Till Finn med de bästa hälsn. /Johan

The first Mesozoic mammal from Scandinavia

JOHAN LINDGREN[1,2], JAN REES[3], MIKAEL SIVERSON[4] and GILLES CUNY[1,5]

Lindgren, J., Rees, J., Siverson, M. & Cuny, G., 2004: The first Mesozoic mammal from Scandinavia. *GFF*, Vol. 126 (Pt. 4, December), pp. 325–330. Stockholm. ISSN 1103-5897.

Abstract: Lowermost Cretaceous (Berriasian) strata of the Skyttegård Member (Rabekke Formation, Nyker Group) on the island of Bornholm, Denmark, have yielded a diverse terrestrial micro-vertebrate fauna. The assemblage is unique in several aspects, including e.g. the first Mesozoic mammal from Scandinavia. Here, we describe the mammal fossil, identified as a multituberculate upper premolar. The tooth is tentatively assigned to the monospecific genus *Sunnyodon*, as it shares the largest number of diagnostic dental features with the approximately coeval *S. notleyi* from the Purbeck Limestone Formation in southernmost England.

Keywords: Berriasian, Bornholm, Cretaceous, Denmark, Multituberculate, Nyker, Rabekke, *Sunnyodon*.

[1] *Geological Museum, University of Copenhagen, Øster Voldgade 5-7, DK-1350 København K, Denmark*
[2] *Department of Geology, GeoBiosphere Science Centre, Lund University, Sölvegatan 12, SE-223 62 Lund, Sweden; johan.lindgren@geol.lu.se*
[3] *Division of Environmental Sciences, Karlstad University, SE-651 88 Karlstad, Sweden; jan.rees@kau.se*
[4] *7 Stuart Street, Mosman Park, 6012 WA, Australia; cardabiodon@iinet.net.au*
[5] *gilles@savik.geomus.ku.dk.*
Manuscript received 8 August 2004. Revised manuscript accepted 8 November 2004.

Introduction

During the initial phase of the Cretaceous, vast parts of what is now the island of Bornholm in the Baltic Sea were developed into coastal plains bordered to the south-west by an attenuated seaway (see Noe-Nygaard et al. 1987, fig. 1). Extensional block faulting, eustasy, and a fluctuating climate resulted in the accumulation of a series of siliciclastic deposits; the Nyker Group (Gravesen et al. 1982). The strata reflect a mosaic of depositional environments, including fluvial channels, alluvial plains with palaeosols, swamps, coastal lagoons, and beaches. Today, these sediments crop out in a narrow belt stretching diagonally across the south-western corner of the island (Fig. 1B).

Vertebrate fossils have been found in several litho-stratigraphical units throughout the Nyker Group (particularly in its upper parts), and recorded remains include isolated teeth, finspines, and cephalic spines of hybodont sharks (Rees 2001; Bonde & Christiansen 2003), scales of various actinopterygians, partial dentitions of *Lepidotes* Agassiz, 1832 and pycnodonts, *Pleuropholis* Wagner, 1863 and two other small, nearly complete stem group teleosteans, crocodile remains including teeth of *Pholidosaurus* von Meyer, 1841 (Bonde & Christiansen 2003; Bonde 2004), turtle scutes, a dentary of a scincomorph lizard (Rees 2000), and a tooth of a dromaeosaurid dinosaur (Bonde & Christiansen 2003; Christiansen & Bonde 2003). The record of a titanosauriform tooth-crown (Bonde & Christiansen 2003) is doubtful due to the extreme wear of the specimen. The most prolific vertebrate-bearing strata known to date are those exposed in the A/S Carl Nielsen's sand pit at Robbedale (for locality description, see e.g. Gravesen et al. 1982; Noe-Nygaard & Surlyk 1988; Bonde 2004). Until now, however, no mammals had been found in Mesozoic sediments on Bornholm, nor in any other Mesozoic deposit in northern Europe.

While searching for selachian teeth in the Rabekke Formation (the lowermost formation of the Nyker Group), one of us (JR) discovered a diverse fossil micro-vertebrate fauna dominated by small crocodilians and turtles. The assemblage was extracted from a thin lens-shaped bed within a carbonaceous claystone of presumably Early Berriasian age (Christensen 1974), situated in a small coastal cliff-section east of the village of Arnager on the south coast of Bornholm (Fig. 1C). Apart from abundant crocodile teeth and turtle carapace fragments, the assemblage also includes numerous actinopterygian scales and jawbone fragments, skeletal elements of amphibians and primitive lizards, dromaeosaurid teeth, and one multituberculate tooth (the tetrapod fauna is currently under study). Below, we describe the multituberculate tooth; the first Mesozoic mammal from Scandinavia.

