Maastrichtian 175 years & Mosasaur Meeting

Maastricht
September 2024

maastrichtian
175 years

The 175th Anniversary of the Maastrichtian – a Celebratory Meeting

Maastricht, September 8-11, 2024

Mosasaur
meeting

7th Triennial Mosasaur Meeting –

A global perspective on Mesozoic marine amniotes

Maastricht, September 12-15, 2024

ABSTRACT VOLUME AND PROGRAMME

edited by

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Natuurhistorisch Museum Maastricht

Maastricht University

Centre Céramique

Abstract volume and programme

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The 175th Anniversary of the Maastrichtian – a Celebratory Meeting

Maastricht, September 8-11, 2024

Programme

Sunday, September 8, 2024

16.00-18.00 h – Registration desk + Ice-Breaker party (Natuurhistorisch Museum Maastricht, De Bosquetplein 7)

Monday, September 9, 2024

8.00-10.00 h – Registration desk (Centre Céramique, Plein 1992)

10.00-10.15 h – Opening address

10.15 h – Start of FIRST SESSION [chairperson to be appointed]

10.15-10.35 h – Mike Reich: A review of Maastrichtian sea cucumbers (Echinodermata, Holothuroidea)

10.35-10.55 h – Christian Voiculescu-Holvad & Emma Sheldon: A gigantic, hook-bearing coleoid from the end-Cretaceous of Denmark

10.55-11.15 h – Docho Dochev & Polina Pavlishina: Maastrichtian inoceramid bivalves, ammonites and dinoflagellate cysts from the Moravitsa section, north-west Bulgaria

11.15-11.40 h – Coffee/tea break

11.40-12.00 h – Dawid Mazurek, Elena A. Jagt-Yazykova, John W.M. Jagt & Dariusz Wieczorek: A Maastrichtian sequence near Włoszczowa (southern Holy Cross Mountains, Poland) – preliminary data

12.00-12.20 h – Norbert Keutgen, Zbigniew Remin & Anna Jadwiga Keutgen: *Belemnella* (Coleoidea, Belemnitellidae) from Altembroeck (north-east Belgium) revisited

12.20-12.40 h – John W.M. Jagt, Mart J.M. Deckers, Johan Laffineur, René H.B. Fraaije & Arno Savelkoul: More latest Cretaceous echinoderm 'odds and ends' from the Maastrichtian type area

12.40-14.00 h – Lunch break: please make your own arrangements for lunch; you will find a range of pubs and restaurants in the direct vicinity of Centre Céramique

14.00 h – start of SECOND SESSION [chairperson to be appointed]

14.00-14.45 h – Neil H. Landman: Ammonites at Cretaceous-Paleogene sites in North America: abundance and short-term survivorship [KEYNOTE LECTURE]

14.45-15.05 h – Marcin Machalski, Neil H. Landman, Matthew Garb, John W.M. Jagt, Elena A. Jagt-Yazykova & J. Kirk Cochran: The Danish Danian ammonites

15.05-15.25 h – Mateus Kroth, João P. Trabucho Alexandre, Mariana Pinheiro Pimenta, Geert-Jan Vis & Eva De Boever: Facies characterisation and stratigraphy of the upper Maastrichtian to lower Danian Maastricht Formation

15.25-15.45 h – Stijn Goolaerts, Bernard Mottequin & John W.M. Jagt: An exceptionally diverse pre-K/Pg boundary nautilid fauna from the Maastrichtian type area (the Netherlands and Belgium)

15.45-16.10 h – Coffee/tea break

16.10 h – start of THIRD SESSION [chairperson to be appointed]

16.10-16.30 h – Pim Kaskes, Johan Vellekoop, Lawrence Percival, John W.M. Jagt, Philippe Claeys & Jan Smit: A geochemical revisit of the expanded Cretaceous-Paleogene (K/Pg) boundary section in the Maastrichtian type area

16.30-16.50 h – Geert-Jan Vis, Ronald Vernes, Mateus Kroth & Armin Menkovic: Rediscovering the Upper Cretaceous and Danian of the south-east Netherlands: recent research initiatives of the Geological Survey of the Netherlands

16.50-17.10 h – James D. Witts, Rowan J. Whittle, Saurav Dutta & Samuel Hunt: Quantifying extinction and ecological change across the Cretaceous-Paleogene (K/Pg) boundary on Seymour Island, Antarctica

17.15 h – End of first day of lectures

Tuesday, September 10, 2024

8.00-10.00 h – Registration desk (Centre Céramique, Plein 1992)

10.00 h – start of FIRST SESSION [chairperson to be appointed]

10.00-10.20 h – Lars P.J. Barten & John W.M. Jagt: Rarer than rare: articulated and associated remains of Late Cretaceous cartilaginous fish from Liège-Limburg (Belgium, the Netherlands)

10.20-10.40 h – Maarten de Rijke, Jonathan J.W. Wallaard, René H.B. Fraaije, John W.M. Jagt & Eric W.A. Mulder: Keeping the light shining on the truly Maastrichtian dinosaurs, those from Maastricht!

10.40-11.00 h – Jonathan J.W. Wallaard, Jelle Heere, Maarten de Rijke & John W.M. Jagt: The Dercetidae from the type Maastrichtian – an enigmatic group of bony fish

11.00-11.20 h – Leon Claessens, Jesse Hennekam, Phil Klahs, Frank Wesselingh, Dylan Bastiaans & John W.M. Jagt: Unlocking the digital potential of the Maastrichtian fossil record

11.20-11.50 h – Coffee/Tea break

11.50 h – start of SECOND SESSION [chairperson to be appointed]

11.50-12.10 h – Sjir Renkens, Raymond van der Ham & Han von Konijnenburg-van Cittert: Plant fossils from the type Maastrichtian

12.10-12.30 h – Sander Houben, Mateus Kroth, Roel Verreussel & Geert-Jan Vis: Palynology of the Eys borehole: a stratigraphical and palaeoenvironmental perspective on the Cretaceous succession of the Ubachsberg Plateau, South Limburg, the Netherlands

12.30-12.50 h – Polina Pavlishina & Docho Dochev: Dinoflagellate cyst biostratigraphy of the upper Campanian-lower Maastrichtian interval in the Oslen Krivodol reference section, north-west Bulgaria

12.50-13.10 h – Cemile Solak, Kemal Taslı & Hayati Koç: Benthic foraminiferal turnover and palaeoenvironmental changes across the Cretaceous-Paleocene transition in shallow-marine platform carbonates, Central Taurides (Türkiye)

13.10-14.40 h – Lunch break: please make your own arrangements for lunch; you will find a range of pubs and restaurants in the direct vicinity of Centre Céramique

14.40 h – start of THIRD SESSION [chairperson to be appointed]

14.40-15.00 h – Jarno J.C. Huygh, Matthias Sinnesael, Pim Kaskes, Johan Vellekoop, Hannah Van der Geest, John W.M. Jagt & Philippe Claeys: Astronomical pacing of flint bands in the Maastrichtian chalk sea of north-western Europe

15.00-15.20 h – Michiel Dusar, Roland Dreesen, C. Wim Dubelaar, David Lagrou & Timo N. Nijland: Maastrichtian building stones from the Mergelland type region; more than Maastricht Stone

15.20-15.40 h – Johan Vellekoop, Pim Kaskes, Matthias Sinnesael, John W.M. Jagt, Sjir Renkens, Eric Nieuwenhuis & Hans J.P. Zijlstra: The Maastrichtian Geoheritage Project, a fertile cross-pollination of citizen scientists and academia

15.40-16.00 h – Christian Salazar & Wolfgang Stinnesbeck: Biostratigraphy and sequence stratigraphy of the Upper Cretaceous (Maastrichtian) Quiriquina Formation in central Chile

16.00 h – Coffee/tea break and POSTER SESSION [chairperson to be appointed]

More than just jaws – the pycnodontiform fish genus *Anomoeodus* from the Maastrichtian type area – ***Lars P.J. Barten, John W.M. Jagt & Jacques Severijns***

The core of Oploo-DB 16: preliminary notes on macrofossil-based proxy correlations with the Maastrichtian type area, around 120 km further south – ***John W.M. Jagt, Nico M.M. Janssen & Geet-Jan Vis***

The Friedrich Vogel Collection (Naturalis, Leiden) of latest Cretaceous and early Paleocene bivalves reassessed – preliminary observations – ***John W.M. Jagt, Marijn Roosen & Natasja den Ouden***

The *pungens* conundrum (Ammonoidea, Scaphitidae) – Maastrichtian, the Netherlands – ***John W.M. Jagt & Elena A. Jagt-Yazykova***

A taxonomic revision of sabellid and serpulid polychaete tube worms from the Maastrichtian chalk of Denmark – preliminary observations **–** ***Tomáš Kočí, Jesper Milàn, Sten L. Jakobsen, Martina Kočová Veselská & Manfred Jäger***

Eric Simon (1948-2018): his contributions to the knowledge of Campanian-Maastrichtian (Late Cretaceous) brachiopods – ***Bernard Mottequin, John W.M. Jagt & Stijn Goolaerts***

Late Cretaceous cockles (Bivalvia, Cardiida) from Liège-Limburg – there is more than meets the eye – ***Jan-Johan ter Poorten & John W.M. Jagt***

Long-bone histology of the Late Cretaceous island-dwelling ankylosaurian dinosaur *Struthiosaurus austriacus* Bunzel, 1871 **–** ***Elżbieta M. Teschner, Christoph Kettler, Jürgen Kriwet & Sebastian Stumpf***

The ChaSE project: Chalk Sea Ecosystem and Cretaceous environmental change in the Chalk Group of the United Kingdom – ***James D. Witts, Deborah Tangunan, Thomas Fogerty, Kim Chandler, Chloe Griffiths, Emma L. Bernard, Katie Collins, Jonathan A. Todd, Zoë Hughes, Marc Jones, Timothy A.M. Ewin, Stephen Stukins, Liam Gallagher, Charlie J. Underwood, Andrew S. Gale, Paul R. Bown & Richard J. Twitchett***

Evening – CONFERENCE DINNER

Restaurant Le Petit Bonheur, Achter de Molens 2, 6211 JC Maastricht, phone + 31-43-321 5109

[Details will be announced during the meeting – **make sure to inform us well in advance of any dietary preferences!]**

Wednesday, September 11, 2024

10.00-17.00 h – Fieldtrip – coach starts at 10.00 **(sharp!)** from Plein 1992, packed lunch will be supplied, together with a field guide

17.00 h – return to Maastricht (Plein 1992) and end of celebratory meeting

7th Triennial Mosasaur Meeting –

A global perspective on Mesozoic marine amniotes

Maastricht, September 12-15, 2024

Programme

Thursday, September 12, 2024

16.00-18.00 h – Registration desk + Ice-Breaker party (Natuurhistorisch Museum Maastricht, De Bosquetplein 7)

Friday, September 13, 2024

8.00-10.00 h – Registration desk (Centre Céramique, Plein 1992)

10.00-10.15 h – Opening address

10.15 h – Start of FIRST SESSION [chairperson to be appointed]

10.15-11.00 h – Melanie A.D. During: Fishes, mosasaurs and the season of the K/Pg extinction [KEYNOTE LECTURE]

11.00-11.25 h – Amelia R. Zietlow: Tylosaurine diversity informed by morphological variation in extant *Varanus*

11.25-11.50 h – John W.M. Jagt, Rudi W. Dortangs, Eric W.A. Mulder & Lars P.J. Barten: How on earth did they do it? Recovery of the first mosasaurs in the Maastrichtian type area in the latter half of the eighteenth century

11.50-12.15 h – Coffee/tea break

12.15 h – Start of SECOND SESSION [chairperson to be appointed]

12.15-12.40 h – Michael J. Polcyn, Louis L. Jacobs, Anne S. Schulp & Pedro Claude Nsungani: Putting an ocean where one had not previously existed: an update on the marine amniote record of Angola

12.40-13.05 h – Anthony E. Maltese & Michael J. Polcyn: The oldest occurrence of a selmasaurin plioplatecarpine mosasaur from the Coniacian of Kansas, USA

13.05-13.30 h – Femke Holwerda, John W.M. Jagt & Anne S. Schulp: 2D and 3D dental microwear analysis informs us about the feeding ecology of type-Maastrichtian mosasaurs

13.30-13.55 h – Eric W.A. Mulder: On the desirability to designate a lectotype for the Late Cretaceous turtle *Allopleuron hofmanni* (Gray, 1831) from the Maastrichtian type area

13.55-15.15 h – Lunch break: please make your own arrangements for lunch; you will find a range of pubs and restaurants in the direct vicinity of Centre Céramique

15.15 h – Start of THIRD SESSION [chairperson to be appointed]

15.15-15.40 h – Lars P.J. Barten, John W.M. Jagt & Eric W.A. Mulder: Gut contents of a subadult individual of *Mosasaurus hoffmannii* Mantell, 1829 from the Maastrichtian type area (the Netherlands) hint at the species' dietary preferences

15.40-16.05 h – Dylan Bastiaans, Jeroen J.F. Kroll, Dirk Cornelissen, John W.M. Jagt, Lars Barten, Frans Kerren, Jacques Knops, Eric Nieuwenhuis, Jacques Philippens, Lex Meijer, Paul Kisters & Anne S. Schulp: Mosasaur 'Carlo', an unusual globidensine mosasaur from the upper Maastrichtian Gulpen Formation of the Maastrichtian type area (southeast Netherlands, northeast Belgium) – an update

16.05-16.30 – Jacques Knops: What do we tell visitors? The 'mosasaur story' at the Natural History Museum of Maastricht

16.30-16.55 – Dunya Handor, Jesse Hennekam, John W.M. Jagt & Eric W.A. Mulder: The De Heer Collection of dissociated mosasaur vertebrae and carapace peripherals of cheloniid turtles

17.00 h – End of first day of lectures

Saturday, September 14, 2024

8.00-10.00 h – Registration desk (Centre Céramique, Plein 1992)

10.00 h – Start of FIRST SESSION [chairperson to be appointed]

10.00-10.25 h – Johan Lindgren: Soft-tissue fossils – implications for the life and habits of ancient marine reptiles

10.25-10.50 h – Mats E. Eriksson, Randolph De La Garza, Esben Horn & Johan Lindgren: Deconstructing ichthyosaur soft tissues and reconstructing *Stenopterygius* (Reptilia, Ichthyopterygia)

10.50-11.15 h – Juliette C.L. Menon, Walter G. Joyce, Serjoscha W. Evers & Donald B. Brinkman: New perspectives on sea turtles from the Cretaceous to the Neogene

11.15-11.40 h – Miguel Marx, Mats E. Eriksson, Benjamin P. Kear, Sven Sachs & Johan Lindgren: Osteological correlates for a dorsal fin in plesiosaurs?

11.40-12.05 h – Coffee/tea break

12.05 h – Start of SECOND SESSION [chairperson to be appointed]

12.05-12.30 h – Alberto Cabezuelo-Hernández, Carlos de Miguel Chaves, Francisco Ortega & Adán Pérez-García: New data on the holotype of the bizarre eosauropterygian, *Paludidraco multidentatus* (Nothosauroidea, Simosauridae)

12.30-12.55 h – Anne S. Schulp, Colijn Dijkers, Hanneke Jacobs, Dylan Bastiaans, John W.M. Jagt, Ana Soraya Marques & Michael J. Polcyn: Mosasaurus 3D: scanning, digital reconstruction and 3D-printing of a large *Prognathodon* skeleton for museum display

12.55-13.20 h – Leon Claessens & Jesse Hennekam: Vertebrate palaeontology at Maastricht University

13.20-14.45 h – Lunch break: please make your own arrangements for lunch; you will find a range of pubs and restaurants in the direct vicinity of Centre Céramique

14.45 h – Start of THIRD SESSION [chairperson to be appointed]

14.45-15.10 h – Adiël A. Klompmaker, Harry L. Blewitt, P. George Martin & T. Prescott Atkinson: Late Cretaceous marine tetrapods from the collections of the Alabama Museum of Natural History

15.10-15.35 h – Eric Wetzels, Joes Minis & John W.M. Jagt: Old wine in new bottles? Emerging intellectual networks in Maastricht during the French Period of 1794-1815

15.45-17.00 – POSTER SESSION [chairperson to be appointed]

Mosasaurids from the Maastrichtian phosphates of Morocco: an extraordinary ecological diversity prior to the K/Pg crisis **–** ***Nathalie Bardet, Valentin Fischer, Nour-Eddine Jalil, Fatima Khaldoune, Oussama Khadiri Yazami, Xavier Pereda Suberbiola & Nicholas Longrich***

The Bulgarian fossil record of Mosasauridae **–** ***Vladimir Nikolov***

Mosasaur remains from the Puskwaskau Formation (Santonian-lower middle Campanian) of Alberta, Canada – ***Trevor H. Rempert*, Brennan P. Martens, Alexander P.M. Vinkeles Melchers & Darius Azmayesh-Fard**

The marine reptile fauna of the Bekrit syncline (El Koubbat Formation, lower Maastrichtian), Middle Atlas Mountains, Morocco **– *Alexander P.M. Vinkeles Melchers*, Brennan P. Martens & Trevor H. Rempert**

A calculation of acceleration capabilities of *Mosasaurus hoffmanni* – ***David van der Mark* & Wietse ten Hoor**

Evening – CONFERENCE DINNER

Restaurant Brandsøn, Het Bat 2, 6211 EX Maastricht, phone + 31-43-201 2620

[Details will be announced during the meeting – **make sure to inform us well in advance of any dietary preferences!]**

Sunday, September 15, 2024

10.00-17.00 h – Fieldtrip – coach starts at 10.00 **(sharp!)** from Plein 1992, packed lunch will be supplied, together with a field guide

17.00 h – return to Maastricht (Plein 1992) and end of celebratory meeting

ABSTRACTS

Mosasaurids from the Maastrichtian phosphates of Morocco: an extraordinary ecological diversity prior to the K/Pg crisis

Nathalie Bardet[1], Valentin Fischer[2], Nour-Eddine Jalil[1], Fatima Khaldoune[3], Oussama Khadiri Yazami[3], Xabier Pereda Suberbiola[4] & Nicholas Longrich[5]

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In the fossil record, mosasaurid teeth are both very abundant and usually species-specific, allowing the documentation of both taxonomic diversity and ecological disparity of this group with fewer uncertainties than in other marine reptiles.

With sixteen mosasaurid species described so far, representing a wide range of sizes and morphologies, the upper Maastrichtian phosphates of Morocco undoubtedly represent the richest deposits in the world for this emblematic clade of Mesozoic predators (e.g., Bardet *et al.*, 2015; Longrich *et al.*, 2022; MacLaren *et al.*, 2022).

