



Disponible en ligne sur www.sciencedirect.com



GEOBIOS

Geobios xxx (2008) xxx–xxx

<http://france.elsevier.com/direct/GEOBIO/>

Original article

Theropod dinosaur teeth from the lowermost Cretaceous Rabekke Formation on Bornholm, Denmark

Des dents de dinosaure théropode de la formation Rabekke (Crétacé inférieur basal) à Bornholm, Danemark

Johan Lindgren^{a,*}, Philip J. Currie^b, Jan Rees^c, Mikael Siverson^{d,e},
Sofie Lindström^a, Carl Alwmark^a

^a Department of Geology, GeoBiosphere Science Centre, Lund University, Sölvegatan 12, 22362 Lund, Sweden

^b Department of Biological Sciences, University of Alberta, CW 405 Biological Science Building, Edmonton, Alberta T6G 2E9, Canada

^c Department of Biology, Karlstad University, 65188 Karlstad, Sweden

^d Department of Earth and Planetary Sciences, Western Australian Museum, Francis Street, 6000 Perth, Western Australia, Australia

^e School of Earth and Geographical Sciences, University of Western Australia, 35, Stirling Highway, 6009 Crawley, Western Australia, Australia

Received 16 May 2006; accepted 29 May 2007

Abstract

The dinosaur fauna of the palynologically dated lower Berriasian Skyttegård Member of the Rabekke Formation on the Baltic island of Bornholm, Denmark, is represented by isolated tooth crowns. The assemblage is restricted to small maniraptoran theropods, assigned to the Dromaeosauridae *incertae sedis* and Maniraptora *incertae sedis*. The dromaeosaurid teeth are characterized by their labiolingually compressed and distally curved crowns that are each equipped with a lingually flexed mesial carina and a distinctly denticulated distal cutting edge. A morphologically aberrant tooth crown (referred to as Maniraptora *incertae sedis*) has triangular denticles of uneven width, a feature occasionally found in Upper Cretaceous hesperornithiform toothed diving birds, but also in premaxillary teeth of the velociraptorine *Nuthetes* from the Lower Cretaceous of England.

© 2007 Elsevier Masson SAS. All rights reserved.

Résumé

La faune des dinosaures du membre Skyttegård (Berriasien inférieur basé sur les palynomorphes) de la formation Rabekke sur l'île baltique de Bornholm, Danemark, est représentée par des couronnes dentaires isolées. L'assemblage trouvé est restreint à des petits théropodes maniraptorés, assignés aux Dromaeosauridae *incertae sedis* et Maniraptora *incertae sedis*. Les dents des dromaeosauridés sont caractérisées par leurs couronnes comprimées labiolingualement et récurvées distalement, montrant une carène mésial courbée lingualement et une carène distale clairement denticulée. Il y a une couronne dentaire morphologiquement aberrante (identifiée comme Maniraptora *incertae sedis*) avec les denticules triangulaires et inégalement larges. Cette dernière caractéristique se trouve occasionnellement dans les oiseaux plongeants hesperornithiformes du Crétacé supérieur, mais aussi dans les dents prémaxillaires du vélociraptoriné *Nuthetes* du Crétacé inférieur d'Angleterre.

© 2007 Elsevier Masson SAS. All rights reserved.

Keywords: Bornholm; Cretaceous; Denmark; Dromaeosauridae; Teeth; Theropoda

Mots clés : Bornholm ; Crétacé ; Danemark ; Dromaeosauridae ; Dents ; Theropoda

1. Introduction

The Dromaeosauridae is a monophyletic clade of small- to medium-sized maniraptoran theropods that display a number of conspicuous features, such as well-developed raptorial talons

* Corresponding author.

E-mail address: johan.lindgren@geol.lu.se (J. Lindgren).

on their second pedal phalanges, stiffened tails and large claws for grasping (Ostrom, 1969). Much of what we know about dromaeosaurids is based on more or less complete skeletons from Cretaceous strata in western North America, Mongolia and China (Osborn, 1924; Ostrom, 1969; Currie, 1995; Barsbold and Osmólska, 1999; Xu et al., 1999; Xu and Wu, 2001). Although these spectacular finds are crucial to our understanding of the interrelationships and affinities of the Dromaeosauridae, assemblages of unassociated teeth and bones, such as the one from Bornholm described herein, provide us with a more complete picture of the temporal and spatial distribution of these dinosaurs.

In Denmark, exposed Mesozoic sediments on the mainland and all but one of the islands comprise offshore chalks and marls of Maastrichtian age. Potentially dinosaur-bearing continental, littoral and alluvial strata are restricted to the small Baltic island of Bornholm. Extensive exploration of the Lower Cretaceous sediments on Bornholm by the 'Fossil Project' (a local organization of skilled amateur collectors founded by Regitze Benthien) over the last few years yielded the first two dinosaur fossils from Denmark. A single indeterminable dromaeosaurid tooth crown (MGUH DK No. 315) was described as *Dromaeosauroides bornholmensis* by Christiansen and Bonde (2003), whereas a worn tooth (currently retained in the private collection of Mrs Benthien) was referred to a titanosaurid sauropod (Bonde and Christiansen, 2003; but see also Lindgren et al., 2004). Both specimens were collected from poorly lithified back-barrier and lagoonal sands of the Jydegård Formation (exposed in the A/S Carl Nielsen's gravel pit at Robbedale), deposited during late Berriasian time (Gravesen et al., 1982; Noe-Nygaard and Surlyk, 1988; Bonde, 2004). Recently, a few dinosaur footprints (MGUH Nos. 27754 and 27755), tentatively assigned to the Sauropoda and Thyreophora, were found preserved in sandstone blocks belonging to the Middle Jurassic Bagå Formation, on the west coast of the island (Milàn and Bromley, 2005).

Dinosaur material from other parts of Scandinavia is likewise scarce, with most finds comprising tridactylous footprints (Grallatoridae) from the Rhaetian and Hettangian of northwestern Skåne, the southernmost province of Sweden (Böslau, 1952; Ahlberg and Siverson, 1991; Gierlinski and Ahlberg, 1994; but see also Milàn and Gierlinski, 2004). A series of four consecutive dorsal vertebrae (of which only one, LO 9068t, is preserved in the collections of the Department of Geology, Lund University) were briefly described from Rhaeto-Liassic (Hettangian) beds of the Höganäs Formation in northwestern Skåne (Böslau, 1954). Several isolated teeth and vertebrae from neoceratopsian dinosaurs have been recovered from the lower Campanian of the Kristianstad Basin, southern Sweden (Lindgren et al., 2007). Three theropod teeth were reported by Persson (1959: p. 474, Pl. 20, Fig. 4) from the uppermost lower Campanian at the Ivö Klack site within the Kristianstad Basin. However, these specimens have been re-identified as teleost remains, most likely belonging to protosphyraenids (Lindgren and Siverson, 2002).

The theropod teeth described in this paper were recovered from a thin, lens-shaped bed within the carbonaceous

claystones and siltstones at the type section of the Skyttegård Member of the Rabekke Formation (Nyker Group) (Gry, 1960; Gravesen et al., 1982; Petersen et al., 1996) on the south coast of Bornholm. Apart from theropod teeth, the microvertebrate assemblage also includes numerous actinopterygian scales and jaw fragments, abundant crocodile teeth, turtle carapace fragments, skeletal elements of amphibians and lizards (Rees et al., 2005), and one multituberculate premolar (Lindgren et al., 2004). Despite being dissociated and fragmentary, the specimens from the Skyttegård Member represent a diverse vertebrate assemblage amongst the otherwise poorly known Lower Cretaceous terrestrial tetrapod faunas of northern Europe.