Geological framework and locality description

As a result of its position within the NW–SE trending Fennoscandian Border Zone, the geology of Bornholm is strongly affected by large-scale, rift induced block faulting. Extensional tectonics during the Upper Jurassic formed marked depressions in the crystalline basement through downward faulting of several blocks (Gravesen et al. 1982), which facilitated the deposition of

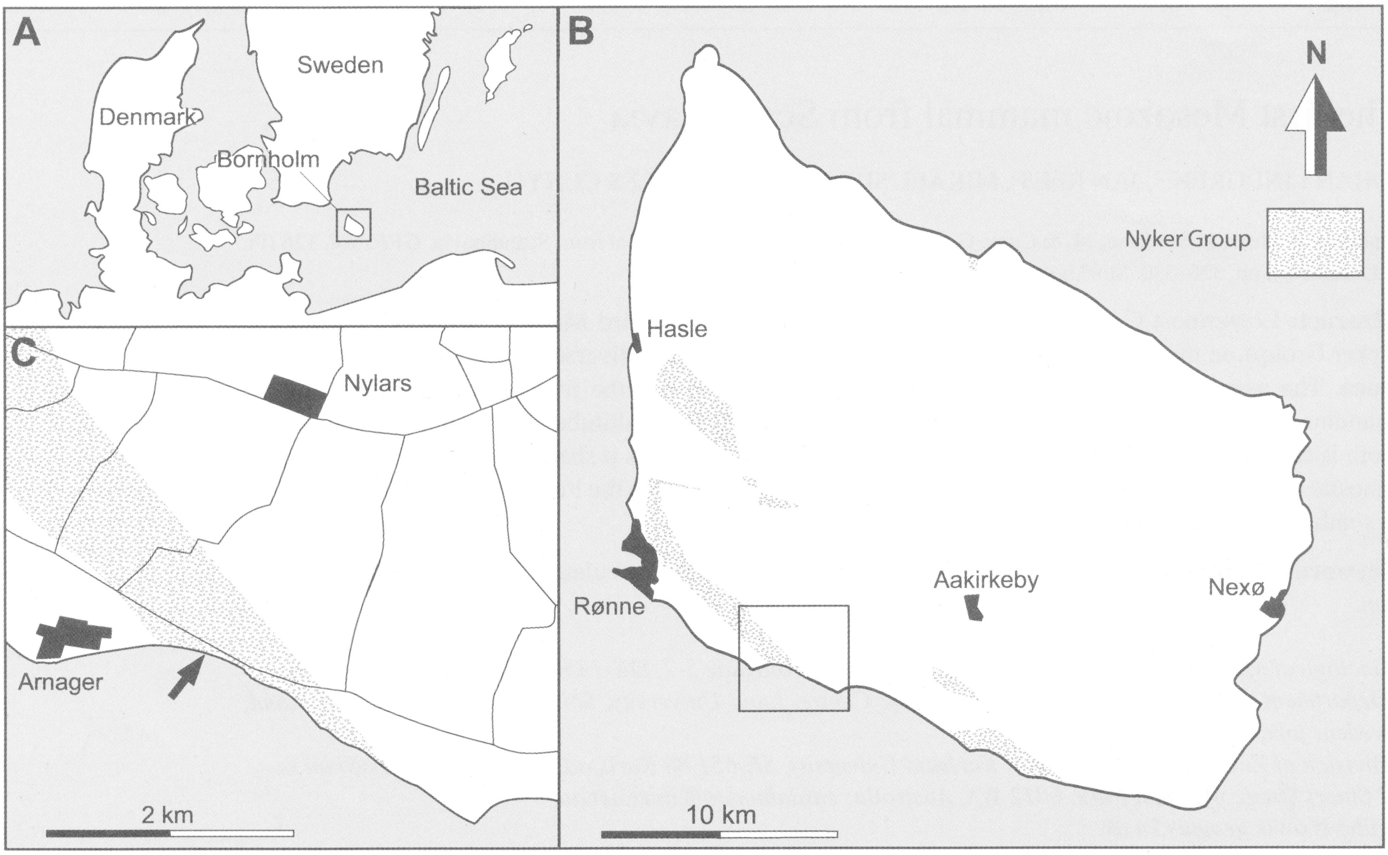

Fig. 1. **A.** Simplified map over southern Scandinavia and northern Germany showing the location of the island of Bornholm in the southern part of the Baltic Sea. **B.** Map over Bornholm showing the distribution of the lowermost Cretaceous Nyker Group on the south-western part of the island (modified from Rees 2000, fig. 1). **C.** Close-up map of Arnager Bay with the location of the outcrop examined marked with an arrow.