Up to now, methods used to link tooth morphology to diets of marine amniotes, such as the one employed by Massare (1987), were essentially **qualitative**. Here, using dental morphologies of most of the Moroccan species, we combine two complementary approaches, namely a thorough comparative anatomy and high-density 3D geometric morphometry (Fischer *et al.*, 2022), so as to determine **quantitatively** the dietary preferences, shape diversity and niche partitioning of these apex predators in the local marine ecosystem, just prior to the Cretaceous-Paleogene (K/Pg) extinction event.

Similar to elsewhere in other regions across the globe, our results show that the Mosasaurinae constitutes the dominant clade in the local assemblage, exhibiting both the greatest systematic diversity (i.e., two-thirds of all taxa represented), the widest range of morphology and size (two to 15 m in overall length) and ecological disparity, reflected by an occupation of all ecological guilds as defined by Fischer *et al*. (2022): durophages, generalists, flesh cutters and flesh piercers. Plioplatecarpines were less diverse, medium-sized predators. The two local halisaurines exhibit the same dental shape, but vary greatly in tooth size (ratio 1:2) and cranial morphology, confirming the hypothesis put forward by Fischer *et al*. (2022) that tooth size is of importance in assessing diet. Noteworthy, durophagous taxa remain unknown within these two non-mosasaurine clades. Tylosaurinae are known only by a very large, generalist taxon. As observed elsewhere, tylosaurines were probably replaced by mosasaurines as apex predators during the Maastrichtian (e.g., MacLaren *et al.*, 2022).

As a whole, mosasaurids were both systematically highly diverse – and still diversifying during the latest Maastrichtian – and ecologically disparate, through niche-partitioning in the shallow-marine environment represented by the uppermost Cretaceous phosphates of Morocco. This high diversity and disparity just prior to the K/Pg biological crisis suggest that their extinction was rather sudden.

REFERENCES

Bardet, N., Houssaye, A., Vincent, P., Pereda-Suberbiola, X., Amaghzaz, M., Jourani E. & Meslouh, S., 2015. Mosasaurids (Squamata) from the Maastrichtian phosphates of Morocco: biodiversity, palaeobiogeography and palaeoecology based on tooth morphoguilds. *Gondwana Research*, 27: 1068-1078. https://doi.org/10.1016/j.gr.2014.08.014

Fischer, V., Bennion, R.F., Foffa, D., MacLaren, J.A., McCurry, M.R., Melstrom, K.M. & Bardet, N., 2022. Ecological signal in the size and shape of marine amniote teeth. *Proceedings of the Royal Society,* B289: 20221214. https://doi.org/10.1098/rspb.2022.1214

Longrich, N.R., Jalil, N.-E., Khaldoune, F., Yazami, O.K., Pereda-Suberbiola, X. & Bardet, N., 2022. *Thalassotitan atrox*, a giant predatory mosasaurid (Squamata) from the Upper Maastrichtian Phosphates of Morocco. *Cretacecous Research*, 140: 105315. https://doi.org/10.1016/j.cretres.2022.105315

MacLaren, J.A., Bennion, R.F., Bardet, N. & Fischer, V., 2022. Global ecomorphological restructuring of dominant marine reptiles prior to the Cretaceous-Palaeogene mass extinction. *Proceedings of the Royal Society* B289: 20220585. https://doi.org/10.1098/rspb.2022.0585

Massare, J.A., 1987. Tooth morphology and prey preference of Mesozoic marine reptiles. *Journal of Vertebrate Paleontology*, 7: 121-137. https://doi.org/10.1080/02724634.1987.10011647

Rarer than rare: articulated and associated remains of Late Cretaceous cartilaginous fish from Liège-Limburg (Belgium, the Netherlands)

Lars P.J. Barten[1] & John W.M. Jagt[2]

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In the Maastrichtian type area (south-east Netherlands, north-east Belgium), isolated teeth of cartilaginous fish (mostly sharks and inclusive of dermal denticles) are common in the uppermost unit (Lanaye Member) of the Gulpen Formation and in all members of the overlying Maastricht Formation of late Maastrichtian age. In fact, these are considered highly collectable by the many amateur palaeontologists who are active in the area and concentrate on recovering huge samples from fossil hash levels (condensed levels) at the base of several units within the Maastricht Formation. These samples are then sieved (various mesh widths) in tap water and the dried residues subsequently handpicked. The fossiliferous base of the Valkenburg Member, which is often, albeit erroneously, referred to as the 'Lichtenberg Horizon', is the most popular of such levels.

However, associated dentitions or post-cranial elements of elasmobranch individuals are extremely rare in the study area. The comparatively poor fossilisation potential of cartilage, the main component of most elasmobranch skeletons, may explain this paucity. However, it should be noted here that in some cases portions of cartilage may be preserved in these limestones. To date, a handful of isolated vertebrae of lamniform and squaliform sharks are known. These may represent partially ossified vertebrae of individuals of an advanced age (Fig. 1, left). Other fragments of cartilage clearly show the typical surface structure (Fig. 1, right) that is reminiscent of the outer surface of a basketball (Welton & Farish, 1993). At least one isolated vertebra of a squatiniform shark, with attached cartilage, is known to us; it is contained in a private collection.

Exceptionally rare are examples of associated remains of elasmobranchs. These include a partial cranial and post-cranial skeleton of a male chimaeroid (*Edaphodon* sp.) from the Gronsveld Member at Eben Emael (CBR-Romontbos quarry; see Duffin & Reynders, 1995) and an elongated, > 1-m long rostrum, with dissociated rostral and oral teeth, of a sclerorhynchid ray (*Ganopristis leptodon* Arambourg), from the Valkenburg Member at the former ENCI quarry near Maastricht. A stratigraphically older find, of early late Campanian age, was made at Haccourt (former CPL SA quarry, now Kreco). This comprises dissociated remains of a single individual of anacoracid shark, of which >25 teeth and some large vertebrae, were recovered from the Zeven Wegen Member (Gulpen Formation). This particular specimen has previously been referred to *Squalicorax lindstroemi* (Davis) (see Jagt & Meeuwsen, 2017), but is perhaps better assigned to *Squalicorax pristodontus* (Agassiz) (L.P.J. Barten, work under way).

Figure 1. *Left:* an isolated, large and partially ossified shark vertebra (NHMM K018 54 50) from the upper Maastricht Formation, former 't Rooth quarry, Bemelen. *Right:* detail of a piece of fossilised cartilage (NHMM 1998 141/A) from the Lanaye Member (Gulpen Formation) at the former ENCI-HeidelbergCement Group quarry, Maastricht, recovered in close proximity of the type specimen of the mosasaur *Prognathodon saturator* Dortangs, Schulp, Mulder, Jagt, Peeters & de Graaf, 2002. Note the remarkable surface structure. (collections of the Natuurhistorisch Museum Maastricht).

Rays assigned to the extinct family Rhombodontidae Cappetta, 1987 are widely distributed in the fossil record, this particular family being represented by several genera and species. These species were diagnosed mostly on the basis of isolated teeth, since skeletal elements or more complete dentitions of *Rhombodus* are few and far between (Cicimurri & Ebersole, 2020). Earlier, caudal spines have also been attributed to *Rhombodus* (Umbgrove, 1926; Hamelink, 1952), but as these were not found in association with teeth, this placement cannot be substantiated. In general, teeth of rhombodontid rays have a typical diamond-shaped crown and a bilobed root (Cappetta, 1987, 2012; Noubhani & Cappetta, 1994). Those of *Rhombodus binkhorsti* Dames, 1881 are no exception; these have been recorded from Maastrichtian strata in Europe (Herman, 1977; Corral *et al*., 2016), Africa (Noubhani & Cappetta, 1994; Cuny *et al*., 2012), Asia and North and South America (Herman, 1977; Cappetta, 1987; Cicimurri & Ebersole, 2020). Isolated teeth of *R. binkhorsti* have been described by several authors from the Maastrichtian type area, and from collections we have seen, it appears that the species occurs most frequently in the upper portion of the Maastricht Formation (Emael and Nekum members). However, Herman (1977) recorded *R. binkhorsti* in north-east Belgium from the 'tuffeau de Maestricht, niveau à coprolithes'. In current terminology, this corresponds to the fossil hash layer resting on top of the Lichtenberg Horizon, at the base of the Valkenburg Member (Maastricht Formation; see Felder & Bosch, 1998). Reynders (1998) noted material of *R. binkhorsti* from the Lanaye Member (Gulpen Formation). Therefore, this species had a considerable stratigraphical range, covering the uppermost Gulpen Formation and the entire Maastricht Formation, although it may not have been equally abundant during deposition of the various units of these formations (see also Albers & Weiler, 1964).

Figure 2. Dorsal, ventral and lateral views, respectively, of NHMM K 4996, a partial dentition, comprising six diamond-shaped teeth, of *Rhombodus binkhorsti* from the Emael Member (Maastricht Formation); CBR Romontbos quarry (Eben Emael, province of Liège, Belgium).

Recently, in the Jan & Marcel Kuypers Collection, now housed at the Natuurhistorisch Museum Maastricht, a partial dentition of *R. binkhorsti* has been recognised (Fig. 2). This specimen (NHMM K 4996) comprises six still articulated, diamond-shaped teeth, recovered from a fossil hash level on top of the Lava Horizon within the Emael Member (Maastricht Formation) at the CBR-Romontbos quarry (Eben Emael, Belgium). NHMM K 4996 constitutes only the fourth record of associated and articulated elasmobranch material from the Maastrichtian type area to date, and is therefore of great importance. The teeth are tightly packed into a solid crushing surface and in that respect are similar to two partial dentitions of *R. binkhorsti* from the Maastrichtian Ripley Formation of Mississippi (Gulf Coast, United States), described and illustrated by Cicimurri & Ebersole (2020). In fact, those specimens constituted the first examples of articulated dentitions of *R. binkhorsti* from North America, thus illustrating how rare finds such as these really are. The partial dentition illustrated here is undoubtedly the first report of associated dental remains of *R. binkhorsti* from Europe. Together with the material from Mississippi, it may help us capture the variation in tooth morphology of this particular ray species and furthermore yield clues as to its dietary preferences. Its solid tooth plate points at a durophagous diet (Enault *et al*., 2016), potential food items including oysters and other bivalves, gastropods and ammonites (Cicimurri & Ebersole, 2020). Representatives of these molluscan groups were all abundantly present in the Maastrichtian sea of the study area.

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More than just jaws – the pycnodontiform fish genus *Anomoeodus* from the Maastrichtian type area*

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**In commemoration of Paul Dols (1965-2017)*

Although remains of teleost fish are frequently encountered in and recovered from the various members of the Gulpen and Maastricht formations (upper Campanian-upper Maastrichtian) in the extended Maastrichtian type area, more or less complete skeletons are comparatively rare. To date, only a handful of (semi-)articulated fish are known from these strata (Friedman, 2012; Jagt & Schwarzhans, 2022). Amongst others, these include partial skeletons of two dercetids (*Cyranichthys jagti* Taverne & Goolaerts, 2015 and *Dercetis triqueter* Pictet), *Omosoma* sp. and *Enchodus faujasi* Agassiz.

The study of fish fossils from the Maastrichtian type area dates back to the turn of the eighteenth and nineteenth centuries. It was Faujas Saint-Fond (1798-1803) (see also Brignon, 2015), who illustrated some isolated cranial remains and teeth, but did not name these; names were later introduced by Louis Agassiz, amongst other scientists. By the latter half of the nineteenth century, the study of fossil fish was taken up in earnest. Forir (1887, 1889) erected the genus *Anomoeodus* and distinguished three species, and recorded several other taxa (see also Lambers, 1998). Recently, the number of teleost taxa was expanded markedly by a study of silicified otoliths (Schwarzhans & Jagt, 2021), amongst others of early gadiforms and perciforms.

Pycnodontiforms represent a group of actinopterygians of near-global distribution during the Mesozoic and Paleogene (Kriwet, 2002, 2005). The genus *Anomoeodus* Forir, 1887 was widely distributed, as is illustrated by records from Europe (Kriwet, 2002; Licht & Kogan, 2011), the United States (Shimada & Everhart, 2009) and North Africa (Cooper & Martill, 2020). Lebrun (2024) presented a recent overview, illustrating several (near-)complete skeletons of various genera and species. However, most pycnodontiforms are diagnosed on the basis of isolated elements, such as scales, isolated teeth or dentitions, only. In fact, merely twelve percent of known pycnodontiforms has been described from dissociated skeletal remains (Kriwet, 2001). *Anomoeodus* is no exception; until now, it was known from the Maastricht type area (south-east Netherlands, north-east Belgium) exclusively as isolated vomerine [upper jaw] and prearticular [lower jaw] dentitions. Three species have so far been recorded (Friedman, 2012), namely *A. foriri* Leriche, *A. fraiponti* Forir and *A.*

subclavatus (Agassiz), but there may be other taxa as well (Fig. 1). *Anomoeodus subclavatus* appears to have been the commonest, with several dentitions currently on record (Umbgrove, 1956; Jagt & Dols, 2010). Friedman (2012) also referred lozenge-shaped scales with an external ornament of irregular ridges to *Anomoeodus*, and mentioned that scales of that particular type had not yet been recorded from the Maastrichtian type area. Here we present a partial postcranial skeleton from the study area that retains these particular scales (Fig. 2).

This specimen (NHMM 2024 007) was recovered by the late Paul Dols from the basal Emael Member (Maastricht Formation) at the CBR-Romontbos quarry, Eben Emael, province of Liège (Belgium). The postcranial skeleton, consisting of extremely fragile and delicate bones, has now been prepared and consolidated. Although damaged and incomplete, it preserves a large portion of the vertebral column. At least twelve vertebrae may be counted, with elongated neural spines and haemal arches, which are either straight or slightly curved caudally. Moreover, several black-coloured scales are seen in close proximity and are here considered conspecific. On the basis of these fragmentary, albeit associated, skeletal elements, a typical laterally flattened (compressed) and deep body shape may be deduced, which is typical of pycnodonts. Moreover, some of the preserved scales may be described as lozenge shaped, in accordance with Friedman (2012), who mentioned that *Anomoeodus* likely was one of the few teleost fishes in the Maastrichtian type area that bore a partial coat of rhombic scales. In view of the fact that *Anomoeodus* is the commonest representative of the Pycnodontiformes in the Maastrichtian type area, and the species *A. subclavatus* the most frequent, we refer to NHMM 2024 007 as *Anomoeodus* cf. *subclavatus*. This find is thus an important specimen for science that may contribute to gaining new insights into the anatomy and morphology of *Anomoeodus*, a genus diagnosed mostly on the basis of dentitions.

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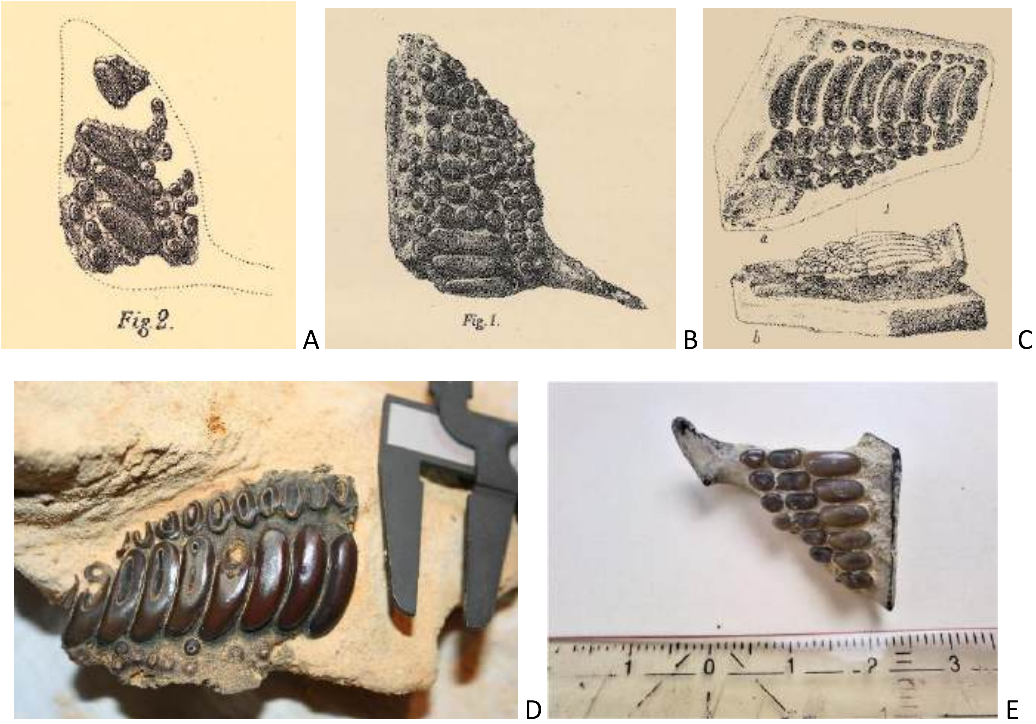

Figure 1. Prearticular dentitions of late Maastrichtian species of *Anomoeodus* from the extended Maastrichtian type area: A. *Anomoeodus foriri*; B. *Anomoeodus fraiponti*; C. *Anomoeodus subclavatus* (all from Forir, 1887, 1889); D. *Anomoeodus subclavatus* (P. Dols Collection); E. *Anomoedus*(?) sp. nov. (J. Severijns Collection).

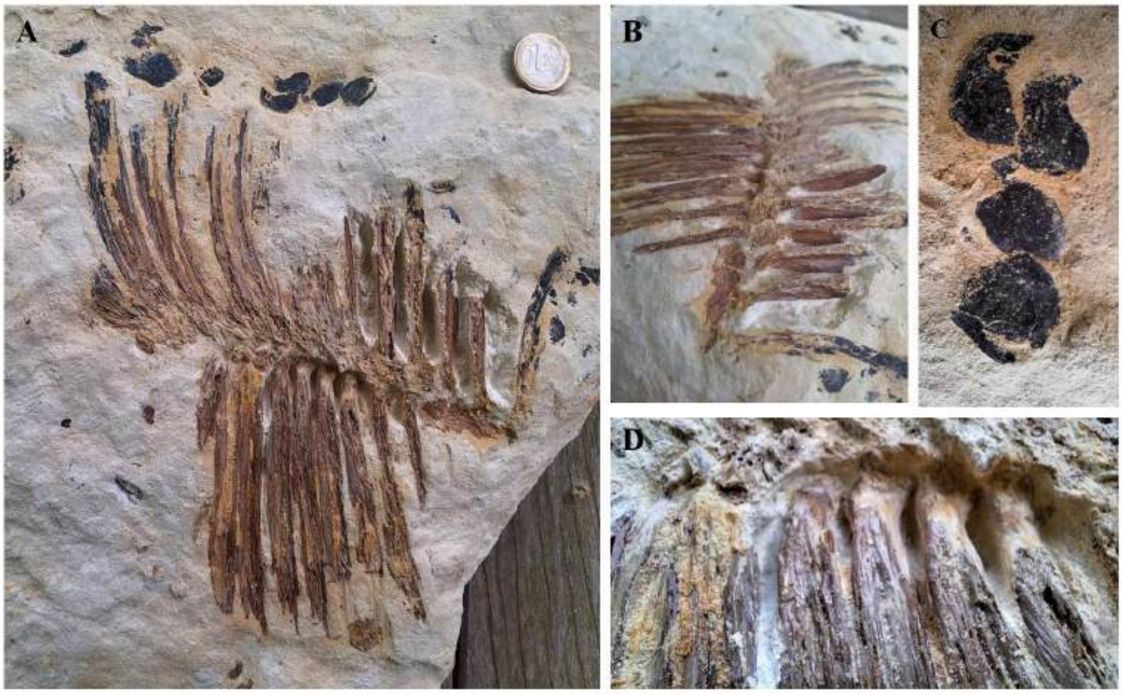

Figure 2. Partial postcranial skeleton (A, B, D), presumably of *Anomoeodus* (*A.* cf. *subclavatus*), with lozenge-shaped scales (C); basal Emael Member (Maastricht Formation), CBR-Romontbos quarry, Eben Emael (Liège, Belgium) (NHMM 2024 007, leg. P. Dols). A 1-euro coin for scale.