2. Geological setting and palynology

The Phanerozoic sequence on Bornholm has been subjected to large-scale, rift-induced block faulting, resulting in a mosaic of paralic facies types. Outcrops of Mesozoic sediments are restricted mainly to low coastal cliff sections and a few inland quarries on the southwestern part of the island. Geologically, Bornholm forms part of the Tornquist-Sorgenfrei Lineament, which, in turn, is situated within the Fennoscandian Border Zone. The terrestrial to marginal marine strata of the principally Lower Cretaceous Nyker Group crop out in the Holsterhus, Nyker, Knudsker, Salene, Bøsthøj and Arnager-Sose fault blocks (Gravesen et al., 1982; Petersen et al., 1996). These blocks were formed during the Triassic and Jurassic as a result of repeated periods of down-faulting and tilting along the Fennoscandian Border Zone (Gravesen et al., 1982). Subsequent erosion produced large quantities of siliciclastic sediments that filled depressions in the crystalline basement. At the time of deposition, Bornholm was situated along the edge of a narrow seaway connecting the Danish Embayment and the Polish Trough (see Noe-Nygaard et al., 1987: Fig. 1).

The Rabekke Formation (the lowermost formation of the Nyker Group) is subdivided into a lower Homanshald Member and an upper Skyttegård Member (Gravesen et al., 1982). In the Arnager-Sose block, an approximately 25 m thick sequence of medium- to coarse-grained fluvial sands of the Homanshald Member rests disconformably upon nearshore marine sandstones of the Lower Jurassic Hasle Formation. The Homanshald Member is replaced upsection by an up to 44 m thick succession of carbonaceous clays and silts belonging to the Skyttegård Member. The entire sequence spans the Berriasian–Valanginian interval, although its lowermost parts may be of Tithonian age (Christensen, 1974).

The outcrop that yielded the theropod teeth is a small, partly overgrown cliff facing Arnager Bay, approximately 1 km east of the hamlet of Arnager on the south coast of Bornholm (N 55°03'13" E14°47'51"; Fig. 1). Normally, the exposed strata have a thickness of less than two metres (although removal of recent beach deposits by winter storms occasionally unveils yet another metre of sediments), extend laterally about 20 m and dip somewhat to the southwest. The section is part of the type locality of the Skyttegård Member (type locality 3b, see Gravesen et al., 1982: Fig. 27) and consists of coal-rich, black

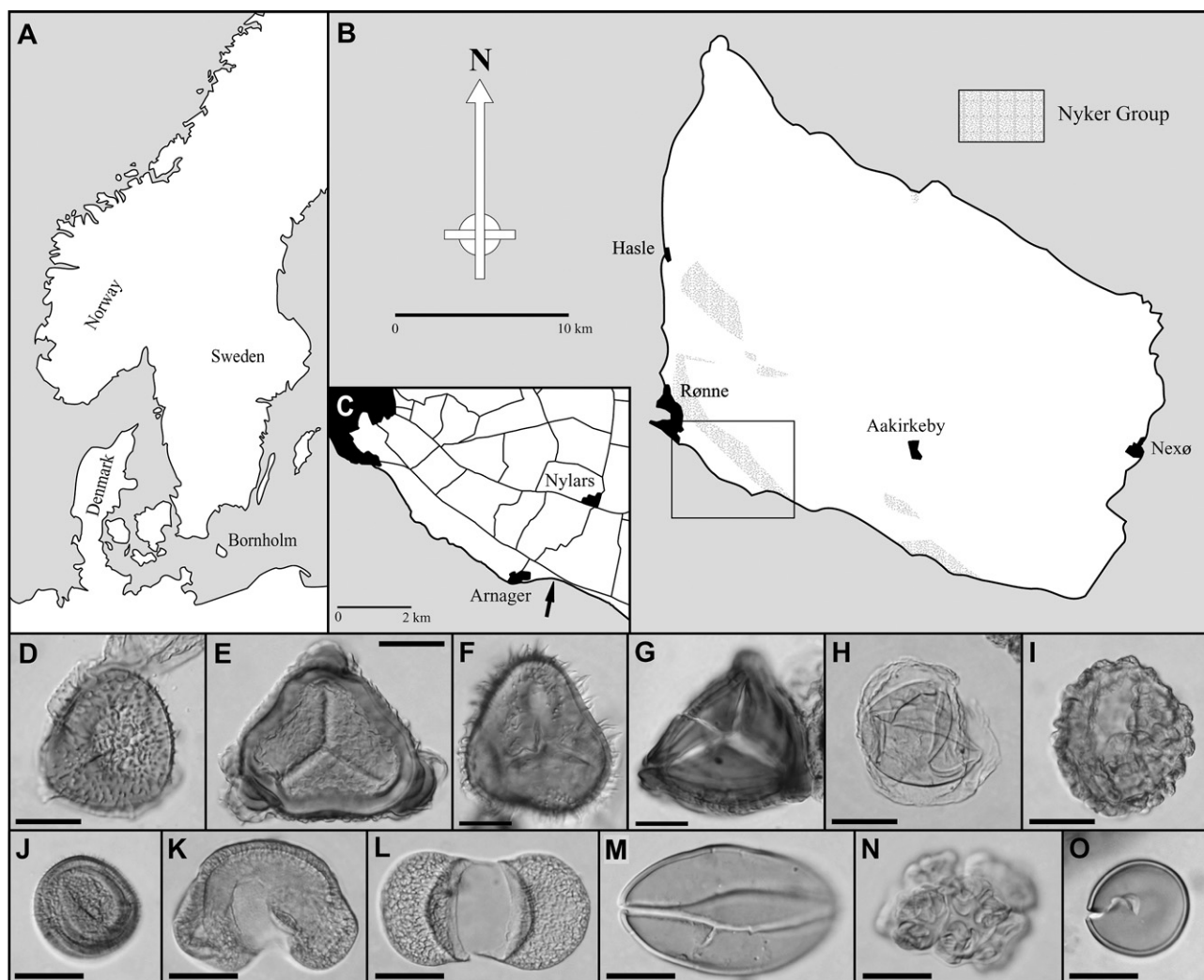


Fig. 1. **A:** simplified map over southern Scandinavia and northern Germany showing the location of Bornholm in the southern part of the Baltic Sea; **B:** map over Bornholm showing the distribution of the lowermost Cretaceous Nyker Group on the southwestern part of the island (modified from Rees, 2000); **C:** close-up map of Arnager Bay with the location of the outcrop examined marked with an arrow; **D–O:** selected palynomorph taxa from the Rabekke Formation, with slide number and England Finder coordinates. Scale bars are 20 µm; **D:** *Aequitriradites spinulosus*, Rabekke A: 3 D38/2 (LO 10184); **E:** *Trilobosporites* sp., Rabekke A: 2 F28/4 (LO 10185); **F:** *Pilosisorites trichopapillosus*, Rabekke A: 4 W36/3 (LO 10186); **G:** *Plicatella* sp., Rabekke A: 4 S38/2 (LO 10187); **H:** *Perinopollenites elatoides*, Rabekke A: 1 K34/2 (LO 10188); **I:** *Cerebropollenites macroverrucosus* (Thiergart) Schulz, 1967, Rabekke A: 1 O34/3 (LO 10189); **J:** *Classopollis echinatus*, Rabekke A: 1 K34/1 (LO 10190); **K:** *Parvisaccites radiatus*, Rabekke A: 4 Q21/2 (LO 10191); **L:** *Alisporites* sp., Rabekke A: 2 F28/1 (LO 10192); **M:** *Schizosporis* sp., Rabekke A: 1 M35/4 (LO 10193); **N:** *Botryococcus braunii*, Rabekke A: 4 M39/2 (LO 10194); **O:** *Ovoidites* sp., Rabekke A: 1 O30/2 (LO 10195).

clays and silts, interbedded by a few distinct lenses of light grey to almost brick-red silty clay stone. The vertebrate material derives from a prominent lenticular bed, up to 15 cm thick and about 10 m wide, located near the base of the exposed sedimentary sequence.