a thick (locally 250 m; see Gry 1960) sequence of siliciclastic strata during the earliest Cretaceous. The Nyker Group, comprising all Lower Cretaceous strata on Bornholm, is sub-divided into three consecutive formations, denominated, from bottom to top, Rabekke, Robbedale, and Jydegård (Gravesen et al. 1982). The sedimentary sequence commences with clayey to sandy limnic and fluviatile deposits of the Rabekke Formation. These strata are overlain by coastal and shallow marine sands of the Robbedale Formation, which, in turn, are disconformably (see Nielsen et al. 1996, fig. 2) replaced upsection by lagoonal and back-barrier clays and sands of the Jydegård Formation (Gravesen et al. 1982). Together, the sediments reflect varying depositional environments ranging from fully terrestrial to shallow marine conditions (Gravesen et al. 1982). Stratigraphically, the Nyker Group spans the Berriasian–Valanginian interval, although its lowermost parts may be of Tithonian age (e.g. Christensen 1974). Trace fossils are fairly common, especially in the Rabekke and Robbedale formations (Nielsen et al. 1996), whereas body fossils are generally less frequent and often restricted to certain horizons.

The Rabekke Formation (Gry 1960) is sub-divided into the lower Homanshald Member and the upper Skyttegård Member (Gravesen et al. 1982). While the Homanshald Member mainly comprises lightly coloured sandy sediments, the Skyttegård Member is principally composed of silts and clays with a high content of plant detritus. The former strata have been interpreted as representing fully continental conditions, whereas the latter probably accumulated within the supratidal and intertidal zones (Gravesen et al. 1982).

The outcrop that has yielded the multituberculate tooth described and illustrated herein is a small, partly overgrown natural cliff-section located approximately one km east of the hamlet of Arnager, on the south coast of Bornholm (N 55°03'13" E 14°47'51"; Fig. 1C). The exposed strata (in October 2003) have a thickness of less than two metres, a lateral extension of about 20 metres, and dip somewhat to the south-west. The section is part of the type locality of the Skyttegård Member (probably the middle portion, see Gravesen et al. 1982, fig. 28), and consists primarily of coal-rich, black clays and silts, interbedded by a few distinct lenses of lightly grey to almost brick-red silty claystone. The lenses are almost devoid of larger coal fragments, although abundant plant debris occurs in finer fractions. According to Petersen et al. (1996), the dark carbonaceous clays were deposited in an anoxic limnic environment with occasional marine influx causing brackish conditions. The lake was surrounded by dense vegetation dominated by gymnosperms which produced the plentiful plant litter found as detrital coal today. The formation of the lenses is currently not fully understood, although the high content of allochthonous tetrapod remains in the A-lens (see below) suggests that at least this bed represents some kind of concentration deposit. Apparently, the inferred flood event responsible for its formation gathered teeth and bones from a variety of habitats before depositing them on the lake floor. Moreover, the presence of scales and jawbone fragments from actinopterygians indicates that the pale sediment accumulated during a period of oxygenation of either the pond itself (which may normally have been stratified with anoxic conditions close to the bottom and oxygenated surface water) or some other open body of water nearby. Another possible explanation to the formation of vertebrate-bearing lenses has been provided by Nessov (1990; see also Nessov & Kielan-Jaworowska 1991), who suggested that concentrations of fossils in swampy environments were largely restricted to channels linking brackish- and freshwater basins. During periods of heavy rain the plains were submerged, causing the death of small land animals, such as dromaeosaurs and mammals, whereas an increased influx of unoxygenated brackish water (presumably originating from the deeper parts of the channels) caused the simultaneous death of amphibians and actinopterygians.

All accessible lenses were sampled for fossils, although only three contained identifiable vertebrate remains. The by far most productive horizon (denominated the A-lens herein), which yielded the mammal tooth described below, is situated near the base of the sedimentary sequence.

Material and methods

The material was obtained by washing and sieving the most prolific vertebrate-bearing lens. Following an initial sample of about seven kg (which yielded 26 crocodile teeth), large bulk samples were collected, with a total of more than 300 kg having been processed to date. The sediments were dried, treated with a solution of sodium carbonate, and washed in order to remove fine-grained fractions of the matrix. The residues were then picked for vertebrate remains in fractions down to 0.5 mm.

Depository acronyms. – DORCM, Dorset County Museum, Dorchester, England; MGUH, Geological Museum, University of Copenhagen, Copenhagen, Denmark.