Gut contents of a subadult individual of *Mosasaurus hoffmannii* Mantell, 1829 from the Maastrichtian type area (the Netherlands) hint at the species' dietary preferences

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Here we present preliminary data on potential stomach contents of a subadult individual (NHMM 2015 027) of the mosasaurid *Mosasaurus hoffmannii*, discovered in April 2015 and nicknamed 'Lars'. It originates from above the Lava Horizon in the middle of the Emael Member (Maastricht Formation) at the former ENCI-HeidelbergCement Group quarry at Sint-Pietersberg, near Maastricht (see Jagt *et al*., 2015, 2016; Barten *et al*., 2023a, b).

Bony material of a cheloniid turtle, possibly *Ctenochelys*

Between a string of seven articulated posterior dorsal and anterior caudal vertebra of specimen NHMM 2015 027, bone fragments of a small-sized turtle were recovered in the field during the earlier stages of the dig in April 2015 (Fig. 1). Although most of the mosasaur rib cage was lost due to quarrying prior to its discovery, the presence of turtle bones in the lower back area of this squamate predator, i.e., where its intestines would have been, suggests that they might well represent remains of the mosasaur's last meal. The discovery of an unidentifiable bone fragment at the same spot supports this hypothesis, because the fragment is severely damaged, reflecting corrosion by acidic gastric juices. During preparation in the museum laboratory, additional turtle bones were uncovered. This material includes two peripheral bones (Fig. 1B-E), triangular in cross-section and with pits for accommodation of ribs clearly visible in both pieces. Also, numerous fragments of the plastron were found (Fig. 1A), several of which could be pieced together and restored partially. Additionally, two vertebrae were recognised, and there are some (still) unidentified, yet distinct, bones that cannot be of a mosasaurine origin in view of their small size (Fig. 1F, G).

Heere *et al*. (2023) have recently recorded a lower jaw from the Emael Member (Maastricht Formation) at the former ENCI-HeidelbergCement Group quarry; this shows a close affinity to that of the marine turtle genus *Ctenochelys*. The peripherals and plastron fragments found near NHMM 2015 027 are closely similar in morphology and size to peripherals and plastron of a juvenile individual of *Ctenochelys stenoporus* (Hay, 1905), as described in detail by Matzke (2007, figs 12, 13). Thus, it seems likely that this individual of *M. hoffmannii* had consumed such a juvenile turtle, just prior to its demise.

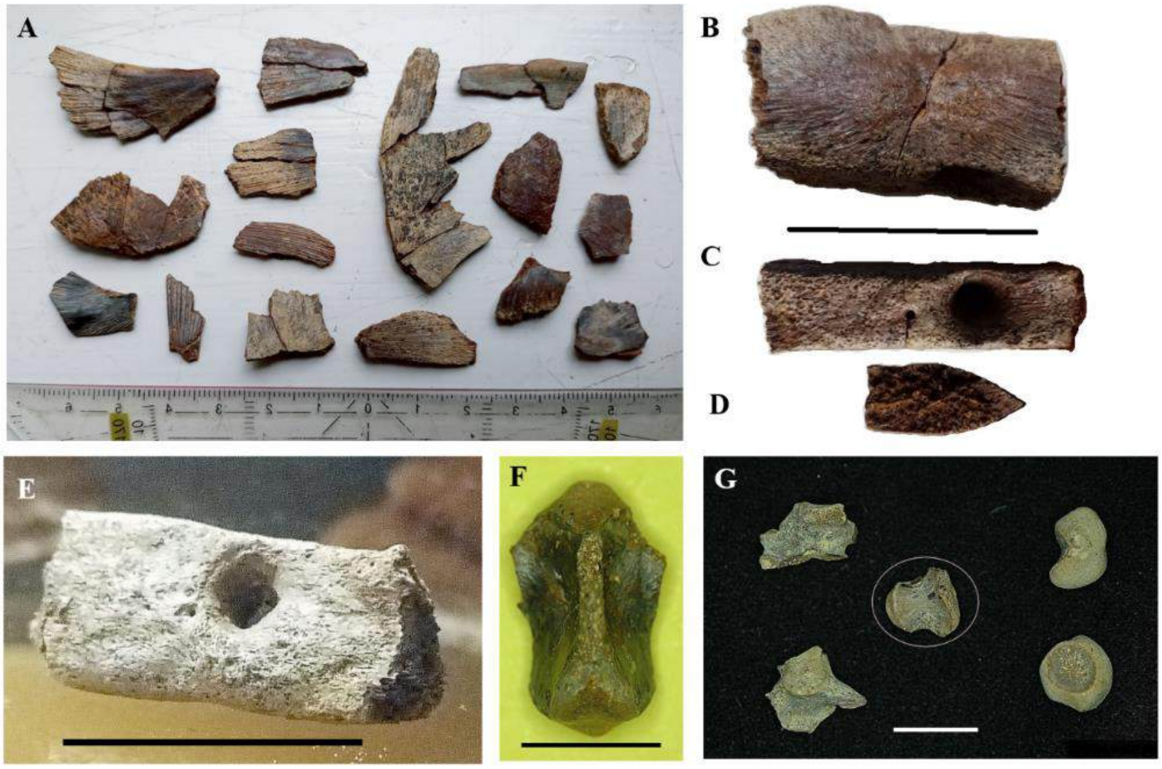

Figure 1. Isolated bones of a chelonioid turtle, possibly *Ctenochelys*, recovered in association with *Mosasaurus hoffmannii* (NHMM 2015 027). **A**. Different plastron fragments, some restored. **B-D**. Several views of a peripheral bone, showing the pit for accommodation of a rib and the triangular cross section. Scale bar equals 30 mm. **E**. A second peripheral with pit visible. Scale bar equals 30 mm. **F**. Turtle vertebra. Scale bar equals 5 mm. **G**. Several corroded and still unidentified bone fragments, including a potential vertebra (circled). Scale bar equals 5 mm. Photographs: Lars P.J. Barten and Eric A.P.M. Nieuwenhuis.

Avian/non-avian dinosaur bones

During wet sieving of matrix originating from the pelvic area of NHMM 2015 027 at the Natuurhistorisch Museum Maastricht, two small, yet well-preserved pedal phalanges (Fig. 2) were noted. One of these has recently been illustrated by Field *et al*. (2024, fig. 8). The size and typical morphology of these pedal phalanges, with their pulley-shaped joints, allows them to be distinguished from phalanges of marine reptiles (such as mosasaurs and turtles) and to be assigned to a (non-)avian dinosaur (Field *et al*., 2024). The discovery of dinosaur or avialan-like bird remains from the type section of the Maastrichtian Stage is already unique by itself. Although this cannot be determined with certainty at the moment, it is possible that these remains represent mosasaur gut contents as well, having been found in close association with NHMM 2015 027. Mosasaurs are known to have preyed upon marine birds such as *Hesperonis* (Martin & Bjork, 1987).

Figure 2. Several views of one of the two (non-)avian dinosaur pedal phalanges, found in association with 'Lars', a partial skeleton of *Mosasaurus hoffmannii*. **A, B**. dorsal views. **C**. ventral view. **D, E**. lateral views. **F**. closeup showing pulley-shaped joint. The other specimen is illustrated in Field *et al*. (2024, fig. 8). Photographs: Lars P.J. Barten.

Our preliminary observations on the putative stomach contents of mosasaur 'Lars' yield new and valuable insights into the dietary preferences of large mosasaurine mosasaurs such as *M. hoffmannii*, the commonest taxon in the Maastrichtian type area. Future research on this subadult individual of *M. hoffmannii* needs to include a detailed dental microwear analysis (see Holwerda *et al*., 2013, 2023), so as to determine whether or not microwear patterns are in correspondence with its preserved gut contents. Moreover, as the specimen represents one of the smaller individuals of *M. hoffmannii* known to date, it might yield novel data on the ontogenetic development of tooth morphology in this species. In that respect, it might contribute to resolving the discussion about whether or not *M. lemonnieri* represents a juvenile form of *M. hoffmannii*, as suggested by Mulder *et al*. (2004) and recently discussed anew by Madzia (2019).

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Mosasaur 'Carlo', an unusual globidensine mosasaur from the upper Maastrichtian Gulpen Formation of the Maastrichtian type area (southeast Netherlands, northeast Belgium) – an update

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Globidensine mosasaurs constitute an important and speciose marine reptile clade that underwent significant diversification during the Campanian and Maastrichtian. They occupied various ecological niches and exploited a wide range of resources as durophages, piscivores and macropredators. Here we introduce a new globidensine mosasaur from the type Maastrichtian that underlines the evolutionary success story of the clade. Previous notes on the specimen, NHMM 2012 072, focused on cranial pathologies (Bastiaans *et al.*, 2020) and provisionally attributed it to *Prognathodon sectorius*. After completion of its preparation, we may now offer a comprehensive description of the morphologically informative material and discuss the affinities.

The mosasaur record from the type Maastrichtian, particularly from the Maastricht Formation, comprises an ecomorphologically diverse fauna comprised of five taxa: *Carinodens belgicus*, *Plioplatecarpus marshi*, *Prognathodon sectorius*, *Mosasaurus hoffmanni* and *Prognathodon saturator* (Schulp *et al.,* 2013). The new specimen, NHMM 2012 072, originates from the upper Lixhe 3 Member of the underlying Gulpen Formation. This level is not typically associated with abundant mosasaur fossils, adding to the significance of this find. In contrast to most mosasaur finds from the Maastrichtian type area, NHMM 2012 072 was found almost fully disarticulated, with poor bone surface preservation and the presence of pyrite and marcasite both in the matrix and fossil, which after oxidation results in a thin gypsum veneer on the bone surface (Ritsema & Groenenberg, 1993). Parts of the premaxilla, anterior maxillae, anterior dentaries, a largely preserved braincase lacking the right paroccipital process, a dentigerous section of the left dentary comprising 10 alveoli, right splenial, left coronoid, presumed left angular, both pterygoids, the right posterior mandibular unit (PMU), left squamosal, fragmentary portions of the mandible, left ectopterygoid, axis; presumed cervical, posterior dorsal, lumbar and caudal vertebrae, isolated ribs and rib fragments, isolated teeth, and potentially a quadrate fragment have been recovered to date. Associated micro- and macrofaunal biota (Jagt, 2023), indicate prolonged sea floor exposure and potential scavenging of the mosasaur carcass by neoselachians.

Generic and specific assignment

NHMM 2012 072 is assigned to the Mosasaurinae based on several synapomorphies and plesiomorphies, including a raised tooth row situated on a distinct ridge above the shelf of the pterygoid; the shape of the basisphenoid pterygoid process retaining a relatively narrow gape with articular facets facing mostly anterolaterally; long basioccipital tubera that are parallel sided in posterior view and protrude ventrolaterally at exactly 45 degrees from horizontal; and a dentary medial parapet equal in height to the lateral wall of the bone (Simões *et al.,* 2017). It can be associated with '*Prognathodon*-type' mosasaurs on the basis of several shared features in most of the species, including the presence of a short but distinct premaxillary rostrum anterior to the first tooth position in most species in the genus; reduced number of dentary positions (from 16 to 15 or 14); the relatively large size of the pterygoid teeth, similar to marginal dentition; the medial inflection of the retroarticular process being extreme (i.e., almost 90 degrees); the angle of the anterior margin of the dorsum sellae relative to the sella turcica, gradually sloping anteroventrally; and the procumbent shape of the premaxillary teeth (Simões *et al.,* 2017; Lively, 2020).

NHMM 2012 072 is distinguished from all currently recognised '*Prognathodon*-type taxa' by a unique combination of features such as the comparatively long and higher rugosity of the basioccipital tubera, the distinct facetting of the tooth crowns in this taxon; as well as the lack of tooth inflation of posterior marginal tooth crowns, which is a common feature in other *Prognathodon* species but completely absent in NHMM 2012 072 (Schulp *et al.,* 2013; Simões *et al.,* 2017; Lively, 2020; Strong *et al.,* 2020; Longrich *et al.,* 2022; Zietlow *et al.,* 2023). It differs from *P. kianda* in having a short rounded or obtuse premaxillary rostrum. NHMM 2012 072 and *P. solvayi* differ from all other '*Prognathodon*-type' mosasaurs in the presence of procumbent teeth. NHMM 2012 072, *P. kianda*, *P. waiparaensis* and *Eremisaurus* all show a dorsal keel on the premaxillary internarial bar on both the dentigerous and internarial portions as opposed to a lack of such keel on all other '*Prognathodon*-type' mosasaurs. NHMM 2012 072, *P. overtoni* and *Gnathomortis stadtmani* all show shallow grooves trending anterodorsally from the lateral maxillary foramina which are lacking in all other mosasaurs in the clade. The shape of the premaxillary-maxillary suture in NHMM 2012 072, *P. overtoni, P. waiparaensis, P. solvayi* and *P. saturator* likely initially rose dorsally and then sloped posterodorsally as opposed to immediately posterodorsally sloping as in *P. kianda*. NHMM 2012 072 shares with *P. kianda, P. waiparaensis, P. solvayi*, *G. stadtmani* and *Eremiasaurus* the lack of coarse texturing on the tooth crowns, contrary to *P. overtoni, P. saturator* and *P. currii*. As opposed to *P. overtoni* and *P. kianda*, NHMM 2012 072 displays complex enamel structures on its tooth crowns in the form of facets, while *P. waiparaensis, G. stadtmani, P. solvayi* and *Eremiasaurus* all show some degree of facetting or fluting. The relatively large size of the pterygoid teeth of NHMM 2012 072 is a feature shared with *P. waiparaensis, P. solvayi* and *P. saturator*, while *P.*

kianda and *G. stadtmani* display relatively reduced pterygoid tooth sizes. NHMM 2012 072 and *G. stadtmani* both display a pterygoid tooth row that terminates well anteriorly of the bifurcation between the quadratic ramus and the basipterygoid process, while for instance *P. waiparaensis* shows a posterior bifurcation instead. NHMM 2012 072, *P. kianda, P. overtoni* and *Eremiasaurus* all show up to 15 dentary tooth positions, while *P. waiparaensis, P. saturator* and *G. stadtmani* have up to 14 and *P. solvayi* and *P. curriii* only 13 alveoli. NHMM 2012 072, *P. kianda, P. overtoni, P. waiparaensis* and *Eremiasaurus* all show an extension of the dentary anterior to the first alveolus, while such a process is absent in *P. solvayi, P. saturator* and *P. currii.* The medial wing of the coronoid in NHMM 2012 072 most likely would not have reached the angular which leaves a broadly exposed prearticular, as opposed to the condition in *G. stadtmani*, where it is only narrowly exposed. The extent of the surangular in NHMM 2012 072, as it does not reach the ventral margin of the mandible, leaves the articular and angular visible in lateral view. A similar condition can be observed in *P. overtoni* and *G. stadtmani*, while the opposite is seen in *Eremiasaurus*.

Additional work on the postcranial, exclusively axial skeleton, of NHMM 2012 072 is needed to obtain crucial additional characters to resolve an unequivocal closeness of the taxon with any '*Prognathodon*-type' mosasauroid. Nonetheless, despite some ambiguity of the specific relationships of NHMM 2012 072, it is clear that it is well-nested within '*Prognathodon*' and closely associated with *P. kianda* and perhaps the European taxa *P. saturator* and *P. solvayi* in some of the latest phylogenetic analyses (e.g., likelihood analyses of Simões *et al.,* 2017; parsimony analyses of Lively, 2020). Most recent phylogenetic analyses, however, recover no monophyletic '*Prognathodon*' clade but rather a paraphyletic assemblage (e.g., Simões *et al.,* 2017; Lively, 2020; Strong *et al.,* 2020; Longrich *et al.,* 2022; Zietlow *et al.,* 2023). This may be due in part to the fact that current phylogenetic analyses may be too influenced by ecologically driven morphologies, as illustrated by cranial proportions and dentition types, that may result in unreliable outcomes for gracile taxa such as *P. kianda*, *Eremiasaurus* and NHMM 2012 072. This emphasises the need for revised taxonomic and phylogenetic analyses of the interrelationships of highly nested mosasaurs and specifically the various species of '*Prognathodon*'.

Ecology

The facetted sharp dentition of NHMM 2012 072 may hint at a similar ecology to that of *Mosasaurus hoffmanni* which displays somewhat similar tooth morphologies. This will be further explored by using quantitative analytical methods such as 3D geometric morphometrics. This illustrates a previously overlooked ecomorphological diversity within '*Prognathodon*-type' mosasaurs and underlines the need for a revision of the genus both taxonomically, phylogenetically and ecologically. Endocranial reconstruction of NHMM 2012 072, although suffering from some degree of mediolateral deformation, shows dorsoventral compression and anteroposterior lengthening of the endosseous labyrinth similar to other highly nested mosasaurs. The relative semicircular canal size in NHMM 2012 072 indicates proportionately larger vestibular systems compared to brain size in highly nested mosasaurs when compared to more early diverging taxa such as *Platecarpus*. NHMM 2012 072 further provides evidence of violent interactions between mosasaurs, as the anterior cranium bears several pathologies with moderate levels of reparative bone formation. This provides unique insights into the trophic organisation and behavioural repertoires in mosasaurs in this latest Cretaceous ecosystem (Bastiaans *et al.,* 2020).