A palynological investigation of the vertebrate-bearing bed yielded a rich and well-preserved palynoflora dominated by the *Perinopollenites elatoides* Couper, 1958 (Taxodiaceae, 52%), *Alisporites* spp. (pteridosperms, 11%), *Callialasporites* spp., and *Auracariacites australis* Cookson, 1947 (Auracariaceae, 5%), together with abundant fern spores assigned to *Deltoidospora* spp. (7%). The co-occurrence of common *Parvisaccites radiatus* Couper, 1958, less abundant *Classopollis echinatus* Burger, 1965 and *Aequitriradites spinulosus* (Cookson and Dettmann) Cookson and Dettmann, 1961, and rare *Pilosisorites tricho-*

papillosus (Thiergart) Delcourt and Sprumont, 1955, *Trilobosporites bernissartensis* (Delcourt and Sprumont) Potonié, 1956 and *Plicatella* spp. verify an Early Cretaceous age (Petersen et al., 1996). In northwestern Europe, *A. spinulosus* and *Plicatella* spp. have their first appearance datums (Fig. 2) in assemblages contemporaneous with the Runctoni standard ammonite Zone (Hoedemaeker and Herngreen, 2003, 2004). Thus, the Skyttegård Member palynoflora and vertebrate fauna are no older than early Berriasian in age (Fig. 2).

The high abundance of the colonial green alga *Botryococcus braunii* Kützing, 1849 in the Skyttegård Member indicates deposition in a freshwater environment and this is further corroborated by abundant zygnematacean zygospores assigned to *Ovoidites* spp. and *Schizospora* spp. Extant zygnematacean green algae can be found in many different habitats, but they

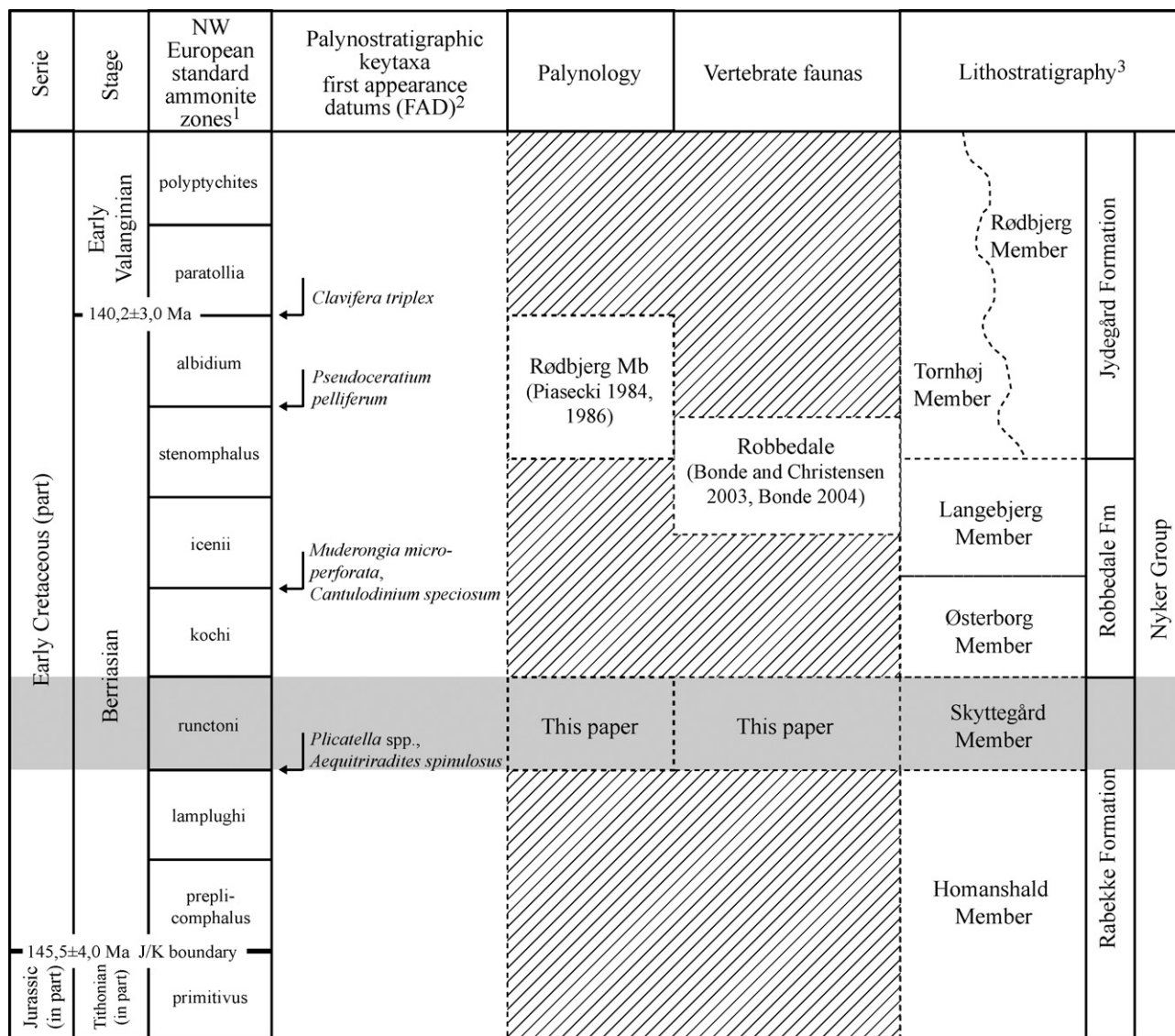


Fig. 2. Lithostratigraphy, palynology and vertebrate faunas of the Early Cretaceous of Bornholm, partly after ¹Herngreen et al. (2003), ²Poulsen and Riding (2003), ³Hoedemaeker and Herngreen (2003, 2004), ⁴Gravesen et al. (1982) and Petersen et al. (1996). Jurassic-Cretaceous boundary is currently placed at the base of the Jacobi Tethyan Ammonite Zone, that can be correlated with the base of the Preplicomphalus Boreal Ammonite Zone (Hunt, 2004).

proliferate in stagnant and oxygen rich water in lakes or ponds where they form green, slimy masses of ‘pond scum’ on the surface (van Geel and Grenfell, 1996). For most extant zygmematacean species, the optimum growth conditions occur where temperatures range from 14 to 22 °C (van Geel and van der Hammen, 1978). This is in agreement with the belemnite palaeotemperatures of 16–23 °C for northwestern Europe (Great Britain and Germany) during the latest Jurassic-earliest Cretaceous (Gröcke et al., 2003). However, zygmematacean zygospores form when living conditions turn harsh, such as during summer droughts or winter freezes (van Geel and Grenfell, 1996). The high abundance of zygmematacean zygospores in the Rabekke Formation, thus suggests that deposition took place within the 14–22 °C temperature range, but with seasonal climatic variations. Modern *Botryococcus Kützing*, 1849 is found in tropical to temperate regions, where it forms a thick surface scum in freshwater bogs, lakes, ponds and

temporary pools. It is also known to tolerate seasonally cooler climates and can be abundant in brackish water environments (Batten and Grenfell, 1996). The total organic content is dominated by fluffy, amorphous organic matter that makes up 58%, while spores, pollen and microalgae compose 22%, wood remains are 15% and non-woody plant tissue and cuticles 5%.