Systematic palaeontology

The terminology is based mainly on that of Kielan-Jaworowska & Ensom (1992) and Hahn & Hahn (2003), while the systematics follows that of Kielan-Jaworowska & Hurum (2001, but see also Hahn [1993] for a discussion regarding the uncertain higher taxonomy of *Sunnyodon* Kielan-Jaworowska & Ensom, 1992). In accordance with the recommendations given by Smith & Dodson (2003), the following descriptive terms are used herein: mesial (anterior), distal (posterior), lingual (towards the tongue), labial (towards the lip), apical (towards the tip of the cusp), and basal (towards the root).

Abbreviations. – B – cusps of the labial (buccal) row, numbered from mesial to distal; L – cusps of the lingual row, numbered from mesial to distal; M – molars, numbered from mesial to distal; P – premolars, numbered from mesial to distal.

Order Multituberculata Cope, 1884

Family Paulchoffatiidae Hahn, 1969

Subfamily *Incertae sedis* (see Hahn 1993)

Genus *Sunnyodon* Kielan-Jaworowska & Ensom, 1992

Type species (monotypy). – *Sunnyodon notleyi* Kielan-Jaworowska & Ensom, 1992, from the Tithonian Cherty Freshwater Member of the Purbeck Limestone Formation in southernmost England.

Sunnyodon? sp.

Fig. 2

Material. – MGUH 27220, a posterior premolar from the upper left jaw.

Description. – MGUH 27220 is an incomplete posteriorly situated upper premolar (probably P4 or P5) lacking the root, the distal end of the crown (see discussion below), and parts of the shelf-like area lingual to the inner row of cusps. As preserved, the base of the crown comprises a strongly vaulted elongate plate measuring 1.24 mm in total length and 0.90 mm in maximum width. An asymmetrical excavation on the mesial margin of the plate divides the mesial rim into a gently bent labial corner and a more acutely inclined lingual one. Unfortunately, parts of the lingual face of the shelf-like plate are broken off, although the preserved mesial portion indicates that a weak ridge originally may have been present. In occlusal view, the labial margin is nearly straight. The inner (lingual) row includes three broad-based conical cusps (L1–L3) which increase in size from front to rear, whereas the outer (labial) row comprises two cusps (B1–B2) of sub-equal size; a smaller mesial one and a somewhat larger distal one. Two tiny cuspules are present; one located meso-lingually to the first cusp of the labial row and one situated immediately anterior to the first cusp of the lingual row. All cusps are ornamented with coarse radiating enamel crests, a few of which ramify halfway down the height of the cusps forming inverted Y. The apices of the cusps are slightly posteriorly pointed, and (with the exception of L3) lack apical wear. The three cusps of the lingual row are bound together by a longitudinally directed enamel ridge, whereas the two tubercles of the labial row are set apart from each other. The first cusp of the outer row is, however, connected to the second cusp of the inner row by an extended radiating enamel crest, while the second cusp of the labial row is linked to the third cusp of the lingual row in the same way.

Discussion. – The order Multituberculata comprises a diverse group of extinct allotherian mammals, characterised by their peculiar multicuspid (i.e. multituberculate) teeth (e.g. Kielan-Jaworowska & Hurum 2001; Sigogneau-Russell & Kielan-Jaworowska 2002). In multituberculates (as well as in other mammals), the dentition has four basic classes; incisors, canines, premolars, and molars. Each of these classes comprises teeth with a highly characteristic morphology (see e.g. Hahn 1969, fig. 20; Hahn & Hahn 2000, fig. 15.2–15.5), which greatly enhances the chances of confidently determine the specific jaw-position of an isolated tooth. The multituberculate tooth-crown from the Rabekke Formation displays several features diagnostic of posteriorly situated, upper premolars, such as an elongate form of the crown, and a relatively large number of conical cusps (see e.g. Hahn 1969, fig. 20; Hahn & Hahn 2000, fig. 15.5B).