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New data on the holotype of the bizarre eosauropterygian, *Paludidraco multidentatus* (Nothosauroidea, Simosauridae)

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Simosauridae is an eosauropterygian clade ranging from the Middle (Anisian or Ladinian) to the Upper Triassic (Carnian) of the Middle East (Haas, 1981; Vickers-Rich *et al*., 1999; Kear *et al*., 2010) and Europe (Rieppel, 1994, 1996; Dalla Vecchia, 2008, 2017; de Miguel Chaves *et al*., 2015, 2018, 2020; Segesdi & Ősi, 2021). The clade is represented by two valid representatives: *Simosaurus gaillardoti* von Meyer, 1842, from the Ladinian of France and Germany, and *Paludidraco multidentatus* de Miguel Chaves, Ortega & Pérez-García, 2018, from the Carnian of Spain. Material of indeterminate attribution from this lineage has been identified in several Middle East and European sites with Middle to Upper Triassic strata (Kear *et al*., 2010; de Miguel Chaves *et al*., 2015; Segesdi & Ősi, 2021).

Simosaurids are mostly known by material attributed to the genus *Simosaurus* (Jaekel, 1905; von Huene, 1921, 1948, 1952, 1959; Kuhn-Schnyder, 1961; Haas, 1981; Rieppel, 1994; Vickers-Rich *et al*., 1999; Kear *et al*., 2010). In this sense, this clade was recognised as monotypic until the recent description of the Spanish form, the traditional diagnosis of Simosauridae therefore being exclusively based on the relatively well-known *S. gaillardoti*. This was interpreted as an active durophagous predator based on its large and blunt conical teeth (Rieppel, 1994). *Paludidraco multidentatus* has recently been defined on the basis of a relatively complete skeleton (holotype) and a partial skull (paratype) (de Miguel Chaves *et al*., 2018). The brief description of the holotype has allowed the recognition of several synapomorphies for the Simosauridae, which is why an amended diagnosis was preliminarily proposed for the clade, awaiting a more detailed assessment of the anatomy of the new species and improvement of its diagnosis. *Paludidraco multidentatus* has been interpeted as a filter feeder based on tooth morphology which shows adaptations to a slow mode of locomotion and, therefore, suggesting a notable ecological disparity in the clade (de Miguel Chaves *et al*., 2018). Although the holotype of *P. multidentatus* is relatively complete and exceptionally well preserved, a detailed characterisation of the poscranium of this bizarre simosaurid has not yet been published.

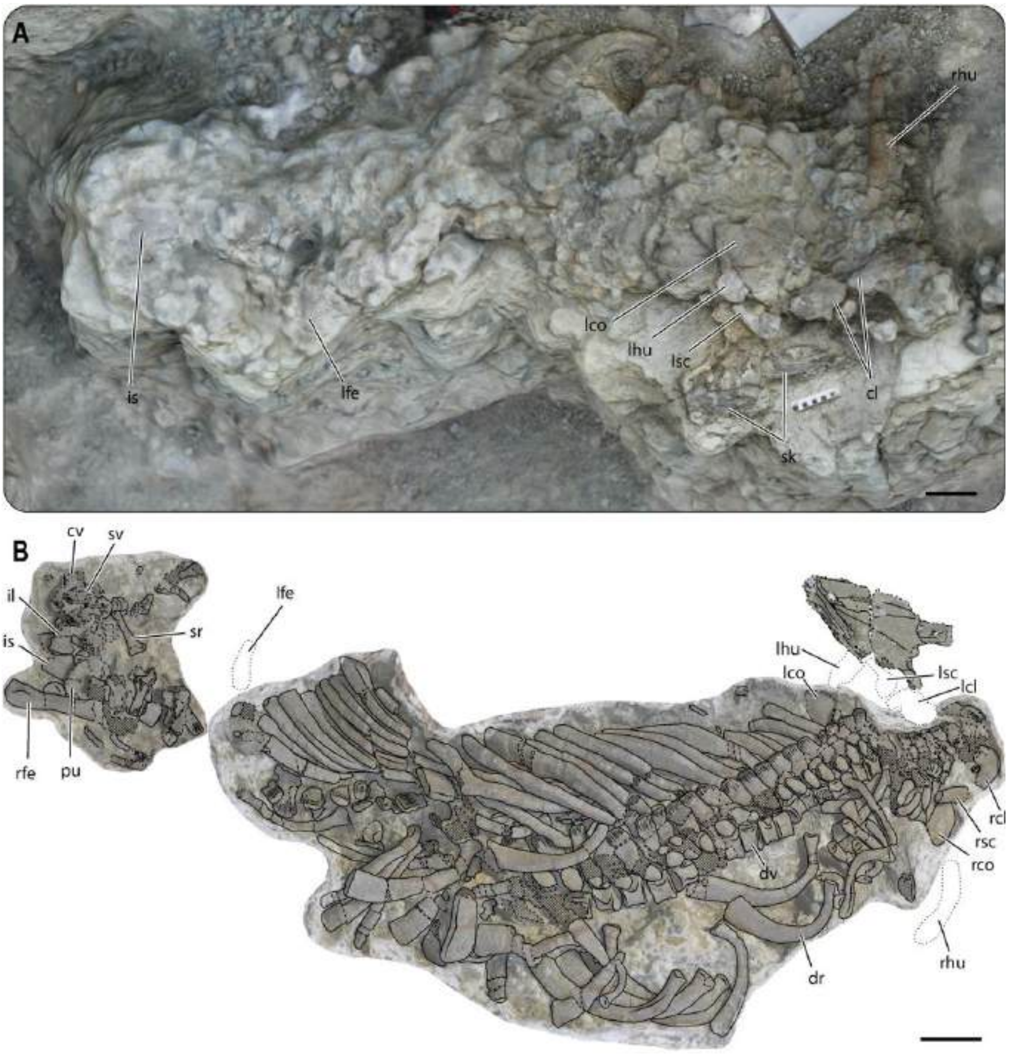

Figure 1. The holotype of *Paludidraco multidentatus* (MUPA-ATZ0101) from the Carnian (Upper Triassic) of El Atance (Guadalajara, Spain). **A.** 3D rendering of the top field view of MUPA-ATZ0101 (modified from García-Ávila *et al*., 2021). **B**. Preliminary stage of preparation of the dorsal view of MUPA-ATZ0101 (modified from de Miguel Chaves *et al*., 2018). Dotted lines indicate the position of the bones removed during the excavation. *Abbreviations*: **cv**, caudal vertebra; **dr**, dorsal rib; **dv**, dorsal vertebra; **lcl**, left clavicle; **lco**, left coracoid; **lfe**, left femur; **lhu**, left humerus; **lsc**, left scapula; **il**, ilium; **is**, ischium; **pu**, pubis; **rcl**, right clavicle; **rco**, right coracoid; **rfe**, right femur; **rhu**, right humerus; rsc, right scapula; **sk**, skull; **sr**, sacral rib; **sv**, sacral vertebra. Scale bars equal 100 mm.

The holotype of *Paludidraco multidentatus* (MUPA-ATZ0101) consists of a relatively complete skeleton that was found partially articulated in the field (Fig. 1A). It was collected from the Keuper Facies of the El Atance fossil site (Guadalajara, Spain), which corresponds to the Carnian (i.e., the Julian substage) (see García-Ávila *et al*., 2021). It was extracted in three main blocks (Fig. 1B): the skull, a large block containing most of the postcranial skeleton, and a smaller block with pelvic and other posterior postcranial elements. The skull is relatively complete, the anterior half being partially distorted due to severe taphonomic deformation. It preserves its relatively complete posterior part (e.g., the entire parietal or both squamosals and quadrates), the complete palate, part of the snout, plus partial left and right mandibular rami (see de Miguel Chaves *et al.*, 2018). The mandibles show numerous and small sickle-like teeth displayed in a pleurodont implantation. The postcranium was preliminary prepared in dorsal view for the first publication (see Fig. 1B). The larger block preserves the last cervical vertebrae, most of the dorsal vertebral series and dorsal ribs, and part of the pectoral girdle (i.e., partial right and left clavicles, remains of both coracoids and partial right scapula). Most of the elements in this block are articulated, preserving its original position. The smaller block preserves vertebrae and ribs from the distal dorsal, sacral and caudal regions, elements of the pelvic region (i.e., both partial ilia, a pubis and an ischium), as well as a partial right femur. Additional elements associated with this specimen were collected during the excavation, which include at least both partial humeri, a partial left scapula, a partial left femur, and several vertebral and rib elements both from the cervical and dorsal regions, all of them being currently under preparation (see Fig. 1B).

Further preparation of the holotype of *Paludidraco multidentatus* for a precise characterisation following the original publication of the taxon is currently almost finished. This includes a thorough preparation of the ventral side of this specimen, the complete removal of the elements extracted in the small block, and the disarticulation of several elements of anatomical and systematic interest from the larger block (i.e., pectoral girdle elements and cervical vertebrae). A detailed characterisation of the postcranial material of *P. multidentatus* that it is being prepared is currently in process, so as to perform a detailed comparative anatomical study with *Simosaurus gaillardoti*. Hence, this will enable a better characterisation of both taxa and provide an updated diagnosis for Simosauridae. The main anatomical information hitherto derived from this study is presented here.

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Vertebrate palaeontology at Maastricht University

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Officially founded in 1976 with the establishment of a medical faculty, Maastricht University is a relatively young university, still less than fifty years old. The university's Faculty of Science and Engineering is even younger, established as recently as 2018. A dynamic and rapidly growing faculty, it was established by bringing several existing and newly established programmes in the sciences under the same roof, with new initiatives being developed each year. One of these recent developments is the addition of vertebrate palaeontology as a curricular and research component of the Maastricht Science Programme.

Maastricht University is positioned on some of the oldest geological bedrock in the Netherlands, in a province with a rich geological and palaeontological history. The Maastricht area marks many major milestones and events in the growth and development of the geological and palaeontological sciences. This includes the establishment of the Maastrichtian Stage in 1849 by André Dumont, the youngest time slice of the Cretaceous, based on limestone outcrops of the Sint-Pietersberg, south of the city. It also includes the 18th-century discovery of the 'Grand Animal de Maestricht', now known as *Mosasaurus*, an animal that played a key role in the recognition of the concept of extinction (Cuvier, 1796, 1799; Homburg, 2015; Jagt *et al.*, 2024).

The new research initiatives, collaborations and programme building at Maastricht University endeavour to bridge the span from Maastricht's storied palaeontological and geological history to the cutting-edge palaeontological science of today. In these initiatives, collaborations with established partners such as the Natural History Museum of Maastricht, Natuurmonumenten and the established community of citizen scientists who have been studying and collecting in the area for many decades is an integral component. One of the upcoming new research initiatives are excavations at the former ENCI quarry, together with our partners at the Natural History Museum of Maastricht, Natuurmonumenten and citizen scientists. Another large-scale collaborative project is the 3D imaging of the fossil fauna from the Upper Cretaceous sedimentay rocks of the region. In their palaeontological studies at Maastricht University, many students are exposed to scientific methods such as geometric morphometrics and digital imgaging (Fig. 1), and the study of Cretaceous fauna locally and in the different corners of the world. Another focal point of vertebrate palaeontological research at Maastricht University is island evolution, with active projects running in the Mediterranean and the Mascarenes.

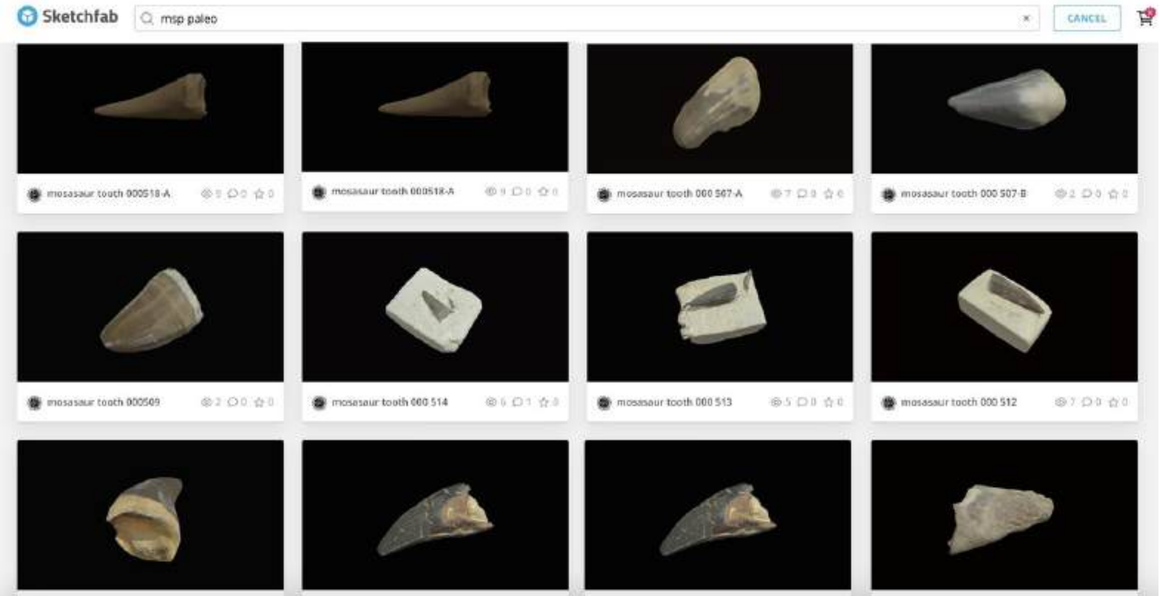

Figure 1. Structured light 3D surface scans of Late Cretaceous mosasaur teeth from the De Heer Collection (Natural History Museum of Maastricht), rendered by Maastricht Science Programme students. These interactive 3D scan models can be accessed on Sketchfab https://sketchfab.com/MSP-Paleo/Collections/Late-Cretaceous

In our presentation, we look forward to sharing information on the latest developments in vertebrate palaeontology at the Faculty of Science and Engineering with you, and to highlight the many exciting collaborative projects that are both underway and in development.

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Unlocking the digital potential of the Maastrichtian fossil record

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The Upper Cretaceous limestone deposits of southern Limburg constitute a unique geological, palaeontological, biological and cultural heritage. The Sint-Pietersberg specifically holds global significance as it contains the original type section of the Maastrichtian Stage, the final millions of years of the Mesozoic (Vellekoop *et al.*, 2022; Jagt *et al.*, 2024). Outcrops of Upper Cretaceous strata yield a rich fossil biota that includes radiations and the origins of new species. The end of the period is marked by the disappearance of (non-avian) dinosaurs and other major vertebrate and invertebrate taxa. The rich invertebrate fauna and iconic extinct vertebrates found within these Upper Cretaceous limestone sediments, such as *Mosasaurus*, have been integral to the establishment of the concept of extinction (Cuvier, 1796, 1799). The local quarries and outcrops continue to offer a remarkable potential and still yield new fossil discoveries and fundamental insights into organismal evolution. For instance, the recently discovered extinct birds *Asteriornis* and *Janavis* have fundamentally revised our understanding of the relationships between basal living bird taxa (Field *et al.*, 2020; Benito *et al.*, 2022).

However, information on the Maastrichtian fauna of southern Limburg is often scattered and can be difficult to access. Additionally, with quarries ceasing commercial operation, access to and detailed knowledge of strata is rapidly disappearing. Here, we introduce our initiative to 3D scan the full diversity of southern Limburg Late Cretaceous faunal remains, from both museum and private collections. The aim is to compile and curate knowledge and to facilitate the study of life from the Maastrichtian type area worldwide.

Three-dimensional scanning will be undertaken at Maastricht University, the Maastricht Natural History Museum, on-site at various other institutes, and *in situ* during excavations. Currently, the majority of specimens are being imaged through structured light surface scanning methods (Fig. 1A-D), but future data collection will also make use of non-contact laser surface scanning, LiDAR, photogrammetry, CT, microCT and synchrotron scanning.

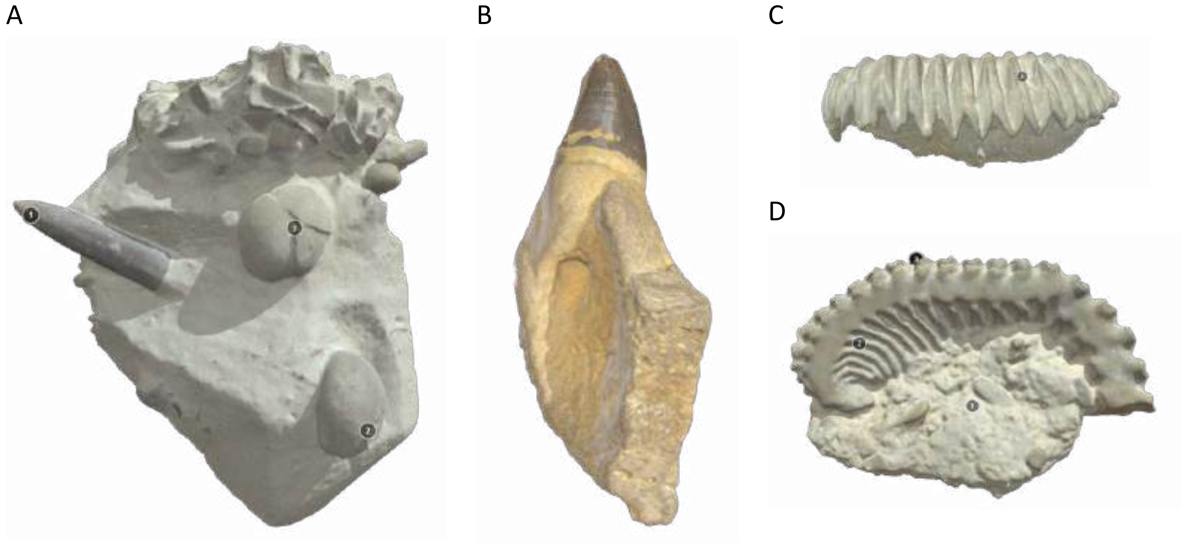

Figure 1. Structured light 3D surface scans of late Maastrichtian fossils rendered by students from the Maastricht Science Programme. **A.** limestone block with belemnite, echinoderms and molluscan shell fragments visible; **B.** Mosasaur tooth from De Heer Collection (Natuurhistorisch Museum Maastricht); **C, D.** Single valve of the bivalve *Agerostrea ungulata* (von Schlottheim), in lateral and dorsal view, respectively (NHMM De Heer Collection). These interactive 3D scan models can be accessed on Sketchfab https://sketchfab.com/MSP-Paleo/Collections/Late-Cretaceous.

The scans and their metadata will be collected, reposited and made available using standard protocols and best practices (e.g., Davies *et al*., 2017). To facilitate data use and the creation of integrated curated datasets, we plan to develop a dedicated internet user portal. To ensure long-term access, scans will be stored in open file formats and files will be duplicated on established digital repositories and interactive platforms such as MorphoSource and Sketchfab. Growth of the database will be guided by research projects, including embedding in undergraduate and graduate research projects at Maastricht University and the Natural History Museum of Maastricht.

