene of Denmark and early mysticete hearing. *Palaeontology*, **52**: 1169-1190.

TÜTKEN, T.; VENNEMANN, T. W.; JANZ, H. & HEIZMANN, H. E. P. (2006): Palaeoenvironment and palaeoclimate of the Middle Miocene lake in the Steinheim basin, SW Germany, a reconstruction from C, O, and Sr isotopes of fossil remains. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **241**: 457-491.

WINGE, H. (1910): Om Plesiocetus og Sqvalodon fra Danmark. *Videnskabelige Meddelelser fra den naturhistoriske Forening i København*, **7**: 1-37.

WOOD, R. C.; JOHNSON-GOVE, J.; GAFFNEY, E. S. & MALEY, K. F. (1996): Evolution and Phylogeny of Leatherback Turtles (Dermochelyidae), with Descriptions of New Fossil Taxa. *Chelonian Conservation and Biology*, **2**: 266-286.