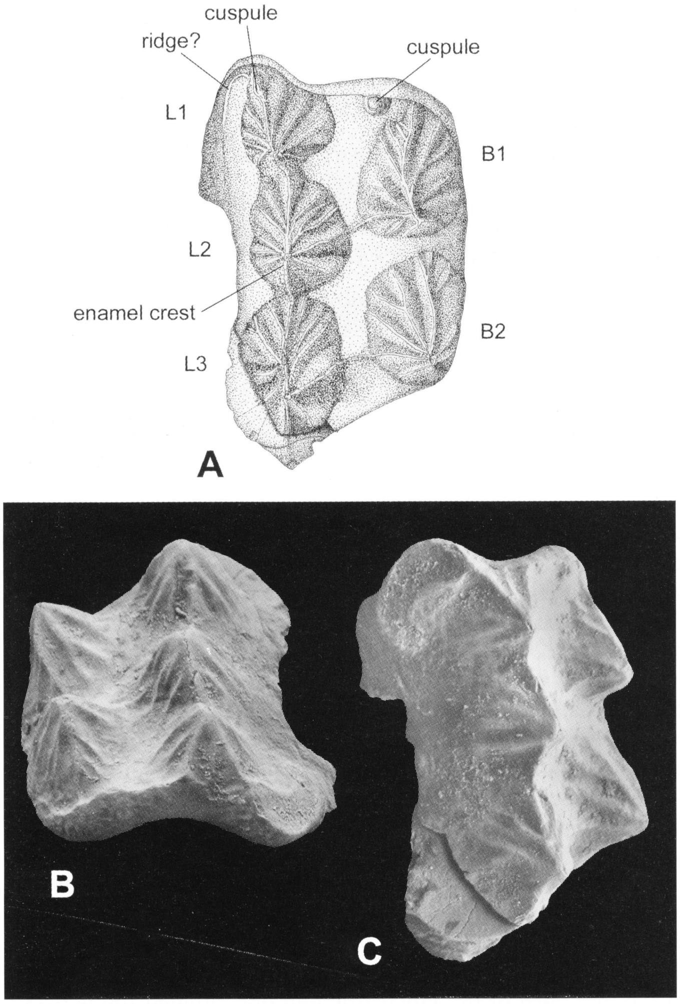

Fig. 2. Sunnyodon? sp. (P4 or P5) from the lower Berriasian Skyttegård Member of the Rabekke Formation (Nyker Group) on the island of Bornholm, Denmark, all ×45. **A.** Camera lucida drawing of MGUH 27220 in occlusal view, showing the dental terminology used in the text (note that both the cusps and the dental plate are covered with enamel). **B.** MGUH 27220 in oblique meso-occlusal view; mesial end facing the viewer. **C.** MGUH 27220 in oblique linguo-occlusal view; mesial end facing the top of the page.

Furthermore, conical cusps covered with radiating enamel crests are typical of premolars and not of incisors, canines or molars (Kielan-Jaworowska & Ensom 1992). Multituberculate premolars from the maxillae have two (or sometimes three, see Kielan-Jaworowska & Ensom 1994, pl. 1, fig. 6) rows of cusps of sub-equal size, whereas the corresponding teeth in the mandibles possess an inner row of markedly enlarged, blade-like cusps (forming a cutting edge) and an outer row of reduced swellings (Hahn & Hahn 2000). Upper premolars with a shortened labial row occur in several multituberculate families, including the Paulchoffatiidae (Hahn & Hahn 2003). In most of these taxa (but see also below) the cusps forming the outer row are restricted to the anterior half of the crown (see e.g. Kielan-Jaworowska & Ensom 1992, pl. 5, fig. 3; Hahn & Hahn 2003, fig. 5B–D). Moreover, the mesial margin of premolars and molars has often a more or less concave appearance (in occlusal view), whereas the distal end of the crown is sub-triangular to gently rounded (e.g. Hahn & Hahn 1998, fig. 1D, E, 2003; fig. 5B, C). Accordingly, MGUH 27220 is here interpreted as representing the mesial three-fourths of a posteriorly situated premolar (probably P4 or P5) from the left maxilla.

The paulchoffatiid *Sunnyodon notleyi* was originally erected upon a single, left ?P5 (Kielan-Jaworowska & Ensom (1992) stated that the tooth was from the right jaw, although this is almost certainly a typographical error as DORCM GS 18 is clearly from the left jaw, see Kielan-Jaworowska & Ensom 1992, pl. 5, figs. 3, 10). The tooth was found in Tithonian strata of the Cherty Freshwater Member of the Purbeck Limestone Formation on the south coast of England (see Kielan-Jaworowska & Ensom 1992). MGUH 27220 is tentatively assigned to *Sunnyodon* as it shares the largest number of diagnostic dental characters with *S. notleyi* (the type and only known species of the genus, see e.g. Kielan-Jaworowska & Ensom 1992, pl. 5, figs. 3, 10), including: (1) the relatively large size of the two labial cusps and their position in the middle of the tooth length. (2) The posteriorly increasing size of the cusps of the lingual row. (3) The connection of all cusps of the lingual row by a longitudinal ridge. (4) The presence of an enamel crest that links the second cusp of the labial row with the third cusp of the lingual row. (5) The coarse radially oriented enamel crests on the cusps. (6) The occurrence of a tiny cuspule meso-lingually to the first cusp of the labial row. (7) The presence of a minute cuspule immediately anterior to the first cusp of the lingual row.