The abundance of *Botryococcus* and zygmematacean zygospores in the vertebrate-bearing bed of the Skyttegård Member suggests that this sediment was deposited in a quiet, small lake, where at least the surface water must have been well oxygenated, free of sediment and with a sufficient nutrient supply to favour algal growth. The abundance of zygmematacean zygospores also suggests that living conditions for these algae were sometimes harsh, perhaps due to a seasonal climate. The large amount of amorphous organic matter suggests that the bottom conditions were anoxic. The presence of rare specimens of marine dinoflagellate cysts in the palynoflora

shows that the area was situated in a near marine environment and had an occasional influx of saltwater. This is in accordance with Petersen et al. (1996) who based on kerogen and biomarker analyses suggested that the black carbonaceous mudstones of the Skyttegård Member were deposited in an anoxic lake in a coastal setting. According to their data, the organic matter in the lake was chiefly derived from gymnospermous vegetation immediately surrounding the lake, mainly consisting of Pinaceae and Cupressaceae (Petersen et al., 1996). The present palynological study indicates that the lake was surrounded by gymnospermous vegetation consisting predominantly of Taxodiaceae, with common pteridosperms, Auracariaceae and ferns. Based on morphological and genetic characters, Taxodiaceae is today included within Cupressaceae (Gadek et al., 2000).

3. Material and methods

The theropod teeth consist only of crowns, perhaps because of the natural process of resorption of the root during tooth-replacement and/or because enamel-covered crowns are more likely to be preserved than the roots. The first explanation seems more likely because of the presence of wear facets on the tooth apices, because of the loss of denticles and because of the presence of resorption pits in the tooth bases. The colours of the teeth vary from black to bleached white, although there is no correlation between colour and state of preservation. A few specimens are broken and fragmentary, suggesting pre-depositional transport over some distance, whereas others are almost intact and probably were shed close to the place of burial.

The teeth were obtained by washing and sieving large bulk sediment samples collected from the vertebrate-bearing lens. The samples were dried, treated with a boiling solution of sodium carbonate and then washed in hot water to remove fine-grained fractions of the matrix. The sifted residues were dried and then picked for vertebrate remains in fractions down to 0.5 mm. Three nearly complete crowns (MGUH Nos. 28403–28405) were hardened by application of polyvinylbutyral dissolved in acetone. All fossils were coated with gold prior to being digitally photographed using a scanning electron microscope. Measurements were taken using a binocular microscope incorporating an optical micrometer calliper. The geographical position (WGS 84 datum) of the locality was recorded using a Garmin II Plus satellite GPS receiver.

Institutional abbreviations are as follows: BMNH, Natural History Museum, London, England; LO, Department of Geology, Lund University, Lund, Sweden; MGUH, Geological Museum, University of Copenhagen, Copenhagen, Denmark; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Canada.

4. Tooth morphology and taxonomy

The utility of isolated teeth in taxonomic studies of theropods has been thoroughly demonstrated in papers by, among others, Currie et al. (1990), Farlow et al. (1991), Rauhut

and Werner (1995), Baszio (1997), and Smith et al. (2005). As emphasised by these authors, differences due to ontogeny and the normal range of variation within a species must be taken into consideration when comparing teeth of different species. Moreover, the gross crown morphology changes along the dental arcade. In order to enhance the utility of isolated teeth in theropod taxonomy, Currie et al. (1990) established a number of descriptive and measurable parameters based on the overall morphology of the crown and on the distribution of denticles (if present) along its carinae. This descriptive approach was subsequently refined by Rauhut and Werner (1995), who introduced a denticle size difference index (DSDI – the ratio of the number of denticles per given length unit of the mesial and distal carina), which facilitates comparison between tooth crowns of different size.

In accordance with the recommendations given by Farlow et al. (1991), the accustomed measurement of tooth size used herein is mesiodistal (fore-aft) basal length (FABL) and it is against this standard that all other measurements are compared. Tooth crown height (TCH) was measured perpendicular to FABL and represents the vertical distance from the base to the tip of the crown (thus disregarding its curvature), whereas tooth basal width (BW) was measured at right angles to both FABL and TCH (see Fig. 3 in Sankey et al., 2002).

5. Systematic palaeontology

DINOSAURIA Owen, 1842

SAURISCHIA Seeley, 1887

THEROPODA Marsh, 1881

MANIRAPTORA Gauthier, 1986

DROMAEOSAURIDAE Matthew and Brown, 1922

Dromaeosauridae incertae sedis

Referred material: MGUH Nos. 28403–28409 and five unnumbered fragments, Geological Museum, Copenhagen.

Description: The three best preserved teeth are described separately, followed by a more general description of the more fragmentary specimens, with special attention given to characters of taxonomic interest.

MGUH No. 28403 (Fig. 3A–C) is an isolated, presumably shed, dentary tooth crown assumed to have come from the distal part of the mandible. As preserved, the strongly labiolingually flattened crown measures 5.0 mm in TCH, 3.5 mm in FABL and 1.3 mm in BW. The original height is estimated to have been around 5.5 mm. The tip of the crown is broken off, although a small wear-facet is still preserved near the apex on the labial face. The crown is strongly curved distally and the apex extends beyond the distal demarcation of the base of the crown. The mesial carina does not reach the base of the crown and basally is somewhat twisted towards the lingual face. A few faintly dimpled enamelled edges that may be worn remnants of serrations are present on a small apical portion of the otherwise smooth mesial carina. The distal carina bears chisel-shaped, elongate denticles. There are on an average seven posterior denticles per millimetre. In lateral view, the apices of the serrations are gently convex and the longitudinal axis of each

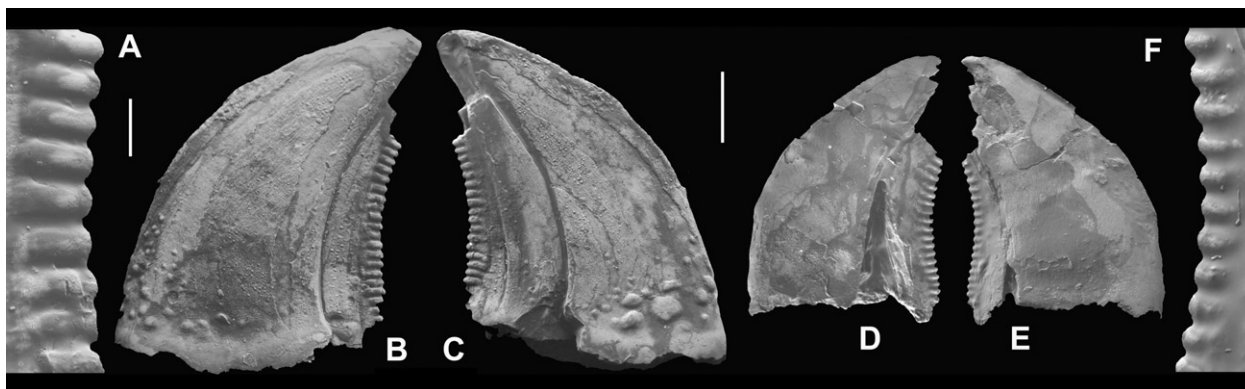


Fig. 3. Two isolated, presumably shed, dromaeosaurid tooth crowns from the lower Berriasian (Lower Cretaceous) Skyttegård Member of the Rabekke Formation (Nyker Group) on the Baltic island of Bornholm, Denmark. A–C: MGUH No. 28403 in B: labial and C: lingual views; A: enlargement of distal denticles; D–F: MGUH No. 28404 in D: labial and E: lingual views; F: enlargement of distal denticles. Scale bars represent 0.2 mm (A, F) and 1 mm (B–E).

denticle is straight. Grooves are present between adjacent denticles, but interdental slits are not visible, probably due to matrix and/or the hardening agent that partly fills the grooves. The grooves do not extend onto the surface of the crown. Fine, hairline striations cover much of the crown surface, although it cannot be determined whether this enamel texture represents original ornamentation or post-depositional damage and abrasion. Prominent granulae of uneven size and shape occupy the more proximal portion of the crown, particularly on the mesial half. A broad and shallow vertical furrow extends vertically along the mid-line of the labial face of the crown, contributing to the somewhat hourglass-shaped basal outline.