We anticipate that our scanning initiative will help digitally unlock the rich biota of the Upper Cretaceous of the southern Limburg region and facilitate quantitative and qualitative studies at species level, focusing on topics such as form and function, taxonomy and phylogeny and down to ecosystem level and beyond. Continued discoveries at classic localities underscore the never-ending potential for new fossil finds and novel insights. The digital curation and open sharing of scan data will help facilitate studies of the Maastricht region's rich geological and palaeontological heritage. It will help expand the worldwide reach of fossil data, while also lowering specimen attrition through physical handling and providing a digital alternative for costly museum travel. We are enthusiastic about, and look forward to, the new opportunities that the project will offer to all.

Acknowledgements

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Maastrichtian inoceramid bivalves, ammonites and dinoflagellate cysts from the Moravitsa section, north-west Bulgaria

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The Moravitsa section is located 1.5 km south of the village of Moravitsa (municipality of Mezdra) in the gully of the River Kamenitsa of north-west Bulgaria. This section is situated in the border part of the Central Balkan-Fore Balkan Tectonic Zone which forms the outer segment of the Balkan Orogen in Bulgaria (*sensu* Ivanov, 2017). Exposed is a continuous upper Campanian-Danian sedimentary succession comprising the K/Pg boundary interval (Sinnyovsky, 2004; Stoykova & Ivanov, 2004) and unconformably overlying Lower Cretaceous (Aptian) sandstones of the Roman Formation. The base of the succession is composed of reddish, bioturbated, glauconitic sandstones of the Darmantsi Formation with a prominent nodular phosphate-bearing level, at the very base of the formation. Upsection, grey limestones and grey nodular limestones are exposed; these are included in the Kunino Formation (Fig. 1). The remainder of the section is represented by thin- to medium-bedded, grey limestones, rich in flint nodules and assigned to the Mezdra Formation; this encompasses the K/Pg boundary.

Fossil record

Inoceramid bivalves are the commonest macrofossils in the Moravitsa section, with nearly 100 per cent of these occurring in the Kunino Formation; this was previously named the “inoceramid bearing horizon” (see Bončev & Kamenov, 1934). Nearly all specimens were collected from a single, 30-cm-thick level cropping out two metres above the base of the formation. The majority are of large size and preserved as internal moulds; linked to their sheer abundance, they often overlap each other. The inoceramid assemblage at this level comprises *Cataceramus barabini* (*sensu* Meek), *Cataceramus bebahoensis, Cataceramus glendivensis*, *Cataceramus* aff. *goldfussianus*, *Platyceramus stephensoni*, *Platyceramus salisburgensis* and “*Inoceramus*” *howletti*. Rare inoceramid specimens were collected from 1.8 m above this inoceramid-rich horizon. The very characteristic “*Inoceramus*” *ianjonaensis morgani* was identified, accompanied by *Cataceramus bebahoensis*.

Ammonites rank second as most frequent macrofossil group in this section. Rare and poorly preserved specimens occur at the base of the Kunino Formation and comprise *Pachydiscus* (*Pachydiscus*) *neubergicus* and *P.* (*P.*) *armenicus* (Fig. 1). Upsection, 1.8 m above these pachydiscids, *Diplomoceras cylindraceum* has been observed. Additionally, fragments and partially preserved specimens of this species have also been obtained upsection from the Kunino-Mezdra lithological transition interval (Fig. 1).

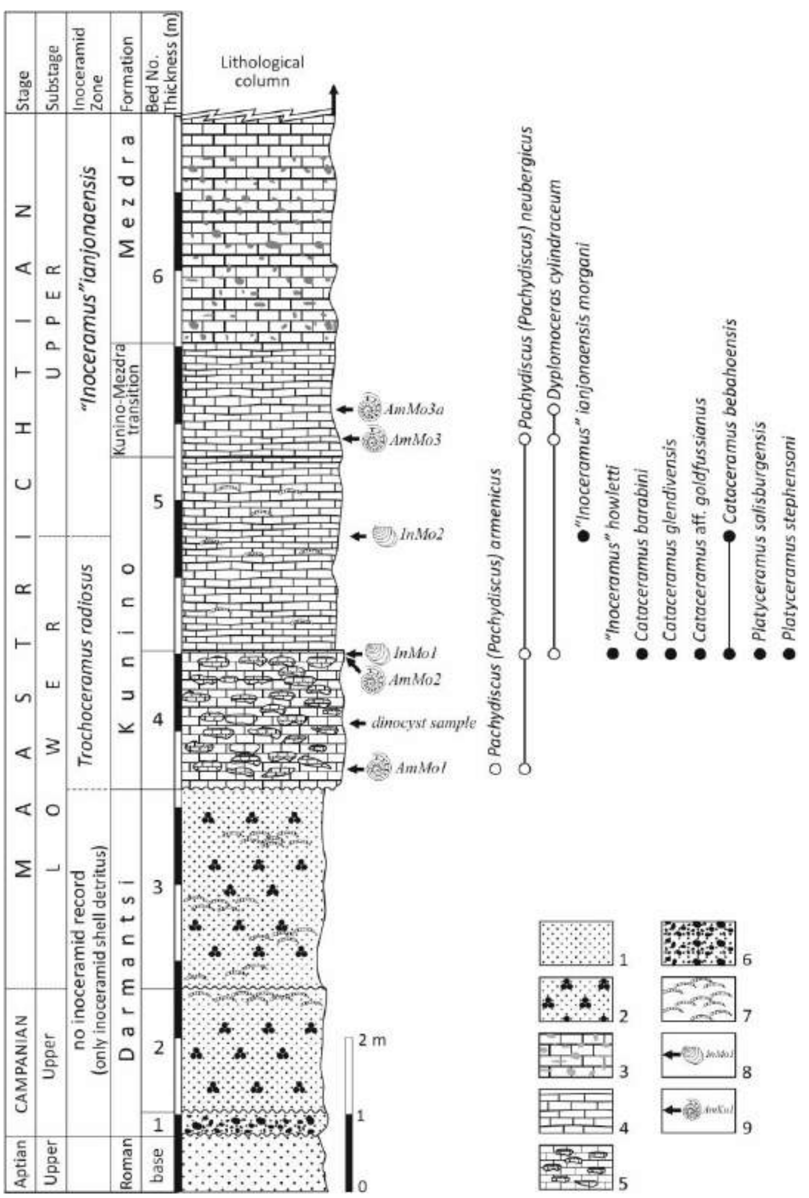

Figure 1. Lithological log of the Moravitsa section with inoceramid and ammonite distribution: **1.** green, yellowish-reddish to grey sandstones; **2.** reddish to rusty, highly bioturbated glauconitic sandstones; **3.** white to grey, medium- to thin-bedded limestone with abundant flint concretions; **4.** white to grey limestones; **5.** white, grey to light-grey nodular limestones; **6.** yellowish, brown and rusty phosphatic nodules; **7.** inoceramid detritus; **8.** occurrence of inoceramid bivalves; **9.** occurrence of ammonites.

One sample obtained at 0.9 m from the base of the Kunino Formation has yielded a dinocyst association of moderate abundance and preservation. The association includes the following taxa: *Cerodinium speciosum*, *Glaphyrocysta wilsonii*, *Florentinia mayi*, *Deflandrea galeata*, *Isabelidinium cooksoniae*, *Isabelidinium bakeri*, *Areoligera senoniensis*, *Areoligera medusettiformis, Pervospaeridium pseudhystrichodinium*, *Achomosphaera sagena*, *Hystrichospaeridium tubiferum* and *H. salpingophorum*. The concurrent presence of *Cerodinium speciosum*, *Glaphyrocysta wilsonii* and *Deflandrea galeata*, as well as the complete absence of *Cannosphaeropsis utinensis*, *Alterbidinium acutulum* and *Hystrichodinium pulcherrimum* marks an age not older than mid-Maastrichtian for the sampled interval, compared to the dinocyst zonations of Kirsch (1991) and Roncaglia & Corradini (1997).

Interpretation

From a sequence-stratigraphical point of view, the glauconitic sandstones of the Darmantsi Formation accumulated in a transgressive system tract with gradual sea level rise in the Moesian Epicontinental Basin during the latest Campanian-earliest Maastrichtian. In the Maastrichtian, the nodular and thin- to medium-bedded limestones of the Kunino Formation formed during a still rising sea level – transgressive system tract. Already during the latest Maastrichtian-Danian, the limestones rich in flint concretions of the Mezdra Formation (lower part) accumulated within a high system tract (Sinnyovsky, 2004).

The Maastrichtian inoceramid diversification and great biostratigraphical value of the group have been demonstrated in several papers (Walaszczyk *et al.*, 2009, 2010; Walaszczyk & Kennedy, 2011). Based on the presence of large-sized "*Inoceramus" howletti* and *Cataceramus* aff. *goldfussianus*, the inoceramid assemblage of the inoceramid-bearing level falls within the upper part of the *Trochoceramus radiosus* Zone (uppermost lower to lowermost upper Maastrichtian), although specimens of the genus *Trochoceramus* have not been recorded. Upsection, and based on the first occurrence of "*Inoceramus*" *ianjonaensis morgani* (see Fig. 1), the lower boundary of the "*Inoceramus*" *ianjonaensis* Zone (lower upper Maastrichtian) is marked (Walaszczyk *et al*., 2009, 2010).

Recently, the Mid-Maastrichtian Event (MME) was studied in detail using integrated biotic, petrological and geochemical data in order to reveal the driving mechanism behind it in the European Chalk Sea (Dubicka *et al*., 2023); a sea level rise of 50-100 m for at least 2 myr with high concentrations of mercury in sea water, most likely caused by intensive oceanic-tectonic activity and formation of vast oceanic plateaus. Moreover, climate warming, caused by greenhouse gases and changes in oceanic circulation, were additional factors leading to the extinction of many marine organisms, including inoceramid bivalves (Dubicka *et al*., 2023). The inoceramids were the dominant group among the marine benthic faunas form the late Albian nearly to the end of the Maastrichtian with great morphological and taxonomic diversity. Prior to their extinction during the early late Maastrichtian, inoceramids experienced one last diversity episode with morphological variety and species richness in the late early Maastrichtian (Dubicka *et al*., 2023).

Although palaeoenvironmental conditions of the Moesian Epicontinental Basin were different from those of the Chalk Sea, we consider that the MME is recorded in the Moravitsa section. One possible scenario of the inoceramid mass occurrence level in the Kunino Formation is that it falls at the beginning of the MME in the late early Maastrichtian (Dubicka *et al.*, 2023) and demonstrates a final bloom and diversity maximum of inoceramid bivalves. The first occurrence of "*Inoceramus*" *ianjonaensis morgani* at 1.8 m above the inoceramid mass occurrence level (i.e., base of the "*Inoceramus*" *ianjonaensis* Zone, lower upper Maastrichtian) coincides with the continuously rising sea level in the transgressive system tract, where thin-bedded limestones of the Kunino Formation accumulated. The maximum sea level in the Moesian Epicontinental Basin during the late Maastrichtian (peak of the MME) led to the formation of flint-rich limestones of the lower part of the Mezdra Formation, where inoceramids are absent and ammonite occurrences are poor. The other outcrops of the Kunino Formation (and basal Mezdra Formation) in the region that yielded an abundant inoceramid record (lower and lower upper Maastrichtian) corroborate this observation (Dochev & Metodiev, 2020; Pavlishina *et al.*, 2020). Another explanation for the inoceramid mass occurrence level is that is an expression of a local bioevent resulting from high productivity and associated with local deepening of the basin. The absence of inoceramids higher in the section might be not related with the decline of the group prior to the final extinction during the late Maastrichtian (Sinnyovksy, 2004).

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Fishes, mosasaurs and the season of the K/Pg extinction

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The Cretaceous-Paleogene (K/Pg) mass extinction was triggered by the Chicxulub asteroid impact, which eliminated approximately 76 per cent of species. The Tanis seiche deposit in North Dakota represents an extraordinary record of the direct effects of the Chicxulub impact. This includes specimens that likely perished by suffocation with impact spherules and/or subsequent entombment in sediment mobilised by the seiche wave.

Osteohistology and stable isotope archives of exceptionally well-preserved perichondral and dermal bones in acipenseriform fishes from the Tanis deposit were used to reveal annual cyclicity across the final years of the Maastrichtian and demonstrate that the catastrophic impact occurred in boreal spring (Fig. 1). Annual life cycles drive the seasonal timing and duration of reproduction, feeding, and hibernation, and in many taxa, reproduction and growth take place during spring. We postulate that the seasonal timing of the Chicxulub impact in boreal spring (During *et al.*, 2022) and austral autumn importantly contributed to selective biotic survival across the K/Pg boundary.

Further analysis on these fishes through synchrotron microtomography provided insights into their osteology, revealing that the Tanis paddlefishes represent new taxa (Hilton *et al.*, 2023). The biodiversity in the Maastrichtian appears to have been thriving. Furthermore, a study on stable isotopes from a mosasaur tooth from the Hell Creek Formation in North Dakota has yielded surprising results, suggesting that these formidable marine reptiles might not have been as exclusively marine as previously assumed. This unexpected discovery opens new avenues for understanding the ecological niches of mosasaurs and their adaptability to different environments.

These findings collectively provide a nuanced understanding of the end-Maastrichtian ecosystems, the timing of the K/Pg impact and its immediate effects on marine and freshwater ecosystems, shedding light on the selective biotic survival during one of Earth's most pivotal mass extinction events.

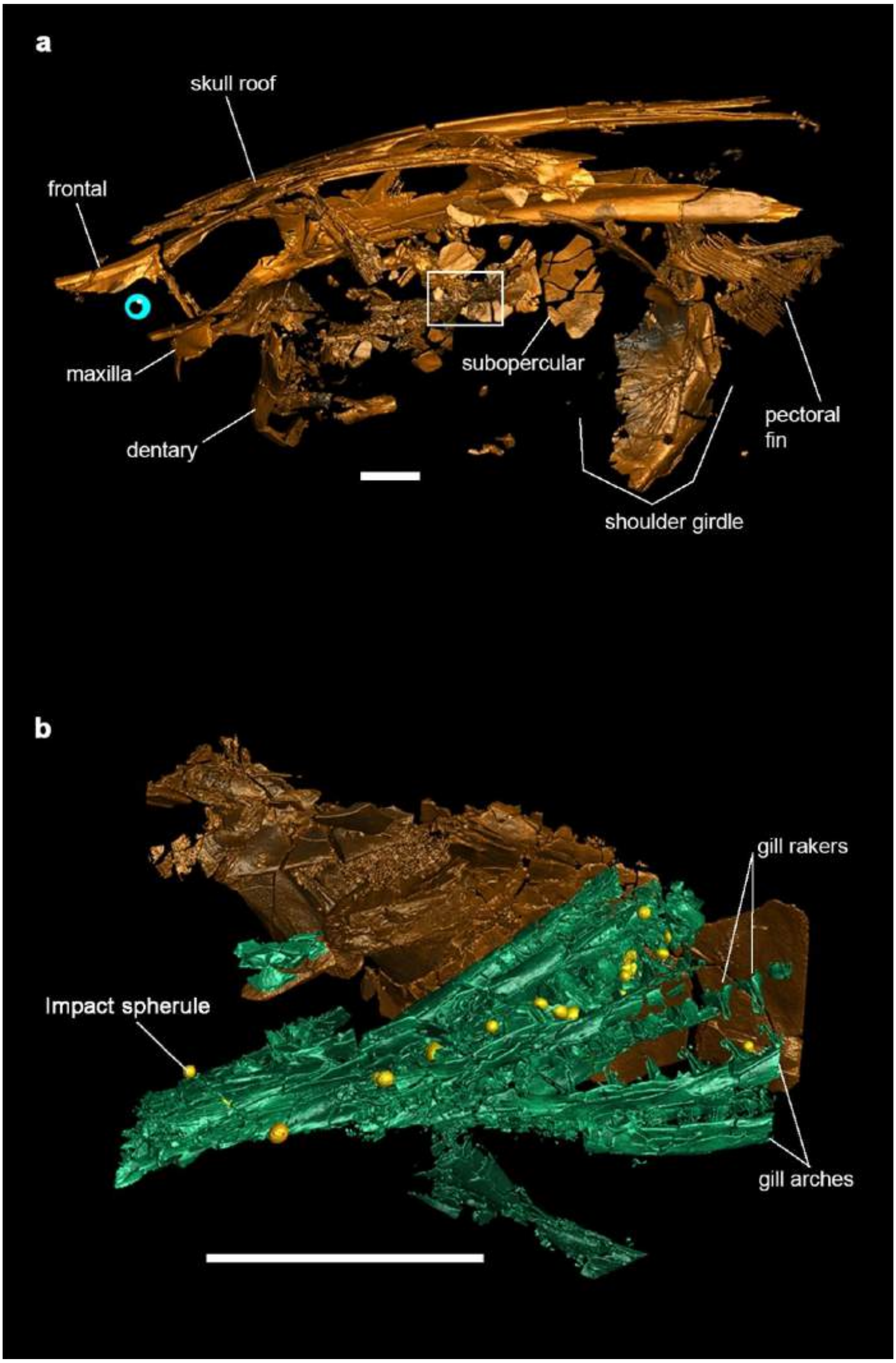

Figure 1. **a**. Three-dimensional model of paddlefish FAU.DGS.ND.161.4559.T, scanned at 43.5 µm voxel size, displayed in left-lateral perspective, highlighting the area for a higher-resolution scan (outlined in white); **b**. Three-dimensional visualisation of the subopercular region, scanned at 13.67 µm voxel size, displayed in right-lateral perspective. This higher-resolution view on the gills from panel a, shows entrapped impact spherules (yellow). Scale bars represent 20 mm.

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Maastrichtian building stones from the Mergelland type region; more than Maastricht Stone

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Introduction. A journey along historical buildings in the chalk district around Maastricht, located in Dutch southern Limburg, the Belgian province of Limburg and the adjacent Aachen-Liège border zone, becomes a discovery tour for local building materials (Dreesen *et al.*, 2019). By origin, they are natural objects, showing peculiar aspects of geodiversity which might have remained unnoticed when they would not have been transformed into cultural objects, and not to forget the influence of time on the state of the buildings. This contribution brings an overview of building stones of Cretaceous age in the Maastrichtian chalk district, as an update to Dusar *et al.* (2009) and a complement to Keuller *et al.* (1910), Felder & Bosch (2000) and Nijland *et al.* (2017).