However, besides these similarities, there are a few features of MGUH 27220 that are different from those of *S. notleyi*, such as: (1) its markedly concave mesial margin. In *S. notleyi* (i.e. DORCM GS 18), there is only a shallow medial depression on the mesial rim (see Kielan-Jaworowska & Ensom 1992, pl. 5, fig. 3), whereas the mesial margin is deeply excavated in MGUH 27220. (2) The shelf-like area lingual to the inner row of cusps appears originally to have been wider in MGUH 27220 than it is in *S. notleyi*. (3) MGUH 27220 is 50 percent larger than DORCM GS 18. Even though these slight, but still distinguishing, characters may be attributed to intraspecific variation (there are even marked differences between teeth from the left and right jaw in the same animal (cf. e.g. the basal outline of the left and right M1 in *Kuehneodon simpsoni* Hahn, 1969, see Hahn & Hahn 2000, fig. 15.3), they prevent us from assigning MGUH 27220 to the approximately coeval *S. notleyi* with confidence. Instead, the multituberculate from Bornholm is kept in open nomenclature pending the discovery of additional topotypic material of *S. notleyi* as well as additional material from the Skyttegård Member.

According to Kielan-Jaworowska & Ensom (1992) and Hahn (1993), *Sunnyodon* is dentally similar to *Paulchoffatia* Kühne, 1961, *Kuehneodon* Hahn, 1969, and *Kielanodon* Hahn, 1987, but differs in the arrangement of the cusps forming the labial row, and in the number and location of the cuspules. The combination of a labial row of cusps located symmetrically in the middle of the tooth length, and two cuspules (excluding the minute bump immediately anterior to L1); one mesial and one distal to the labial row, respectively, separate *Sunnyodon* from other genera of the Paulchoffatiidae (cf. Hahn 1969, fig. 9 *Paulchoffatia*, fig. 20 *Kuehneodon*; Hahn 1987, figs. 7, 8 *Kielanodon*; Kielan-

Jaworowska & Ensom 1992, pl. 5, figs. 3, 10 *Sunnyodon*). Furthermore, *S. notleyi* possesses an incipient posterior lingual ridge, a feature otherwise unknown in this family (Kielan-Jaworowska & Ensom 1992).

In addition to the above mentioned genera, MGUH 27220 superficially resembles two posterior upper premolars assigned to as Pinheirodontine gen. et sp. indet. by Hahn & Hahn (1999, fig. 59A–D) from the Berriasian of Porto Pinheiro at the Atlantic coast of Portugal. The pinheirodontine premolars have a cusp-arrangement similar to that of MGUH 27220, and the mesial margin is excavated in both teeth. They differ, nonetheless, from the Bornholm multituberculate in lacking cuspules, and the shelf-like area labial to the outer row of cusps is more pronounced in the two Portuguese specimens than it is in MGUH 27220.

Palaeobiogeography

The Paulchoffatiidae is an exclusively European family of multituberculates, with a spatial distribution spanning the Iberian Peninsula (Portugal and Spain), possibly Belgium (see below), and the British Isles (Hahn 1993; Kielan-Jaworowska & Hurum 2001). Stratigraphically, the group ranges from the Upper Triassic (Late Norian, see Hahn 1993) or the Middle Jurassic (Upper Bathonian, see Kielan-Jaworowska & Hurum 2001) to the mid-Cretaceous (Barremian), hence being the oldest multituberculate clade known to date (e.g. Hahn & Hahn 1999, fig. 71). The vast majority of described paulchoffatiids originates from the Guimarota Coal Mine (Middle Kimmeridgian) in Leiria, western Portugal (e.g. Hahn & Hahn 2000). So far, eight genera have been identified from partial skulls, mandibles and isolated teeth collected from the lignite-bearing strata exposed in the mine, including the paulchoffatiines *Paulchoffatia*, *Guimar-otodon* Hahn, 1969, *Meketibolodon* Hahn, 1993, *Pseudobolodon* Hahn, 1977, *Henkelodon* Hahn, 1977, *Kielanodon*, and *Meketichoffatia* Hahn, 1993, as well as the kuehneodontine *Kuehneodon*. Paulchoffatiids from other areas of Europe are based solely on isolated teeth and include *Galveodon* Hahn & Hahn, 1992 and *Lavocatia* Canudo & Cuenca-Bescós, 1996, from the Lower Barremian of Galve and Uña in north-eastern Spain (see also Crusafont & Gibert 1976), and *Gerhardodon* Kielan-Jaworowska & Ensom, 1992 and *Sunnyodon* from the Tithonian part of the Purbeck Limestone Formation in southernmost England. Other inferred early paulchoffatiids, such as *Mojo* Hahn et al., 1987, from the Upper Norian of Habay-la-Vieille in southern Belgium, and an enigmatic incisor found in Upper Bathonian deposits of the Kirtlington Mammal Bed in Oxfordshire, England (Freeman 1979), are imperfectly known and their affinity is still being debated (Hahn 1993). The presence of *Sunnyodon*? sp. in the Lower Berriasian of Bornholm, Denmark, extends the geographical range of the Paulchoffatiidae beyond Portugal, Spain and England, and represents the most northerly occurrence of the group so far.