MGUH No. 28404 (Fig. 3D–F) is an incomplete tooth crown, probably from the posterior portion of the maxilla. Much of the apex and part of the labial surface are broken off, but it measures 4.1 mm in TCH, 2.5 mm in FABL and 1.4 mm in BW. An unserrated yet nearly complete (it reaches the base of the crown) and lingually flexed mesial carina and a denticulated distal cutting edge divide the crown into labial and lingual surfaces of sub-equal convexity. The enamelled faces are covered by faint, undulating striae and the upper half of the crown is strongly curved distally. The distal denticles are longer than wide and are separated from one another by indistinct grooves. There are approximately eight distal serrations per millimetre. The closely spaced posterior denticles of MGUH No. 28404 resemble those of MGUH No. 28403, although they have a somewhat more angular lateral outline. The basal cross-section of the crown is teardrop-shaped, with the rounded base of the teardrop on the mesial side of the crown.

MGUH No. 28405 (Fig. 4A–D) is a fairly well preserved, 1.5 mm tall (TCH), 1.2 mm long (FABL) and 0.75 mm wide (BW) distally situated crown, probably from the upper jaw. The tooth is strongly curved distally from about the mid-point of its height, and the enamelled faces are smooth. Conspicuous wear-facets are present on the labial face of the broken and worn apex and along the mesial edge of the crown, whereas the distal carina is reasonably intact and equipped with prominent serrations. The denticles are almost as high as they are wide and curve slightly towards the tip of the crown. Each denticle is blunt and broad-based. The grooves are inconspicuous and interdental slits cannot be seen. In cross-section, the labial

face is gently convex, whereas the lingual face is more strongly convex. A shallow, vertical groove follows the curvature of the crown along the centre of the labial face.

Fragments of theropod teeth have tentatively been assigned to the Dromaeosauridae based upon the presence of well-developed serrations that overlap in gross denticle morphology with those of MGUH Nos. 28403 and 28404. In MGUH Nos. 28406 and 28407, the denticles are somewhat hooked towards the tip of the crown (Fig. 4I–L, O–Q), whereas they are straight in MGUH No. 28408 (Fig. 4E–F). The labial and lingual surfaces of MGUH No. 28406 are covered by a small number of vertical ridges, although this may be due to secondary cracking of the enamel (Fig. 4I–L). One specimen, MGUH No. 28409 (Fig. 4R), lacks enamel (probably because of etching by digestive acids), but has a characteristic labiolingually flattened cross-section, similar to that of MGUH No. 28403.

Remarks: In a work devoted to theropod teeth from Dinosaur Provincial Park (Alberta, Canada), Currie et al. (1990) observed that isolated maxillary and dentary teeth of dromaeosaurids can be readily distinguished from those of other toothed theropods. Dromaeosaurid teeth are unique in that they are markedly labiolingually compressed and strongly curved distally. Moreover, they are equipped with mesial and distal carinae and prominent denticles are present on at least the posterior cutting edge. The mesial carina is often sigmoid in mesial view and somewhat twisted towards the lingual face (Currie et al., 1990; but see also Sankey et al., 2002). Barsbold (1983) divided the Dromaeosauridae into the subfamilies Dromaeosaurinae and Velociraptorinae. This distinction is reflected also in the dental apparatus. Whereas the denticles are blunt and almost as high as they are long in *Dromaeosaurus* Matthew and Brown, 1922 (the only valid genus currently included in the Dromaeosaurinae), velociraptorines, such as *Atrociraptor* Currie and Varricchio, 2004, *Deinonychus* Ostrom, 1969, *Saurornitholestes* Sues, 1978, and *Velociraptor* Osborn, 1924, possess elongate denticles and there is also a significant size disparity between the denticles on the mesial carina and those on the distal cutting edge (Ostrom, 1969; Currie et al., 1990; Barsbold and Osmólska, 1999).

With the exception of MGUH No. 28410a–d (see below), the theropod tooth crowns from the Rabekke Formation correspond