Maastricht stone. Maastricht stone, locally known as 'mergel', forms the most representative stone in the chalk district and is closely linked to the Maastrichtian type section of André Dumont at the Lichtenberg quarry face, as this outcrop resulted from intensive quarrying in the Sint-Pietersberg (Montagne Saint-Pierre).Maastricht Stone is truly exceptional because of its unique properties, i.e., it is 'extremely weak, yet time-resistant' (Dubelaar *et al.*, 2006, p. 12). The Maastricht Formation consists of bioclastic grainstones with some flint nodules in discontinuous layers, reaching up to 50 m in thickness. Lithostratigraphical subdivision is related to astronomical cycles, from 20-kyr precession cycles for individual beds to 120-kyr obliquity cycles for the members, up to 400-kyr eccentricity cycles, subdividing the Maastricht Formation into a lower (Valkenburg to Emael members) and an upper part (Nekum and Meerssen members). In the type area, it has never been buried under more than *c.* 50 m of sedimentary cover (or about 100 m at its base). Consequently, the sediments were not much compacted. Hence, Maastricht limestone retains an extremely high porosity and a relatively low mechanical strength. Despite its extremely high porosity (up to 50 per cent) and very low compressive strength (< 5 MPa) Maastricht stone is a very durable rock type, which is evidenced by many building elements of several centuries old still in good condition. This is mainly due to the large pore size with practical absence of small pores and the formation of 'calcin', a thin protective layer. Rocks of the Maastricht Formation have been quarried both for building stone and as soil conditioner in hundreds of underground galleries, extending over an east-west distance of 40 km around the city of Maastricht. Differences in grain texture and fossil contents allow subdivision into different stone types. Roosburg block extracted from the lowermost Valkenburg to Gronsveld members is creamy white, very fine grained and most resistant to weathering. Sibbe block from the Emael Member is more orange-yellow in colour and granular in texture with excellent resistance to weathering and characterised by frequent serpulid-oyster layers. Light-yellow Nekum Member is solid (e.g., Sicher block) to more friable (e.g., Kanner block) with abundant echinoid debris and complete echinoderms. Outside its own region, use is documented in 14th- to 17th-century churches upstream the River Meuse (Maas) and in several towns in the so-called Rivierenland and Utrecht downstream, during the 15th and 16th centuries.

Kunrader limestone. Time-equivalent strata to the lower Maastricht Formation along the Rur Valley Graben were deposited under more neritic conditions, prone to alternation between subsidence and inversion, while karstification removed the equivalent of the upper Maastricht Formation. They are exposed in the Kunrade area between Valkenburg, Aachen (locally known as Vetschauer limestone) and Heerlen. Kunrader beds are affected by meteoric dissolution and precipitation, resulting in a diagenetic alternation on decimetric scale between loose and compact calcarenites. Kunrader limestone is weather proof, suitable for coursed rubble masonry. Historically its use did not extend much beyond the outcrop area. During the 20th century it has been extensively used all over Dutch southern Limburg. Isolated use in the 1930s and 1950a occurred as far away as Amsterdam and the provinces of Groningen and Drenthe in the north of the Netherlands.

Vijlen Chalk. Although not being entirely frost-resistant white chalk with splintery flint and occasional belemnites of the Vijlen Member (Gulpen Formation) was used in rural vernacular architecture, such as in barns, cellars and bakehouses (local name 'bakovensteen') along the southern boundary of southern Limburg. Similar chalkstone is encountered and used on a very small scale in the westernmost part of the Hesbaye (Biez chalk, Walloon Brabant).

Flint. Flint is intimately connected to chalk, although a completely different material. Its lithification process remains elusive but is linked to cooler climate cycles with higher incidence of biogenic silica production, precpitating mostly as chalcedony. Flint concretions are varied in form, from spiny bioturbations to continuous layers, the former used in their natural state for garden landscaping or follies, the latter hewn as rough building blocks, mostly derived from the Lanaye Member (Gulpen Formation). Flint was already mined in the Neolithic flint mines of Sint-Geertruid remaining in production until the end of the 20th century for application in mills. Flint became a building material in Roman times and is widespread in the Hesbaye region.

Silicified chalk. Among the flints concentrated in the residual deposits on top of eroded Cretaceous strata are many light yellow to caramel brown-coloured stones with a fine granular texture, resembling the original chalk. These silicifications are interpreted as a late diagenetic transformation of carbonates from the Gulpen Formation. A special case are the so-called ‘star stones’ (sterrenstenen), large residual blocks of silicified chalk containing flint nodules with smooth fracture surfaces, resulting from two different silicification events. Because of their irregular formats and unworkability use as building material has been restricted to rural constructions, near the respective extraction sites along the southern boundary of southern Limburg and in Hesbaye.

Heerd. Heerd is quarry terminology for a rock too hard to saw whereby the petrographic name is reserved for strongly cemented Maastrichtian limestones. Heerd results from selective dissolution and sparitic precipitation as a process comparable to the lithification of the Kunrader limestone but occurring within the Maastricht Formation. Hence, heerd is a rare material with variable facies, from rather chalky to coarse bioclastic and fossiliferous. Heerd is a conservative element in buildings, possibly predating the start of underground quarrying in the 13th century. In Utrecht, a 15th/16th-century (?) ornament in heerd from the Dom church has been encountered during excavations.

Tauw. Tauw is quarry terminology for a ‘tough’ stone, resistant to cleavage while absorbing shock energy. Contrary to heerd, tauw is silicified Maastricht Stone. At present, two types are distinguished. Vechmaal tauw originated as a silicification of a serpulid marker bed near the top of the Nekum Member, exposed in the Vechmaal underground quarry and occurring as elongated building stones in the Hesbaye part of Belgian Limburg, centred around the city of Borgloon. The Vechmaal tauw diagenesis occurred in three phases: 1) cementation of pores, 2) replacement of micritic components, 3) dissolution of sparitic fossils and cements. The former diagenetic phases probably occur in synchronicity with flint formation in the original sedimentary setting. The latter phase occurs as part of the post-Cretaceous weathering and creates a secondary porosity.

Elst tauw originates in its type area by silicification of the basal members of the Maastricht Formation exposed *in situ* in the Elst sand pit and found back as building stone or garden architecture in the Jeker valley between Tongeren and Maastricht. Elst tauw is orange-yellow, hewn into larger formats than Maastricht stone and contains purplish flint nodules. The silicification process was pedogenetic, postdating the Cretaceous depositional period and predating the Oligocene marine transgression, when a substantial part of the Maastricht Formation was already removed by dissolution/erosion. The Elst tauw diagenesis also occurred in two phases, affecting the top metre of the remaining calcarenite below the eluvial flint: 1) in the freshwater-marine water mixing zone calcitic bioclasts were partly dissolved and replaced by pyrite, 2) cementation of the pores by cryptocristalline quartz or megaquartz in the largest pores, 3) oxidation of the pyrite and complete dissolution of the bioclasts resulting in a secondary porosity of 12 per cent and rusty staining. The impervious flint nodules resisted the latest phase and have remained pyrite-rich, causing the strong purplish colouration.

Phosphatic chalk. A residual phosphate pebble bed at the base of the flint eluvium was extensively quarried underground in the Liège-Hesbaye region. Further west in the border zone with the province of Brabant, Orp chalk of Campanian age, rich in fossils and dispersed phosphate nodules in a layer not exceeding 1 m, was quarried at least from the 12th to the 17th century. A typical example is the internal cladding of St Adela's church in Orp-le-Grand. **Geoheritage value.** Historical building stones in monuments and vernacular buildings have been extracted from the subsoil during many centuries of human involvement with the land. Stony materials were collected or quarried at many places where today no longer direct access to the subsoil exists. They represent unique sources of information on the different lithologies and facies types or on their alteration processes, enabling us to improve our knowledge of both the regional geo-history and the building history.

Maastricht stone is the most important historical building stone in the Maastricht Chalk district. It is omnipresent in local architecture from the late Middle Ages to the 20th century, while older use has been evidenced by archaeological remains. Moreover, Maastricht stone deserves the qualification as heritage stone because of the obvious link to the remarkable though vulnerable underground quarries and the surrounding attractive landscape (Lahaye *et al.*, 2022).

Contrary to the widespread Maastricht stone and to a lesser extent Kunrader stone and flint, the other lesser-known stone types have not been used far beyond their extraction sites. Observation as building stone is indicative of their natural occurrence in the subsoil and a testimony to the complex geological history, with interplay between sedimentation or weathering and tectonics.

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Deconstructing ichthyosaur soft tissues and reconstructing *Stenopterygius* (Reptilia, Ichthyopterygia)

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The dolphin-like ichthyosaurs (colloquially known as 'fish lizards'; Fig. 1) represent an extinct lineage of marine reptiles that successfully roamed the oceans for much of the Mesozoic Era, leaving behind a rich fossil record from the Lower Triassic to the Upper Cretaceous. Similar to other fossil vertebrates, our understanding of these iconic animals predominantly stems from careful examination of naturally biomineralised hard parts, such as teeth and bones. However, the discovery of soft-tissue structures in exceptionally preserved specimens deriving from Konservat-Lagerstätten has unveiled novel avenues for exploring their anatomical and physiological attributes.

This presentation will delve into the annals of ichthyosaur research, covering over three centuries since their initial discovery. It will reveal how our comprehension of their morphology and ecological adaptations has progressively evolved through successive investigations, and how this has influenced reconstructive efforts. Particular focus will be devoted towards the record of soft-tissue structures and how these offer insights into ichthyosaur biology, ecology and physiology. Building on this historical backdrop, we extrapolated novel perspectives from an exquisite sub-adult specimen of the Jurassic parvipelvian *Stenopterygius* (Urweltmuseum Hauff Bodman, Bodman-Ludwigshafen, specimen MH 432), recovered from the Posidonia Shale of Holzmaden, southern Germany (Lindgren *et al.*, 2018). The study by Lindgren *et al.* (2018) reported groundbreaking results, notably including the discovery of soft tissues with parts of the original biomolecular inventory retained. The pristine nature of the fossil material provided unprecedented insights into the anatomy and biology of *Stenopterygius*, such as the presence of blubber (suggesting homoeothermy) and pigmentation (revealing countershading for camouflage).

Ultimately, the integration of empirical evidence from the fossil record, coupled with cutting-edge analyses of soft-tissue structures, has culminated in a state-of-the-art, life-sized sculptural reconstruction (Eriksson *et al.*, 2022). Replicas like these serve multifaceted purposes, functioning as invaluable tools for research, education and public outreach, providing both scientists and the general public with opportunities to engage closely with these fascinating, but now long-extinct creatures.

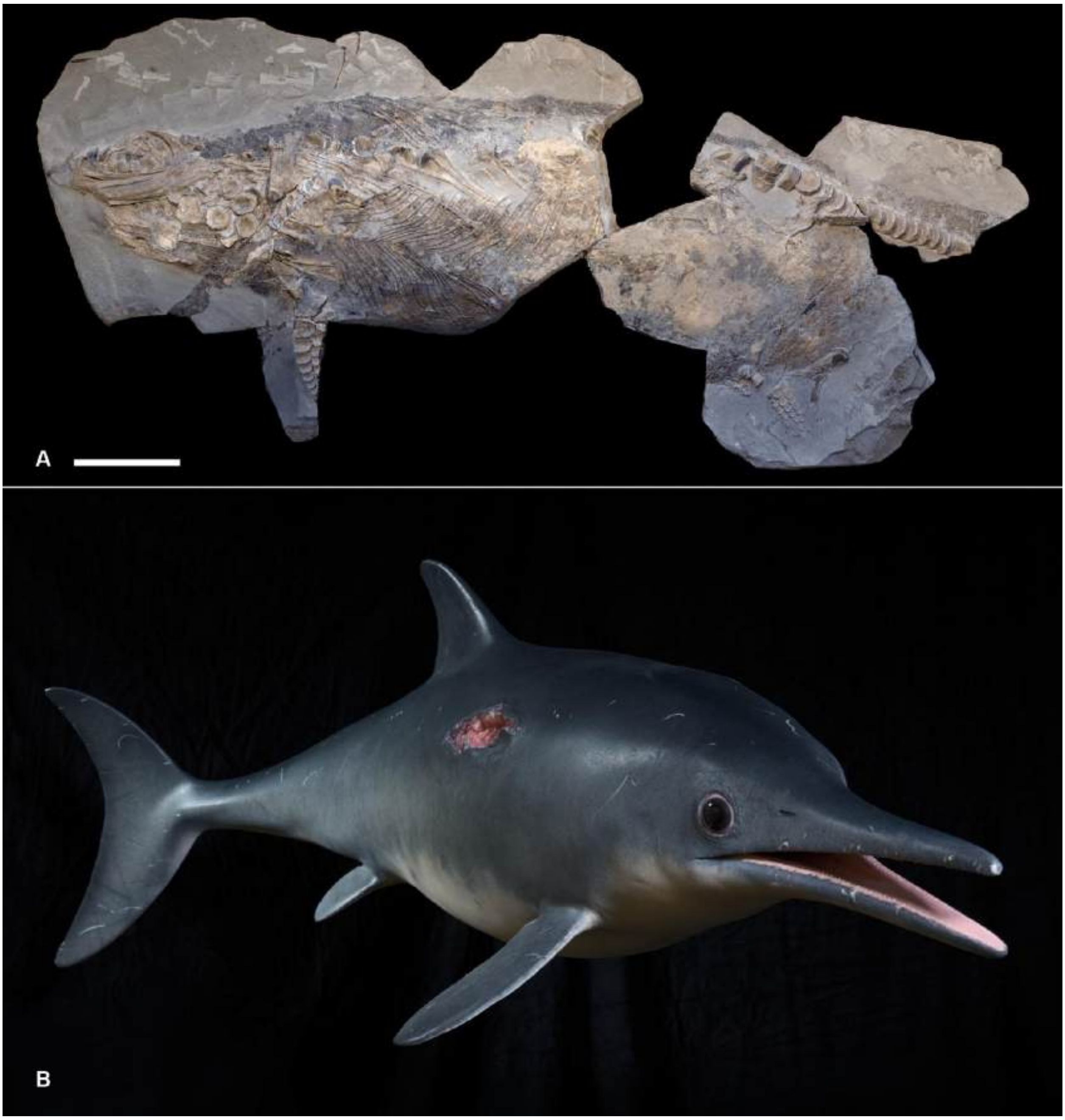

Figure 1. **A**. Photograph of *Stenopterygius* specimen MH 432 from the Lower Jurassic of Holzmaden, southern Germany, which was subjected to a multiproxy analysis by Lindgren *et al.* (2018). Scale bar equals 50 mm. **B**. Photograph showing the resulting sculptural reconstruction of the same individual in oblique, right lateral view (Eriksson *et al.*, 2022). Note the distinctive predation wound (constructed to reveal the blubber), smaller scratches and the minute teeth visible in the lower jaw. Additionally, note the counter-shaded appearance of the animal, with a darker back and lighter belly, consistent with deductions from the fossil specimen. The sculpture measures 1.6 m in length. For this project, two identical copies of the sculpture were produced. One is permanently displayed at the Department of Geology, Lund University, Sweden, while the other resides at Urweltmuseum Hauff Bodman, Bodman-Ludwigshafen, Germany, alongside its inspiration, specimen MH 432.

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An exceptionally diverse pre-K/Pg boundary nautilid fauna from the Maastrichtian type area (the Netherlands and Belgium)

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Not much is known about how the Nautilida (Cephalopoda, Mollusca) survived the end-Cretaceous extinction. This lack of understanding stems largely from the paucity of well-preserved and well-studied nautilid faunas of late Maastrichtian and earliest Paleocene age. Here, we present a revision of the nautilid assemblages from the type-Maastrichtian, based on an exhaustive examination of a vast number of specimens from the Maastricht and Kunrade formations housed in several European natural history collections. Employing both traditional and innovative methods, including micro-CT imaging and a novel approach to septal spacing analysis, we have been able to identify six species, belonging to three genera. This represents the most speciose late Maastrichtian nautilid fauna identified to date. Simultaneously, it displays a significant disparity in shell shapes, ranging from rounded to angular and from depressed to compressed cross sections, with a fully closed to partially open umbilicus, and sutures varying from straight to sinusoidal. Additionally, there are variations in the position of the siphuncle, and in embryo and adult sizes, ranging from small to very large. However, in features of ornament, this fauna is less diverse, with a complete absence of ribbed morphologies, except for reticulate ornament seen on embryonic shells and some rib-like folding on the body chamber. Uncertainties arise regarding the distribution of two of these six species, which may not extend into the uppermost Maastrichtian, as these have so far only been identified in material from the Kunrade Formation. Moreover, the presence of one species in the study area prior to the final ~100 kyr of the Maastrichtian appears questionable because it has been identified exclusively in material from the Nekum Member (Maastricht Formation). It may be speculated that the entry of the latter species, and potentially the disappearance of the other two referred to above, may be associated with palaeoenvironmental changes, resembling minor-scale alterations observed in type-Maastrichtian ammonite faunas from the pre-K/Pg boundary interval. Finally, a single fragmentary nautilid shell from the basal Paleocene (i.e., top of Maastricht Formation, top of subunit IVf-7) is tentatively assigned to one of these six species. By the time nautilids reappear in the fossil record of the region in beds post-dating the K/Pg boundary crisis, i.e., of mid-Danian age, all six seem to have vanished from the area.