Acknowledgements. – The initial fieldwork was carried out by JR during a post-doctoral fellowship financed by Nordisk Forskerutdanningsakademi (NorFa), with additional funding provided by the Geological Museum in Copenhagen. Further fieldwork was supported by grants from Crafoordska stiftelsen. JL acknowledge Kulturarvstyrelsen in Denmark for providing him with a research fellowship at the Geological Museum in Copenhagen. Anders Lindh and Anita Löfgren took the SEM photographs. Zofia Kielan-Jaworowska and Gerhard Hahn reviewed the manuscript and provided useful comments which greatly improved the text. Finally, Regitze Benthien assisted in numerous ways. To all our sincere thanks.

References

Agassiz L.J.R., 1832: Untersuchungen über die fossilen Fische der Lias-Formation. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde 3*, 139–149.

Bonde, N., 2004: An Early Cretaceous (Ryazanian) fauna of 'Purbeck-Wealden type' at Robbedale, Bornholm, Denmark. *In* G. Arratia & A. Tinori (eds.): *Mesozoic Fishes 3 – Systematics, Paleoenvironments and Biodiversity*, 507–528. Verlag Dr. Friedrich Pfeil, München.

Bonde, N. & Christiansen, P., 2003: New dinosaurs from Denmark. *Comptes Rendus Palevol 2*, 13–26.

Canudo, J.I. & Cuenca-Bescós, G., 1996: Two new mammalian teeth (Multituberculata and Peramura) from the Lower Cretaceous (Barremian) of Spain. *Cretaceous Research 17*, 215–228.

Christensen, O.B., 1974: Marine communications through the Danish Embayment during uppermost Jurassic and lowermost Cretaceous. *Geoscience and Man 6*, 99–115.

Christiansen, P. & Bonde, N., 2003: The first dinosaur from Denmark. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 227*, 287–299.

Cope, E.D., 1884: The Tertiary Marsupialia. *American Naturalist 18*, 686–697.

Crusafont, M. & Gibert, J., 1976: Los primeros multituberculados de España, nota preliminar. *Acta Geologica Hispanica 11*, 57–64.

Freeman, E.F., 1979: A Middle Jurassic mammal bed from Oxfordshire. *Palaeontology 22*, 135–166.

Gravesen, P., Rolle, F. & Surlyk, F., 1982: Lithostratigraphy and sedimentary evolution of the Triassic, Jurassic and Lower Cretaceous of Bornholm, Denmark. *Geological Survey of Denmark, Series B 7*, 1–51.

Gry, H., 1960: Geology of Bornholm. Guide to Excursions Nos. A 45 and C 40. *International Geological Congress. 21st Session*, Copenhagen. 16 p.

Hahn, G., 1969: Beiträge zur Fauna der Grube Guimarota Nr. 3. Die Multituberculata. *Palaeontographica, Abteilung A 133*, 1–100.

Hahn, G., 1977: Neue Schädel-Reste von Multituberculaten (Mamm.) aus dem Malm Portugals. *Geologica et Palaeontologica 11*, 161–186.

Hahn, G., 1987: Neue Beobachtungen zum Schädel- und Gebiss- bau der Paulchoffatiidae (Multituberculata, Ober-Jura). *Palaeovertebrata 17*, 155–196.

Hahn, G., 1993: The systematic arrangement of the Paulchoffatiidae (Multituberculata) revisited. *Geologica et Palaeontologica 27*, 201–214.

Hahn, G. & Hahn, R., 1992: Neue Multituberculaten-Zähne aus der Unter-Kreide (Barremium) von Spanien (Galve und Uña). *Geologica et Palaeontologica 26*, 143–162.

Hahn, G. & Hahn, R., 1998: Neue Beobachtungen an Plagiaulacoidea (Multituberculata) des Ober-Juras 3. Der Bau der Molaren bei den Paulchoffatiidae. *Berliner Geowissenschaftliche Abhandlungen E 28*, 39–84.