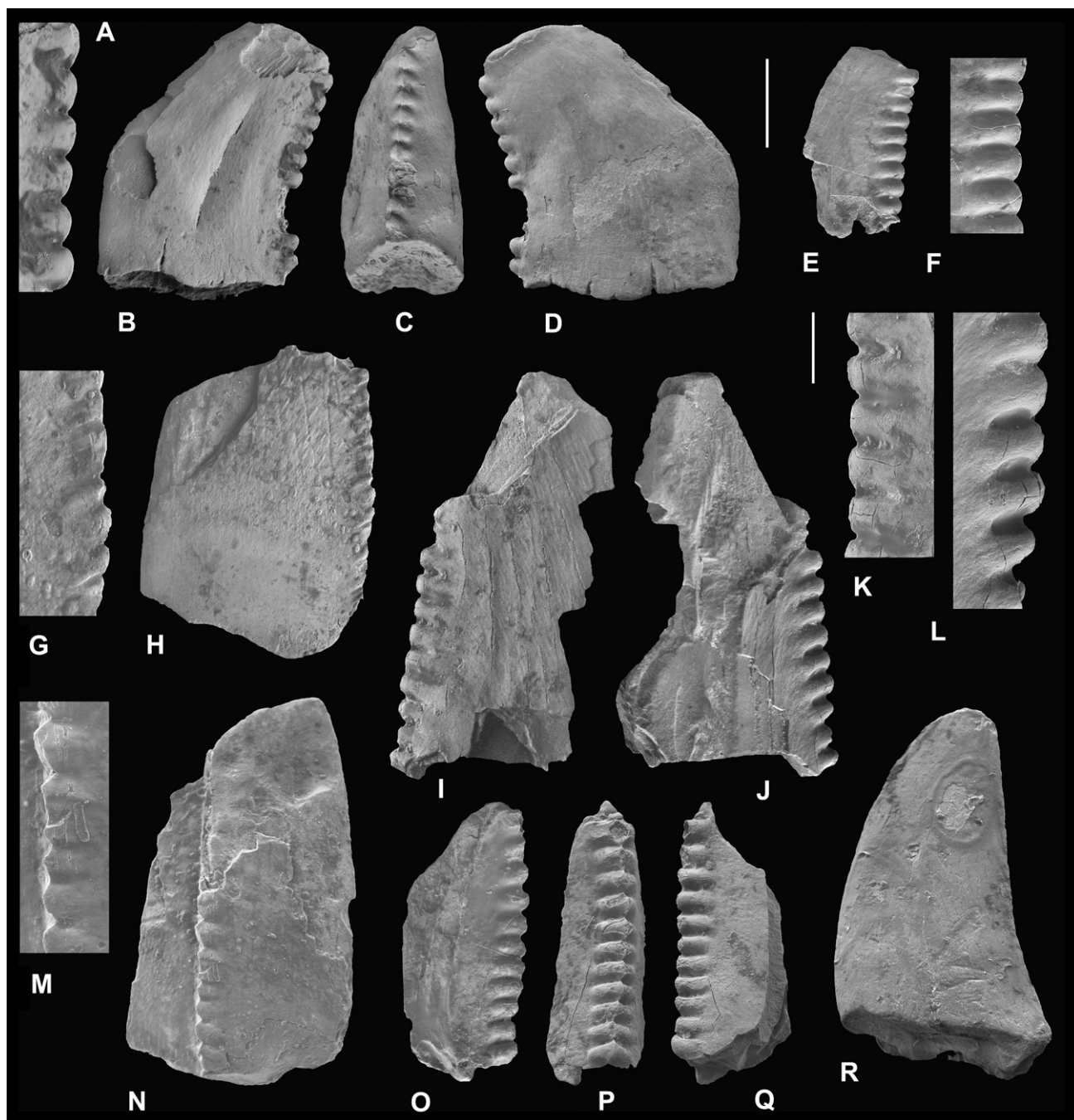


Fig. 4. Selected theropod teeth from the lower Berriasian (Lower Cretaceous) Skyttegård Member of the Rabekke Formation (Nyker Group) on the Baltic island of Bornholm, Denmark. **A–D**: a possible dromaeosaurine dromaeosaurid ('tooth morphotype three'), MGUH No. 28405, in **B**: labial, **C**: distal and **D**: lingual views; **A**: enlargement of distal denticles; **E, F**: Dromaeosauridae *incertae sedis* ('tooth morphotype one'), MGUH No. 28408 in **E**: lateral view, **F**: enlargement of distal denticles; **G, H**: Maniraptora *incertae sedis*, MGUH No. 28410a in **H**, oblique lingual? view, **G**: enlargement of denticles; **I–L**: Dromaeosauridae *incertae sedis* ('tooth morphotype two'), MGUH No. 28406, in **I**, labial? and **J**, lingual? views; **K, L**: enlargement of distal denticles; **M, N**: Maniraptora *incertae sedis*, MGUH No. 28410b in **N**, oblique lingual view, **M**: enlargement of denticles; **O–Q**: Dromaeosauridae *incertae sedis* ('tooth morphotype two'), MGUH No. 28407 in **O**, labial?, **P**: distal and **Q**: lingual? views; **R**: Dromaeosauridae *incertae sedis*, MGUH No. 28409, a stomach acid-etched lateral crown in lingual? view. Scale bars equal 0.5 mm (**B–E, H–J, N–R**) and 0.1 mm (**A, F, G, K–M**).

well in gross crown morphology and denticle distribution pattern with maxillary and dentary teeth from Cretaceous dromaeosaurids of North America, Mongolia and China (Ostrom, 1969; Currie et al., 1990; Barsbold and Osmólska, 1999; Xu et al., 1999, 2000; Xu and Wu, 2001; Sankey et al., 2002). Moreover, teeth lacking denticles on their mesial carina

have been reported in a few velociraptorine dromaeosaurids, including *Nuthetes* Owen, 1854 from the Berriasian, Lower Cretaceous of England (Milner, 2002) and *Saurornitholestes* from the Campanian, Upper Cretaceous of North America (Currie et al., 1990). Hence, the Danish theropod teeth are assigned to the Dromaeosauridae.

There are at least three distinct tooth morphotypes present in the Rabekke dromaeosaurid collection. Teeth of the first morphotype, represented by MGUH Nos. 28403 (Fig. 3A–C), 28404 (Fig. 3D–F) and 28408 (Fig. 4E, F), have chisel-like denticles that are markedly longer than wide. All crowns but one in this group lack denticles on the mesial carina although MGUH No. 24803 possesses a few low bumps that may be the worn bases of denticles. These tooth crowns agree well in overall morphology with teeth of velociraptorine dromaeosaurs, although they can be distinguished from those of other genera by their straight posterior denticles (the denticles are somewhat apically hooked in *Atrociraptor*, *Deinonychus*, *Saurornitholestes*, and *Velociraptor*). Zinke (1998) suggested that hooked denticles may be an advanced character of the Velociraptorinae, which would indicate a more basal position within the Dromaeosauridae for these Rabekke specimens. Straight denticles are found on teeth assigned to the basal velociraptorine *Nuthetes* (Milner, 2002: Pl. 1), but these serrations are more stoutly proportioned and much blunter than are those on teeth included in ‘tooth morphotype one’ (personal observation of BMNH R48207).

Fragments included in the second morphotype group (e.g., MGUH Nos. 28406 and 28407) have elongated, apically inclined denticles (Fig. 4I–L, O–Q). Unfortunately, there are no complete tooth crowns presently known, making it impossible to determine the original shape of the crowns. Although it is plausible that these teeth belong to the same taxon as those included in the ‘tooth morphotype one’ group, the likely presence of a second velociraptorine-like tooth crown species in the Rabekke theropod collection cannot be ruled out at this point.

The third tooth morphotype is represented by MGUH No. 28405 (Fig. 4A–D). In this specimen, the distal denticles are wider than long, and the gross crown morphology is roughly similar to that of *Dromaeosaurus* (Currie et al., 1990). Although definitive characters are lacking, it is reasonable to assume that this crown originates from a small (juvenile?) dromaeosaurine dromaeosaurid.

Maniraptora incertae sedis

Referred material: MGUH No. 28410a–d.

Description: MGUH No. 28410a–d (Fig. 4G, H, M, N) comprises four fragments, presumably from a single premaxillary tooth crown (based on colour, size, state of preservation and denticle morphology). The densely spaced denticles follow an asymmetrically rounded carina (flexed towards the inferred lingual face of the crown). Each denticle is flattened, triangular in lateral outline and separated from its neighbours by shallow grooves. Moreover, the widths of the denticles are highly variable; some are narrow whereas others are almost as wide as they are long. The serrations are somewhat apicodistally directed and one or two low crests extend along the sides of each denticle and coalesce with a large number of faint ridges and minute granulae that cover much of the crown surface. This is especially noticeable on the inferred lower portion of the crown. There are on average 8.5 denticles per millimetre (calculated from data obtained from MGUH No. 28410a and b).

Remarks: Judging from its acutely angular denticles and surface texture, MGUH No. 28410a–d cannot be confidently assigned to the Dromaeosauridae. However, premaxillary teeth of *Nuthetes* differ from maxillary and dentary teeth of the same taxon by having serrations that have coalesced into ‘double’ denticles (Milner, 2002: Pl. 1, Figs. 3–5). Moreover, hairline striations cover the enamelled surfaces (the labial and lingual faces are smooth in maxillary and mandibular teeth of *Nuthetes*) and centrally located, faint ridges follow the longitudinal axis of each denticle (Milner, 2002: Pl. 1, Fig. 5). Consequently, MGUH No. 28410a–d is possibly the remains of a premaxillary tooth from a theropod that is dentally different from the teeth described here as ‘Dromaeosauridae incertae sedis’. The inconsistent size of the denticles also suggests another possibility. Unquestionable theropod teeth have denticles that increase consistently in size (both in height and basal width in labial or lingual views) from their smallest dimensions at the base of the tooth crown, maintain almost the same dimensions for most of the height of the carina and then decrease in size gradually near the tip of the tooth. Animals that generally lack serrations except in the largest individuals (such as large monitor lizards and even a large cf. hesperornithiform bird tooth – TMP 89.103.29) have serrations that vary in size throughout the length of the carina. This suggests the possibility that MGUH No. 28410a–d may not be a non-avian theropod.