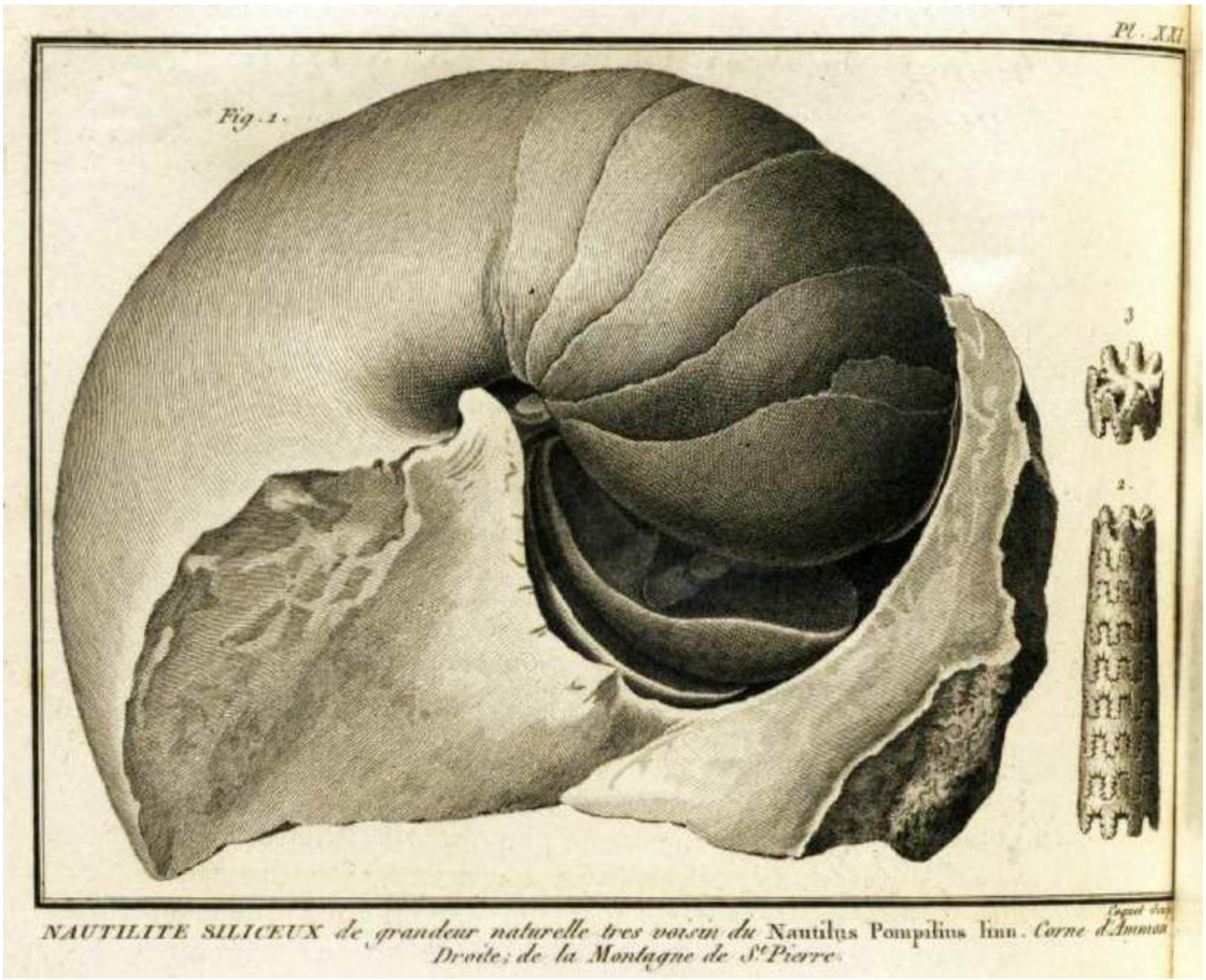

Figure 1. The oldest representation of a nautilid from the type area of the Maastrichtian Stage is depicted in a drawing by Nicolas Maréchal, published in 1801 in Faujas Saint Fond's renowned work *Histoire naturelle de la Montagne Saint-Pierre de Maëstricht* (1799-1803). This drawing was subsequently republished in 1804 in the Dutch translation of the same work, entitled *Natuurlijke historie van den St. Pietersberg bij Maastricht* (1802-1804). This particular fossil is described as a 'Nautilite siliceux très voisine de *Nautilus Pompilius* Linn.' or 'Kei-achtige Nautiliet veel gelijkende naar den *Nautilus Pompilius* van Linn.'; it is a nautilid shell of considerable size preserved in a flint nodule. Most likely, this specimen originated from the Nekum Member (Maastricht Formation) of the Sint-Pietersberg area, south of Maastricht. The drawing also highlights a notable characteristic of specimens from this interval: not all chambers were filled with sediment, and in them, the silicified siphuncle is often found displaced, lying at the bottom of the chamber.

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The De Heer Collection of dissociated mosasaur vertebrae and carapace peripherals of cheloniid turtles

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The key objective of this study has been to attempt identifications of disarticulated mosasaur vertebrae at genus and species level, determine their original position in the vertebral column and assess taphonomic processes in order to gain more insight into the Late Cretaceous environmental setting these animals inhabited. The research centred on two species of mosasaur, viz. *Mosasaurus hoffmannii* (Mosasauridae) and *Plioplatecarpus marshi* (Plioplatecarpinae; see Lingham-Soliar, 1994, 1995) both quite common in the area during the late Maastrichtian (Mulder *et al*., 1998). The Late Cretaceous epoch was characterised by extensive epicontinental seas and stable conditions with high temperatures and sea levels, fostering a diverse marine ecosystem. Mosasaurs, as endothermic creatures with high metabolic rates, thrived in this environment, particularly in the coastal seas around Maastricht, known for their rich biodiversity (Lingham-Soliar, 1995; Mulder *et al.*, 1998, 2000, 2016; Mulder, 1997, 1999, 2003; Jagt, 2005).

The present study hypothesises locomotion-related differences in vertebral morphology between mosasaur species, exploring the feasibility of identifying species based on dissociated vertebrae and characterising vertebral cross sections with comparative literature and collections. Furthermore, bioerosional taxa are identified and classified and their producers discussed, aiming to decipher 0trophic processes and scavenging behaviours within Late Cretaceous marine ecosystems. The presence of biofilm structures on bone surfaces offers further insights into taphonomic processes. Comparisons between taphonomic signatures of cheloniid turtle bones and mosasaur bones were made in order to reveal possible differences between species and yield new insights into predatory relationships.

The present study focused on an extensive collection of disarticulated mosasaur vertebrae from the former Nekami ('t Rooth) quarry near Bemelen, southern Limburg, the Netherlands, complemented by analyses of cheloniid turtle bones. This dual approach aims to discern potential differences in taphonomic influences on bone preservation amongst different vertebrate species in the same environment.

A total of 121 mosasaur vertebrae, housed at the Natuurhistorisch Museum Maastricht (NHMM) and Maastricht University (UM), were examined. Additionally, a smaller assortment of 81 cheloniid turtle carapace bones and other skeletal elements in the same collection (L. de Heer Collection) were assessed. Stratigraphically, the material is presumed to have originated from the upper levels of the Maastricht Formation, i.e., Emael and Nekum members, and possibly the overlying Meerssen Member. Morphological studies were conducted in order to categorise vertebral cross sections and identify species, drawing upon available items of literature. Each part of the vertebral column for each species was extensively described and photographed for documentation. Outer surface and taphonomy analyses involved examining marks under a stereomicroscope and classifying them into different ichnotaxa so as to identify fouling organisms.

Bioerosional traces include *Radulichnus transversus* and *Linichnus serratus* (compare Jagt *et al*., 2020). Decortication patterns hint at scavenging by large aquatic carnivores, shaping the fate of the vertebral remains. The formation of biofilms underscores the intricate interplay between decortication and subsequent fouling by cheilostome bryozoans, adding levels to the taphonomic history.

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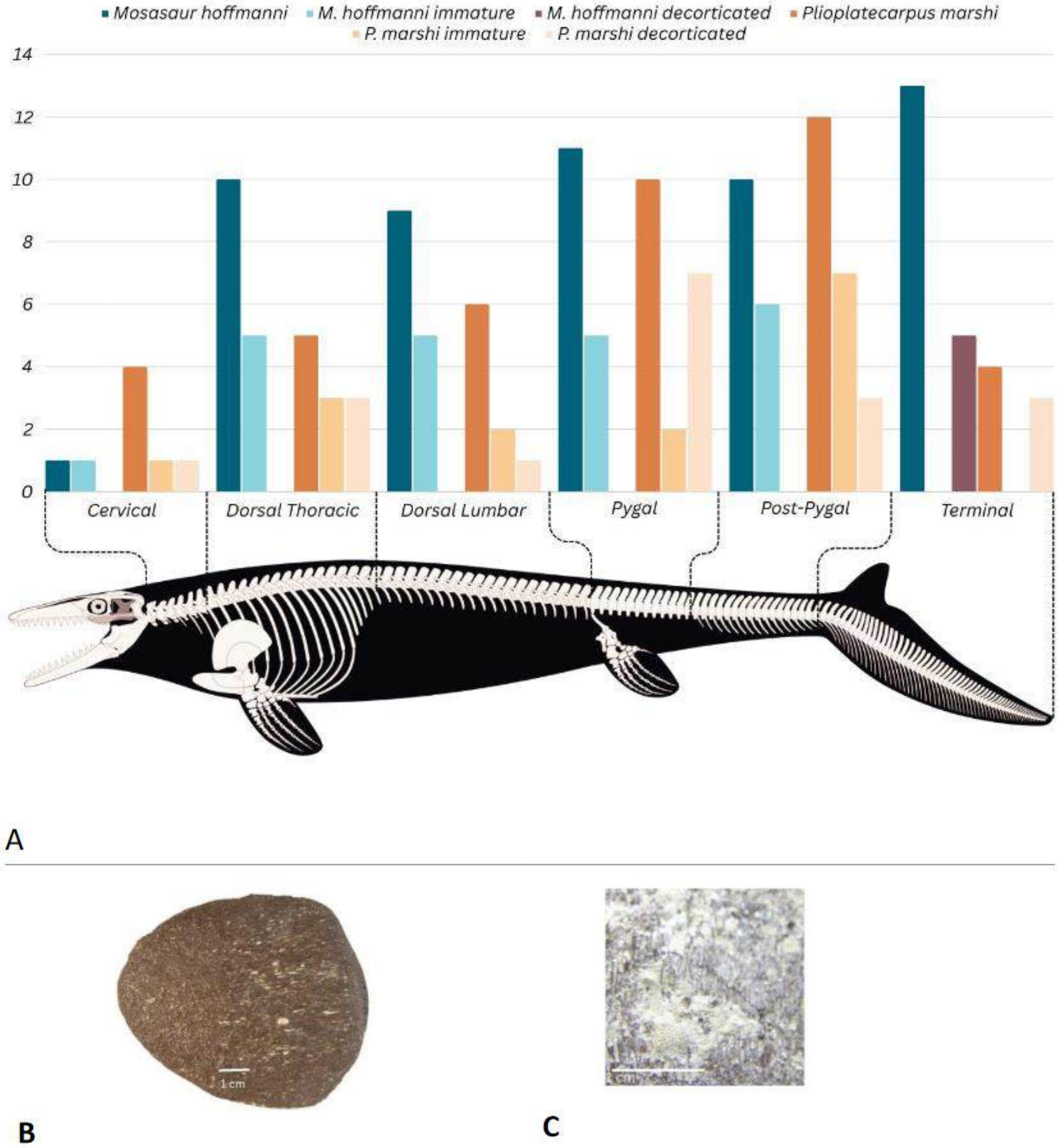

Fig. 3. (A) Each identified vertebrae per species along the vertebral column., and then classified in juvenile and decortication. (B) Specimen UM.K.857.20.01, completely decorticated vertebrae and (C) Specimen NHMM.K.897.20.01, decorticated vertebrae with a *Cheilostome bryozoan* colony present.

2D and 3D dental microwear analysis informs us about the feeding ecology of type-Maastrichtian mosasaurs

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The telltale microscopic traces left behind on tooth enamel as a result of tooth-tooth occlusion and tooth-food interaction are helpful in assessing diet and oral processing in extant and extinct vertebrates. First used in human archaeology (Teaford & Oyen, 1989) and more generally in mammal palaeobiology (e.g., Loffredo & DeSantis, 2014), this technique has now become an established tool in studying reptile palaeobiology as well (e.g., Fiorillo, 1998).

Here we present results of investigations into the diet of mosasaurs that we have performed over the past decade (Holwerda *et al*., 2013, 2023). More specifically, we shall focus on the added insights gained from the application of microwear analysis to a selection of type-Maastrichtian mosasaur teeth and tooth crowns. Two different microwear methods, each with their own specific advantages, are currently employed. We have applied both 2D and 3D microwear analysis (DeSantis *et al*., 2013) on mosasaur taxa from the Maastrichtian type area (Schulp, 2006).

Currently, five mosasaur taxa are recognised from this area (Vellekoop *et al*., 2022), ranging from the diminutive and presumably durophagous mosasaur *Carinodens belgicus* (Woodward) (= *Carinodens fraasi*), via the medium-sized *Plioplatecarpus marshi* and *Prognathodon sectorius*, to the large *Mosasaurus hoffmanni* and *Prognathodon saturator* (Schulp *et al*., 2013, and references therein). Based on previous investigations into tooth morphology (e.g., Massare, 1987), stable isotope analysis (Schulp *et al*., 2013), actuo-palaeontological experiments (Schulp, 2005) and extrapolation from stomach contents recorded from sites elsewhere (Konishi *et al*., 2011), we may hypothesise about the feeding specialisations of these five mosasaur taxa. With exploration of dental microwear we now add an additional avenue of investigation towards testing these hypotheses.

The analysis of 2D microwear has a major advantage in that it requires only regular Scanning Electron Microscopy (SEM) imaging, meaning that data can be acquired with relatively little effort and at reasonable cost. Moreover, it is a ‘staple’ instrument in most research institutions (Holwerda *et al*., 2013). A disadvantage is that the interpretation of the images is affected by a degree of inter-observer bias, and the reproducibility of the observations is considered limited at best. The alternative, 3D microwear analysis, or Dental Microwear Texture Analysis (DMTA), involves a high-resolution 3D scan of the surface, followed by a surface roughness analysis along the parameters as set out in the ISO 25178 norm, resulting in a quantitative (and as such potentially less ambiguous) description of the surface roughness parameters. The application of 3D surface analysis requires casts of the tooth surface to be made, and access to more specialised analytical equipment, leaving the method less accessible and more expensive at that (DeSantis *et al*., 2013; Holwerda *et al*., 2023).

Fuelled by a methodological interest, we have performed both 2D and 3D microwear on teeth of all five mosasaur taxa reported from the type Maastrichtian. Some of the 2D analyses were performed in quadruplo by four different observers so as to assess inter-observer bias (e.g., Mihlbachler *et al*., 2012). Interestingly, despite these different approaches, the general picture emerging from both the 2D and 3D microwear analyses was mostly in agreement between the two methods, the inter-observer bias in the 2D analyses was recognised as expected but the overall interpretations did not diverge too widely, and the microwear patterns recognised in both the 2D and 3D analyses did *grosso modo* correspond to the presumed diets suggested by earlier research.

In all our samples, *Carinodens* showed considerable wear, which agrees with the presumed durophagous diet (Dollo, 1913). The DMTA analysis did, however, add a layer of piscivory in the interpretation (Holwerda *et al*., 2023), when compared to extant archosaur feeding guilds. Perhaps the most surprising outcome was the microwear observed in the sample of *Plioplatecarpus marshi*. Based on tooth morphology along the ternary ecospace outlined by Massare (1987), a piscivorous diet seemed likely; the microwear we have encountered in our sample, both at two-dimensional and three-dimensional level, indicates intensive damage, pointing at a high proportion of much harder food in their diet. The DMTA results even point to ‘harder invertebrate’ feeding, but did also find piscivory likely. It is yet unclear what exactly was on this species’ menu, and what this harder invertebrate prey might have encompassed. *Prognathodon sectorius* was found to have no microwear indicative of rough usage, which the DMTA confirmed. It seems this smaller mosasaur mostly preyed on ‘softer’ animals such as fish and squid. *Mosasaurus*, with 2D microwear pointing at a diet of both softer and harder prey, was found by the DMTA to fit into many feeding guilds, confirming the hypothesis that this mosasaur was a successful generalist.

The only noticeable difference between 2D and 3D microwear was seen in *Prognathodon saturator*. According to 2D analysis, this mosasaur fed on harder prey items, which agrees with its robust cranial build and strong conical teeth. However, DMTA found this mosasaur to have preyed on softer invertebrates. While the type Maastrichtian shallow subtropical sea undoubtedly provided a plethora of such prey items, *Prognathodon* from, for instance, Canada is found with turtle remains as stomach content (Konishi *et al*., 2011), indicating feeding on large vertebrates.

Our recommendation for future uses is to perform exploratory microwear analysis using the less cost-intensive two-dimensional method, and should there be promising results, to perform an in-depth analysis using DMTA. These two methods combined on the type Maastrichtian ecosystem at higher trophic levels has revealed a clear niche differentiation between the smaller mosasaurs and the larger ones, and to some extent between each size category as well.

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Palynology of the Eys borehole: a stratigraphical and palaeoenvironmental perspective on the Cretaceous succession of the Ubachsberg Plateau, South Limburg, the Netherlands

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In 2018 TNO-Geological Survey of the Netherlands drilled a fully cored borehole near the village of Eys on the Ubachsberg Plateau. This borehole is located to the east of the classic type-Maastrichtian section of the former ENCI quarry and its surroundings. The objectives of this borehole were twofold; firstly, it targeted an area for which borehole or outcrop data were lacking, and secondly, at this location a unique cored record of the older siliciclast-dominated Aachen and Vaals formations could be obtained. The 182-m deep borehole terminated in the Aachen Formation and recovered about 171 m of overlying Cretaceous strata. It also demonstrated a conspicuous lithological transition from a sandstone (Vaals Formation) to a limestone predominance (Gulpen or Maastricht formations).

In order to obtain chronostratigraphical control on and an understanding of the environmental evolution of the Cretaceous succession in this “eastern” part of South Limburg, a quantitative analysis of 41 core samples was carried out. Encouragingly, both palynomorph preservation and richness turned out excellent for all of the Cretaceous succession, thereby providing a new regional standard from a palynological point of view.

The continental basal part of the borehole (provisionally assigned to the Aachen Formation, Hergenrath Member) is, as expected, dominated by terrestrial palynomorphs, notably pollen of the *Trudopollis-Normapollis* complex. In addition, abundant reworked early Namurian (Carboniferous) spores were encountered. Successively, marine organic-walled dinoflagellate cysts become dominant upsection. This allows for the identification of 30 palynostratigraphical events facilitating correlations to regional standards and zonations (e.g., Schiøler & Wilson, 1993; Slimani, 2001; Pearce *et al*., 2020 and Vellekoop *et al*., 2022). In summary, we infer a late Santonian age for the first marine incursion within the Aachen Formation, and an early Campanian age for the siliciclastic marine sandstones provisionally assigned to the Vaals Formation. The sharp contact with the overlying argillaceous limestone facies is accompanied by a major hiatus that extends into the middle part of the upper Maastrichtian. Biostratigraphically, these strata thus correspond to the Valkenburg Member of the Maastricht Formation as encountered at the former ENCI quarry, suggesting that Gulpen-equivalent strata are absent at Eys. The absence of the marker species *Palynodinium grallator* in the uppermost sample indicates that the uppermost Maastrichtian is not present in the Eys borehole.

In terms of organic-walled assemblage structure a clear subdivision can be made between the siliciclast-dominated lower Campanian and the overlying upper Maastrichtian limestone- dominated succession. The former is dominated by proximal marine, largely eutrophic components, whereas the latter is extremely diverse, cyclic and dominated by open-marine taxa. Nevertheless, (perhaps seasonal) fresh-water influence as displayed by incursions of the acritarch *Paralecaniella indentata* is manifest throughout. The quantitative organic-walled dinoflagellate cyst distribution patterns complement those for the ENCI quarry (Schiøler *et al*., 1997). This core is currently studied in much greater detail with regard to sedimentology and lithofacies (see contributions of Geert-Jan Vis and Mateus Kroth). Combined, this palynological data set will support a better understanding of the regional facies-, age- and/or tectonostratigraphical relationships in the Cretaceous in the greater South Limburg area.