Hahn, G. & Hahn, R., 1999: Pinheirodontidae n. fam. (Multituberculata) (Mammalia) aus der tiefen Unter-Kreide Portugals. *Palaeontographica, Abteilung A 253*, 77–222.

Hahn, G. & Hahn, R., 2000: Multituberculates from the Guimarota mine. *In* T. Martin & B. Krebs (eds.): *Guimarota – a Jurassic Ecosystem*, 97–108. Verlag Dr. Friedrich Pfeil, München.

Hahn, G. & Hahn, R., 2003: New multituberculate teeth from the Early Cretaceous of Morocco. *Acta Palaeontologica Polonica 48*, 349–356.

Hahn, G., Lepage, J.C. & Wouters, G., 1987: Ein Multituberculaten-Zahn aus der Ober-Trias von Gaume (S-Belgien). *Bulletin de la Société belge de Géologie 96*, 39–47.

Kielan-Jaworowska, Z. & Ensom, P.C., 1992: Multituberculate mammals from the Upper Jurassic Purbeck Limestone Formation of southern England. *Palaeontology 35*, 95–126.

Kielan-Jaworowska, Z. & Ensom, P.C., 1994: Tiny Plagiaulacoid multituberculate mammals from the Purbeck Limestone Formation of Dorset, England. *Palaeontology 37*, 17–31.

Kielan-Jaworowska, Z. & Hurum, J.H., 2001: Phylogeny and systematics of multituberculate mammals. *Palaeontology 44*, 389–429.

Kühne, W.G., 1961: Eine Mammaliafauna aus dem Kimeridge Portugals. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 1961*, 374–381.

Meyer H. von 1841: *Pholidosaurus schaumburgensis*, ein Saurus aus dem Sandstein der Wald-Formation Nord-Deutschlands. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde 4*, 413–418.

Nessov, L.A., 1990: Small ichthyornithiform bird and other bird remains from Bissekty Formation (Upper Cretaceous) of Central Kizylkum Desert. *In* R.L. Potapov (ed.): *Ornithological Investigations in Palearctic*, 59–62. USSR Academy of Sciences, Leningrad.

Nessov, L.A. & Kielan-Jaworowska, Z., 1991: Evolution of the Cretaceous Asian therian mammals. *In* Z. Kielan-Jaworowska, N. Heintz & H.A. Nakrem (eds.): Fifth Symposium on Mesozoic Terrestrial Ecosystems and Biota: Extended Abstracts, 51–52. *Contributions from the Paleontological Museum, University of Oslo 364*.

Nielsen, J.K., Hansen, K.S. & Simonsen, L., 1996: Sedimentology and ichnology of the Robbedale Formation (Lower Cretaceous), Bornholm, Denmark. *Bulletin of the Geological Society of Denmark 43*, 115–131.

Noe-Nygaard, N. & Surlyk, F., 1988: Washover fan and brackish bay sedimentation in the Berriasian-Valanginian of Bornholm, Denmark. *Sedimentology 35*, 197–217.

Noe-Nygaard, N., Surlyk, F. & Piasecki, S., 1987: Bivalve mass mortality caused by toxic dinoflagellate blooms in a Berriasian-Valanginian lagoon, Bornholm, Denmark. *Palaios 2*, 263–273.

Petersen, H.I., Bojesen-Koefoed, J.A. & Nytoft, H.P., 1996: Depositional environment and burial history of a Lower Cretaceous carbonaceous claystone, Bornholm, Denmark. *Bulletin of the Geological Society of Denmark 43*, 133–142.

Rees, J., 2000: An Early Cretaceous scincomorph lizard dentary from Bornholm, Denmark. *Bulletin of the Geological Society of Denmark 48*, 105–109.

Rees, J., 2001: Jurassic and Early Cretaceous selachians – focus on southern Scandinavia. *Lund Publications in Geology 153*, 1–19.

Sigogneau-Russell, D. & Kielan-Jaworowska, Z., 2002: Mammals from the Purbeck Limestone Group of Dorset, southern England. *Special Papers in Palaeontology 68*, 241–255.

Smith, J.B. & Dodson, P., 2003: A proposal for a standard terminology of anatomical notation and orientation in fossil vertebrate dentitions. *Journal of Vertebrate Paleontology 23*, 1–12.

Wagner A., 1863: Monographie der fossilen Fische aus den lithographischen Schiefern Bayerns, Zweite Abtheilung. *Abhandlungen der (Königlichen Bayerischen) Akademie der Wissenschaften 3*, 611–748.