6. Palaeoecology

During early Berriasian time, the coastal plain, lake and lagoonal settings on what is now Bornholm provided suitable habitats for diverse communities of terrestrial, freshwater and brackish water animals. This is reflected in the Rabekke vertebrate assemblage, which comprises a mixture of aquatic (bony fishes), semi-aquatic (crocodilians, amphibians and turtles; Rees et al., 2005) and terrestrial (dinosaurs and mammals; Lindgren et al., 2004) components. On a broad taxonomic level, the fauna is similar in composition to assemblages from the approximately coeval strata of the Guimarota coal mine in western Portugal (Rauhut, 2000) and the Purbeck Limestone Formation and Wealden Group in southernmost England (Milner and Batten, 2002; Sweetman, 2004 and references therein). Hence, it is likely that the fauna mirrors the general assembly of tetrapod communities in comparable environments across west-central Europe during latest Jurassic and earliest Cretaceous times. The occurrence of dromaeosaurid teeth in the Skyttegård Member is hardly surprising, given the almost worldwide distribution of the Dromaeosauridae and other small-bodied maniraptoran theropods in the Lower Cretaceous (Ostrom, 1969; Rauhut and Werner, 1995). For dromaeosaurids, other small theropods, and perhaps also primitive birds, the thickly foliated woodlands on ancient Bornholm must have offered numerous potential habitats and plenty of prey (in the form of tiny vertebrates and insects).

One interesting aspect of the Rabekke dinosaur fauna is the apparent absence of large theropods, sauropods, ornithomimids and other ornithischian dinosaurs. Although certainly at least in

part a result of taphonomic processes (the Skyttegård assemblage is strongly biased towards smaller fossils ranging in size from 1 to 10 mm), the marshy terrain and dense vegetation might have been an unsuitable habitat for large and heavy animals, as has been argued for the lithologically similar localities of Guimarães and Uña in Portugal and Spain (Rauhut, 2001, 2002). The total dominance of carnivorous dinosaurs is also noteworthy, but again, may be a consequence of environmental factors and/or taphonomy (see e.g., Norman and Barrett, 2002). Future research in Berriasian sediments stratigraphically and laterally adjacent to the vertebrate-bearing bed on Bornholm may reveal the presence of larger animals, such as herbivorous dinosaurs, in the Rabekke Formation.

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 of Copenhagen. Further fieldwork was supported by grants from Crafoordska stiftelsen. JL acknowledges Kulturarvstyrelsen in Denmark for providing him with a research fellowship at the Geological Museum in Copenhagen and 'Fossilprojektet på Bornholm' for further financial assistance. PJC was supported by the Natural Sciences and Engineering Research Council of Canada (203091-02). Regitze Benthien and Gilles Cuny assisted in numerous ways. Finally, we thank Paul M. Barrett for his constructive review. To all, our sincere thanks.

References

Ahlberg, A., Siverson, M., 1991. Early Jurassic dinosaur footprints in Helsingborg, southern Sweden. *Geologiska Föreningens i Stockholm Förhandlingar* 113, 339–340.

Barsbold, R., 1983. Carnivorous dinosaurs from the Cretaceous of Mongolia. *Transactions of the Soviet-Mongolian Palaeontological Expedition* 19, 5–117 (in Russian).

Barsbold, R., Osmólska, H., 1999. The skull of *Velociraptor* (Theropoda) from the Late Cretaceous of Mongolia. *Acta Palaeontologica Polonica* 44, 189–219.

Baszio, S., 1997. Systematic palaeontology of isolated dinosaur teeth from the latest Cretaceous of south Alberta, Canada. *Courier Forschungsinstitut Senckenberg* 196, 33–77.

Batten, D.J., Grenfell, H.R., 1996. Botryococcus. In: Jansonius, J., McGregor, D.C. (Eds.), *Palynology: Principles and Applications*. American Association of Stratigraphical Palynologists Foundation, Salt Lake City, pp. 205–214.

Böläu, E., 1952. Neue Fossilfunde aus dem Rhät Schones und ihre paläogeographisch-ökologische Auswertung. *Geologiska Föreningens i Stockholm Förhandlingar* 74, 44–50.

Böläu, E., 1954. The first finds of dinosaurian skeletal remains in the Rhaetic-Liassic of N.W. Scania. *Geologiska Föreningens i Stockholm Förhandlingar* 76, 501–502.

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

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

Burger, D., 1965. Some new species of *Classopollis* from the Jurassic of the Netherlands. *Leidse Geologische Mededelingen* 33, 63–69.

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.

Cookson, I.C., 1947. Plant fossils from the lignites of the Kerguelen Archipelago. British, Australian and New Zealand Antarctic Research Expedition (1929–31), Report A/2, 129–142.

Cookson, I.C., Dettmann, M.E., 1961. Reappraisal of the Mesozoic microspore genus *Aequitriradites*. *Palaeontology* 4, 425–427.

Couper, R.A., 1958. British Mesozoic microspores and pollen grains – a systematic and stratigraphic study. *Palaeontographica B* 103, 75–179.

Currie, P.J., 1995. New information on the anatomy and relationships of *Dromaeosaurus albertensis* (Dinosauria: Theropoda). *Journal of Vertebrate Paleontology* 15, 576–591.

Currie, P.J., Varricchio, D.J., 2004. A new dromaeosaurid from the Horseshoe Canyon Formation (Upper Cretaceous) of Alberta, Canada. In: Currie, P.J., Koppelhus, E.B., Shugar, M.A., Wright, J.L. (Eds.), *Feathered Dragons: Studies on the Transition from Dinosaurs to Birds*. Indiana University Press, Bloomington, Indiana, pp. 112–132.

Currie, P.J., Rigby, J.K., Sloan, R.E., 1990. Theropod teeth from the Judith River Formation of southern Alberta, Canada. In: Carpenter, K., Currie, P.J. (Eds.), *Dinosaur systematics: Perspectives and Approaches*. Cambridge University Press, Cambridge, pp. 107–125.

Delcourt, A.F., Sprumont, G., 1955. Les spores et grains de pollen du Wealdien du Hainaut. *Mémoires de la Société elge de Géologie, de Paléontologie et d'Hydrologie, Nouvelle Série* 5, 1–73.

Farlow, J.O., Brinkman, D.L., Abler, W.L., Currie, P.J., 1991. Size, shape and serration density of theropod dinosaur lateral teeth. *Modern Geology* 16, 161–198.

Gadek, P.A., Alpers, D.L., Heslewood, M.M., Quinn, C.J., 2000. Relationships within Cupressaceae sensu lato: a combined morphological and molecular approach. *American Journal of Botany* 87, 1044–1057.

Gauthier, J., 1986. Saurischian monophyly and the origin of birds. In: Padian, K. (Ed.), *The Origin of Birds and the Evolution of Flight*. *Memoirs of the California Academy of Sciences*, San Francisco 8, pp. 1–55.

Gierlinski, G., Ahlberg, A., 1994. Late Triassic and Early Jurassic dinosaur footprints in the Höganäs Formation of southern Sweden. *Ichnos* 3, 99–105.

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.

Gröcke, D.R., Price, G.D., Ruffell, A.H., Mutterlose, J., Baraboshkin, E., 2003. Isotopic evidence for Late Jurassic–Early Cretaceous climate change. *Palaeogeography, Palaeoclimatology, Palaeoecology* 15, 97–118.

Gry, H., 1960. Geology of Bornholm. Guide to Excursions Nos. A45 and C40. In: *International Geological Congress. 21st Session, Copenhagen*.

Herngreen, G.F.W., Kouwe, W.F.P., Wong, T.E., 2003. The Jurassic of the Netherlands. *Geological Survey of Denmark and Greenland Bulletin* 1, 217–229.

Hoedemaeker, P.J., Herngreen, G.F.W., 2003. Correlation of Tethyan and Boreal Berriasian – Barremian strata with emphasis on strata in the subsurface of the Netherlands. *Cretaceous Research* 24, 253–275.

Hoedemaeker, P.J., Herngreen, G.F.W., 2004. Erratum to 'Correlation of Tethyan and Boreal Berriasian – Barremian strata with emphasis on strata in the subsurface of the Netherlands'. *Cretaceous Research* 25, 137–150.

Hunt, C.O., 2004. Palynostratigraphy of the classic Portland and Purbeck sequences of Dorset, southern England and the correlation of Jurassic–Cretaceous boundary beds in the Tethyan and Boreal realms. In: Beaudoin, A.B., Head, M.J. (Eds.), *The Palynology and Micropalaeontology of Boundaries*. Geological Society, London, Special Publication 2230, pp. 175–186.

Kützing, F., 1849. *Species Algarum*. FA Brockhaus, Leipzig.

Lindgren, J., Siverson, M., 2002. *Tylosaurus ivoensis*: a giant mosasaur from the early Campanian of Sweden. *Transactions of the Royal Society of Edinburgh, Earth Sciences* 93, 73–93.

Lindgren, J., Rees, J., Siverson, M., Cuny, G., 2004. The first Mesozoic mammal from Scandinavia. *Geologiska Föreningen* 126, 325–330.

- Lindgren, J., Currie, P.J., Siverson, M., Rees, J., Cederström, P., Lindgren, F., 2007. The first neoceratopsian dinosaur remains from Europe. *Palaeontology* 50, 929–938.
- Marsh, O.C., 1881. A new order of extinct Jurassic reptiles (Coeluria). *American Journal of Science* 21, 339–340.
- Matthew, W.D., Brown, B., 1922. The family Deinodontidae, with notice of a new genus from the Cretaceous of Alberta. *Bulletin of the American Museum of Natural History* 46, 367–385.
- Milàn, J., Bromley, R.G., 2005. Dinosaur footprints from the Middle Jurassic Bagå Formation, Bornholm, Denmark. *Bulletin of the Geological Society of Denmark* 52, 7–15.
- Milàn, J., Gierlinski, G., 2004. A probable thyreophoran (Dinosauria, Ornithischia) footprint from the Upper Triassic of southern Sweden. *Bulletin of the Geological Society of Denmark* 51, 71–75.
- Milner, A.C., 2002. Theropod dinosaurs of the Purbeck Limestone Group, southern England. *Special Papers in Palaeontology* 68, 191–201.
- Milner, A.R., Batten, D. (Eds.), 2002. Life and environments in Purbeck times, 68. *Special Papers in Palaeontology*.
- 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.
- Norman, D.B., Barrett, P.M., 2002. Ornithischian dinosaurs from the Lower Cretaceous (Berriasian) of England. *Special Papers in Palaeontology* 68, 161–189.
- Osborn, H.F., 1924. Three new Theropoda, *Protoceratops* Zone, central Mongolia. *American Museum Novitates* 144, 1–12.
- Ostrom, J.H., 1969. Osteology of *Deinonychus antirrhopus*, an unusual theropod from the Lower Cretaceous of Montana. *Bulletin of the Peabody Museum of Natural History* 30, 1–165.
- Owen, R., 1842. Report on British fossil reptiles. Part II. Reports of the British Association for the Advancement of Science 1841, 60–294.
- Owen, R., 1854. On some fossil reptilian and mammalian remains from the Purbecks. *Quarterly Journal of the Geological Society of London* 10, 420–433.
- Persson, P.O., 1959. Reptiles from the Senonian (U. Cret.) of Scania (S. Sweden). *Arkiv för Mineralogi och Geologi* 2, 431–478.
- 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.
- Potonié, R., 1956. Synopsis der Gattungen der Spores dispersae. I. Teil – Sporites. *Geologisches Jahrbuch Beihefte* 23, 3–103.
- Poulsen, N.E., Riding, J.B., 2003. The Jurassic dinoflagellate cyst zonation of subboreal Northwest Europe. *Geological Survey of Denmark and Greenland Bulletin* 1, 115–144.
- Rauhut, O.W.M., 2000. The dinosaur fauna from the Guimarota mine. In: Martin, T., Krebs, B. (Eds.), *Guimarota – a Jurassic Ecosystem*. Verlag Dr. Friedrich Pfeil, München, pp. 75–82.
- Rauhut, O.W.M., 2001. Herbivorous dinosaurs from the Late Jurassic (Kimmeridgian) of Guimarota, Portugal. *Proceedings of the Geologists' Association* 112, 275–283.
- Rauhut, O.W.M., 2002. Dinosaur teeth from the Barremian of Uña, Province of Cuenca, Spain. *Cretaceous Research* 23, 255–263.
- Rauhut, O.W.M., Werner, C., 1995. First record of the family Dromaeosauridae (Dinosauria: Theropoda) in the Cretaceous of Gondwana (Wadi Milk Formation, northern Sudan). *Paläontologische Zeitschrift* 69, 475–489.
- Rees, J., 2000. An Early Cretaceous scincomorph lizard dentary from Bornholm, Denmark. *Bulletin of the Geological Society of Denmark* 48, 105–109.
- Rees, J., Lindgren, J., Evans, S., 2005. Amphibians and small reptiles from the Berriasian Rabekke Formation on Bornholm, Denmark. *Geologiska Föreningen* 127, 233–238.
- Sankey, J.T., Brinkman, D.B., Guenther, M., Currie, P.J., 2002. Small theropod and bird teeth from the Late Cretaceous (Late Campanian) Judith River Group, Alberta. *Journal of Paleontology* 76, 751–763.
- Schulz, E., 1967. Sporenpaläontologische Untersuchungen rätio-liassischer Schichten im Zentralteil des Germanischen Beckens. *Paläontologische Abhandlungen B* 2, 541–633.
- Seeley, H.G., 1887. On the classification of the fossil animals commonly named Dinosauria. *Proceedings of the Royal Society of London* 43, 165–171.
- Smith, J.B., Vann, D.R., Dodson, P., 2005. Dental morphology and variation in theropod dinosaurs: implications for the taxonomic identification of isolated teeth. *The Anatomical Record A* 285, 699–736.
- Sues, H.D., 1978. A new small theropod dinosaur from the Judith River Formation (Campanian) of Alberta, Canada. *Zoological Journal of the Linnaean Society* 62, 381–400.
- Sweetman, S.C., 2004. The first record of velociraptorine dinosaurs (Saurischia, Theropoda) from the Wealden (Early Cretaceous, Barremian) of southern England. *Cretaceous Research* 25, 353–364.
- van Geel, B., Grenfell, H.R., 1996. Spores of Zygnemataceae. In: Jansonius, J., McGregor, D.C. (Eds.), *Palynology: Principles and Applications*. American Association of Stratigraphical Palynologists Foundation, Salt Lake City, pp. 173–179.
- van Geel, B., van der Hammen, T., 1978. Zygnemataceae in Quaternary Colombian sediments. *Review of Palaeobotany and Palynology* 25, 377–392.
- Xu, X., Wu, X.-C., 2001. Cranial morphology of *Sinornithosaurus millenii* Xu et al., 1999 (Dinosauria: Theropoda: Dromaeosauridae) from the Yixian Formation of Liaoning, China. *Canadian Journal of Earth Sciences* 38, 1739–1752.
- Xu, X., Wang, X.-L., Wu, X.-C., 1999. A dromaeosaurid dinosaur with a filamentous integument from the Yixian Formation of China. *Nature* 401, 262–266.
- Xu, X., Zhou, Z.H., Wang, X.-L., 2000. The smallest known non-avian theropod dinosaur. *Nature* 408, 705–708.
- Zinke, J., 1998. Small theropod teeth from the Upper Jurassic coal mine of Guimarota (Portugal). *Paläontologische Zeitschrift* 72, 179–189.