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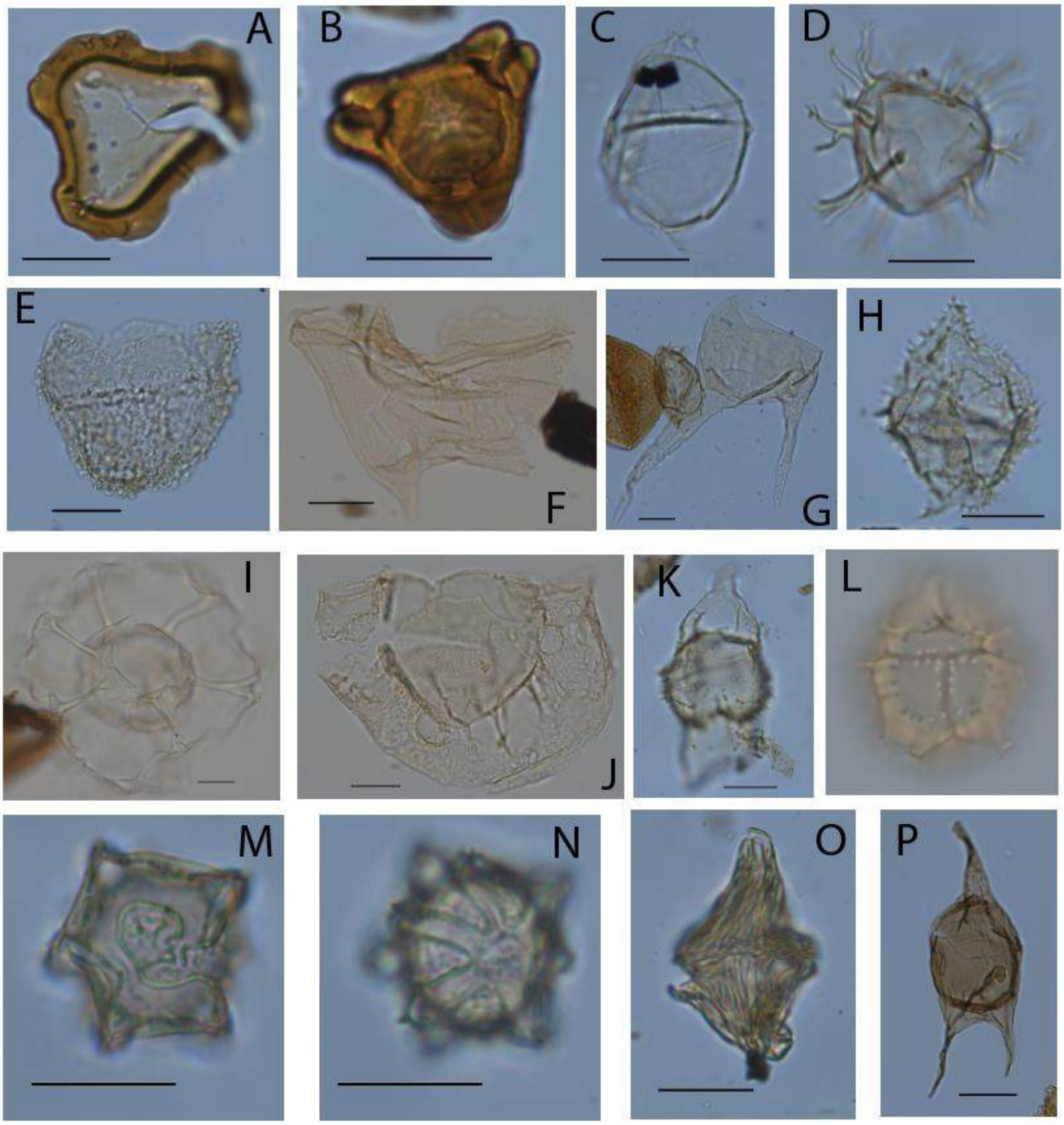

Figure 1. Selection of palynomorphs from the Eys borehole (C-P: organic-walled dinoflagellate cysts). Scale basr equal 20 µm). **A.** *Tripartites vetustu*s (Namurian spore); **B.** *Nudopollis apertus* (Santonian pollen grain); **C.** *Palaeohystrichophora* cf. *infusoroides*; **D**. *Surculosphaeridium longifurcatum*; **E.** *Senoniasphaera reticulate*; **F.** *Palaeoperidinium pyrophorum*; **G.** *Odontochitina costata*; **H.** *Spinidinium echinoideum*; **I.** *Adnatosphaeridium buccinum*; **J.** *Glaphyrocysta perforata*; **K.** *Chatangiella manumii*; **L.** *Cladopyxidium septocrispum*; **M, N.** *Microdinium bensonii*; **O.** *Dinogymnium* sp.; **P.** *Cerodinium diebelii.*

Astronomical pacing of flint bands in the Maastrichtian chalk sea of north-western Europe

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The type area of the Maastrichtian Stage features prominent Upper Cretaceous chalk successions, often containing rhythmically paced nodules and/or bands consisting of flint – a cryptocrystalline α-quartz-dominated sedimentary rock (W.M. Felder & Bosch, 1998, 2000; Zijlstra, 1987, 1994). The Campanian-Maastrichtian European Basin Si cycle was enriched in dissolved Si, originating from both Boreal and Tethyan realms (Engelke *et al.*, 2017; Ashckenazi-Polivoda *et al.*, 2018; Jurkowska & Świerczewska-Gładysz, 2020). Rapid diagenetic changes in the Cretaceous carbonate mud effectively removed biogenic Si from the water column. The decisive factor in flint nodule formation is believed to be the dissolution of calcium carbonate in the sulphate-reduction zone, providing alkalinity and accommodation space for silica precipitation (Jurkowska & Świerczewska-Gładysz, 2020). The presence of clays, however, can slow down the crystallisation of silica polymorphs by competing with opal-CT formation for alkalinity (Kastner *et al.*, 1977). Finally, fixation of the redox boundary of the sulphate-reduction zone during periods of reduced sedimentation rates has been considered a driving mechanism behind the periodic distribution of flint nodules and bands in chalk (Zijlstra, 1987, 1994; Madsen & Stemmerik, 2010; Jurkowska & Świerczewska-Gładysz, 2020). Even though the deposition of chalk in the shallow epicontinental seas of the European basins under greenhouse conditions is well understood, the possible astronomical influence on the often rhythmically distributed flint remains poorly documented (Zijlstra, 1987, 1994; Madsen & Stemmerik, 2010; Lindgreen *et al.*, 2011).

Earlier studies focusing on type-Maastrichtian sequences have suggested that the flint band distribution and variations in bioclast composition reflected astronomical forcing patterns akin to precession and eccentricity (Zijlstra, 1987, 1994; P.J. Felder, 1997; P.J. Felder *et al.*, 2003; Keutgen, 2018). In the present study, chalk and flints of the lower Maastrichtian part of the Gulpen Formation in the Hallembaye section (north-east Belgium) were sampled and analysed using micro-X-Ray Fluorescence (µXRF) spectroscopy. In addition, a semi-quantitative lithological assessment of flint distribution was carried out by assigning a flint score (FS) proxy. Both FS and chalk Ti/Al – a diagenesis-resistant proxy for changes in the composition or provenance of terrigenous material (i.e., clays) – were subjected to a cyclostratigraphical analysis (Westphal *et al.*, 2010). This section was chosen specifically for its gradual upward evolution of flint expression, gradually evolving from none to randomly dispersed flint nodules towards well-expressed, regular thick flint bands.

Building on the robust bio-chemostratigraphical framework for this section (Vellekoop *et al.*, 2022), two complementary astrochronologies have been developed for the Vijlen, Lixhe 1 and Lixhe 2 members – ranging from the Froidmont Horizon to the Boirs Horizon. A high-resolution floating astrochronology has been constructed based on the dominant obliquity-imprint recognised in the chalk Ti/Al. Flint nodules and bands are spaced at Milankovitch time scales. A mixed imprint of obliquity (Vijlen and Lixhe 1 members) and precession-eccentricity (Lixhe 2 Member) has been recognised in the FS. A second astrochronology based on the FS proxy has been constructed in absolute time, utilising the 173-kyr inclination and 405-kyr eccentricity metronomes as a tuning target (Laskar, 2020). Both astrochronologies have been combined by anchoring the high-resolution Ti/Al floating astrochronology to the Boirs Horizon, dated at 68.63 Ma by the FS astrochronology. The updated anchored astrochronology calibrates the investigated interval at Hallembaye from 68.63 ± 0.04 Ma to 70.36 ± 0.04 Ma. An anti-phased relationship between Ti/Al and FS has been revealed, implying that flint development occurred during periods of decreased seasonal contrast (i.e., small variations in obliquity/inclination). In addition, geochemical analyses indicate an upward decrease of clay input and increase in degree of flint silicification, corroborating that clays indeed hamper silica polymorph crystallisation (Kastner *et al.*, 1977; Jurkowska & Świerczewska-Gładysz, 2020). To conclude, temporal variations in the hydrological cycle and consequent changes in aeolian and fluvial input into the European Basin appear astronomically controlled. Astronomical forcing governed favourable conditions towards diagenetic flint formation by controlling palaeoenvironmental conditions and the Si cycle.

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More latest Cretaceous echinoderm ‘odds and ends’ from the Maastrichtian type area

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Upper Cretaceous (lower Campanian to uppermost Maastrichtian) siliciclastic and carbonate strata in the extended type area of the Maastrichtian Stage (south-east Netherlands, north-east Belgium) are renowned for their diverse and well-preserved echinoderm faunas. During recent decades, numerous novel records and new taxa have been published, mostly amongst ophiuroids, asteroids and crinoids. It would appear that the end is not sight yet – still new forms are being recorded and stratigraphical ranges updated. With taxonomic assessments now worked out in detail for most groups, other aspects of these faunas may be considered, such as their palaeoecology, palaeobiology and ichnology (compare Belaústegui *et al*., 2017; Jagt *et al*., 2018). Here we record and briefly discuss three notable recent finds; all involve well-known species, but novel features can now be documented.

Ophiuroid family planners?

In the upper Maastricht Formation (Emael, Nekum and Meerssen members), three species of brittlestar are locally common. One of these is *Felderophiura vanderhami* Jagt, 1991, of which dozens of articulated discs and arms are currently known, even from historical collections (Jagt, 1991, 2000a; Jagt & Neumann, 2010), as well as many thousands of dissociated disc and arm ossicles. The present example (Fig. 1) is of note in comprising two individuals of *F. vanderhami*, one in dorsal, the other in ventral aspect, with at least two arms (the others only partially preserved, or missing altogether) of either individual draped over each other in such a way as to suggest that this is not merely an accidental association. In most ophiuroid taxa, the sexes are separate, although a certain number are hermaphroditic or protandric. The disc holds the gonads and these open between the arms and into pouches – the genital bursae. Normally, fertilisation occurs externally, with gametes shed into the water through bursal sacs, but brooding of developing larvae in bursae is known from numerous species (Hyman, 1955). Could the present example be an instance of ‘family planning’ and is this a snapshot of two brittle stars ‘*in flagrante delicto*’?

Figure 1. Two individuals of *Felderophiura vanderhami* Jagt, 1991, possibly preserved '*in flagrante delicto*' (A. Savelkoul Collection); Emael Member, Maastricht Formation, 't Rooth quarry (Bemelen). Associated are oysters ('*Acutostrea' uncinella* group) and a brachiopod; the latter appears to be close to, if not conspecific with *Almerarhynchia kunradensis* Simon, 2003, from the Kunrade Formation (upper Maastrichtian) in the Heerlen-Benzenrade area (Simon, 2003).

Nerve canals preserved

Amongst stalked crinoids in the upper Maastrichtian of Liège-Limburg, the 'bourgueticrinid' (*sensu* Hess, 2011), *Dunnicrinus aequalis* (d'Orbigny), with five arms and no further divisions, is the commonest species. At certain levels, even complete 'meadows' have been found preserved in obrution deposits (Jagt *et al*., 1998, 2018). In nodular and platy flint of the uppermost Gulpen Formation (Lanaye Member), all echinoderm calcite has been dissolved, leaving three-dimensionally preserved details of internal cup details, including nerve canals of these crinoids (Fig. 2A-D). A direct comparison with diagrams of nerve canals for the genera *Bourgueticrinus*, *Bathycrinus* and *Rhizocrinus* supplied by Wienberg Rasmussen (1978, fig. 565) may help in elucidating the taxonomic position of *Dunnicrinus*.

Large, larger, largest …

The true giant amongst regular echinoids from the upper Maastricht Formation is a species described by Schlüter (1892, p. 214, pl. 21, fig. 6) as *Cidaris gigas*, on the basis of two articulated interambulacral plates in the collections of the Museum für Naturkunde (Berlin, possibly from the Binkhorst van den Binkhorst Collection). No ambulacral columns are preserved in the type specimen, but current assignment to the subgenus *Temnocidaris* (*Stereocidaris*) is based on an adapical IA plate with ambulacral plates illustrated by Jagt (2000b, pl. 3, fig. 1). On account of large scrobicular circles, wide extrascrobicular zones, with a dense, uniform cover of granules and conspicuous neural grooves, the present test fragment (Fig. 2E; NHMM JJ 13473), is considered conspecific with Schlüter's type material. A comparison with complete cidaroid tests of Late Jurassic (Kimmeridgian) age, illustrated in Hess (1975, pl. 29, figs 1, 2; pl. 30, fig. 1), suggests that NHMM JJ 13473 had reached a test diameter of at least 130 mm. None of the Late Cretaceous cidaroids from the United Kingdom and northern Germany, figured by Smith & Wright (1989) and Salah (1982), respectively, come close.

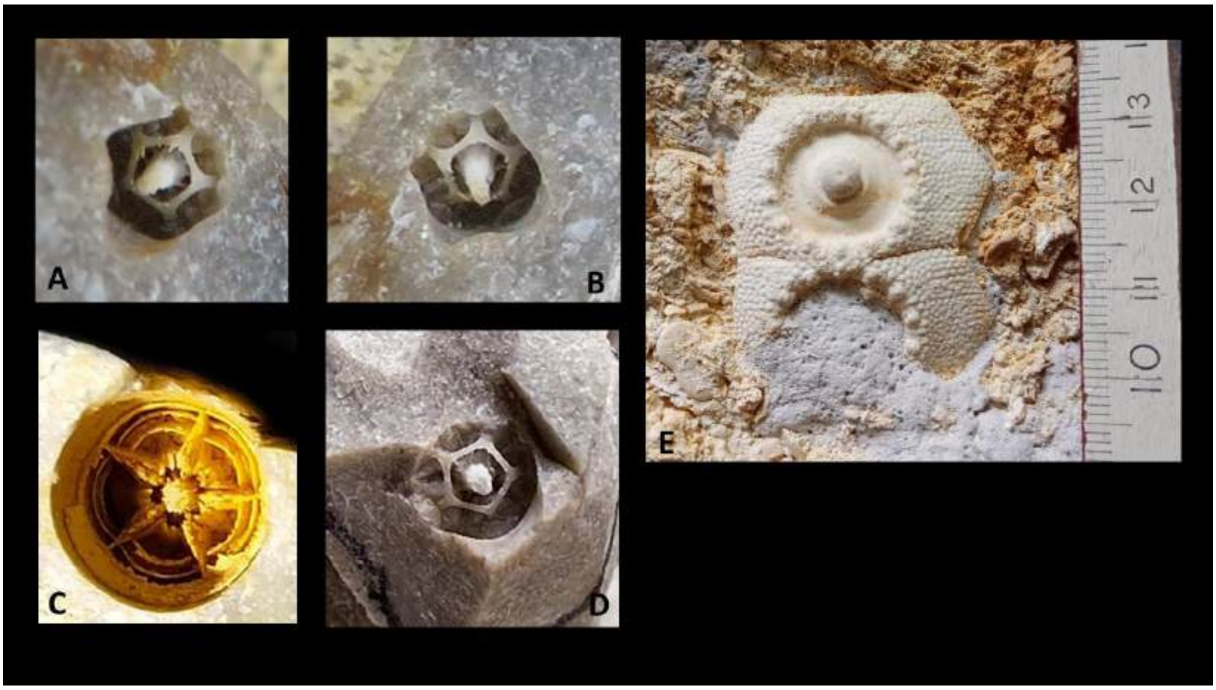

Figure 2. A-D. Flint-filled nerve canals and reflection of growth phases in aboral cups of *Dunnicrinus aequalis* (d'Orbigny), all around 2-3 mm in diameter; Lanaye Member, Kreco quarry (Haccourt, Belgium; Deckers and Laffineur collections). **E.** Two articulated ambital interambulacral plates of *Temnocidaris* (*Stereocidaris*) *gigas* (Schlüter, 1892), the largest cidaroid test plates known to date from the Maastrichtian type area, suggesting an estimated test diameter of at least 130 mm.

Acknowledgements. We thank the managements of Kreco, the former ENCI-HeidelbergCement Group and Ankerpoort-'t Rooth quarries for permission to collect over recent years.

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The core of Oploo-DB 16: preliminary notes on macrofossil-based proxy correlations with the Maastrichtian type area, around 120 km further south

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Located to the south-west of Boxmeer in the province of Noord-Brabant (the Netherlands) is 'Diepboring' (DB) 16 at Oploo, sunk between December 1911 and March 1913, by the Rijksopsporing voor Delfstoffen (State Exploration for Mineral Resources). Portions of the core are contained in the borehole archives of TNO - Geological Survey of the Netherlands (Utrecht/Zeist). At various levels these core pieces yield a range of macrofossil taxa (mostly molluscs, but also brachiopods), as well as ichnofossils (bioturbation) that allow proxy correlations with strata in the extended type area of the Maastrichtian Stage, around 120 m further to the south.

Although work on these cores has just started, we here present some preliminary data. The Santonian-Campanian part of the sequence penetrated yielded the ichnotaxon *Gyrolithes davreuxi* de Saporta (see Bromley & Frey, 1974) at depths of 787 and 790 m (Fig. 1A). This ichnotaxon is well known from discrete levels within the 'smectite facies' of the Vaals Formation in the Haccourt area (Liège, north-east Belgium), of early Campanian age (*lingua/quadrata* Zone, sensu germanico). In the lower part, referred to as 'Emscher' on associated labels, numerous inoceramid bivalves occur, mostly Sphenoceramus of the *cardissoides* group (Fig. 1B); a single specimen of the ammonite *Hauericeras pseudogardeni* (Fig. 1D) at a depth of 998 m corroborates the middle to late Santonian age (compare Jagt *et al*., 1995; Kennedy & Christensen, 1997; Kennedy & Kaplan, 2000).

Of note is also the mud shrimp *Mesostylus faujasi* (Fig. 1C) at a depth of 597.20-600.70 m, which in the Liège-Limburg/Campine area ranges from the 'middle' Santonian to the uppermost Maastrichtian, and is more of a facies indicator (Mourik et al., 2006; Karasawa, 2003; Goolaerts & Mottequin, 2023).

For now, the most interesting observation concerns the Maastrichtian portion of the succession. This has an amazing 'brachiopod coquina bed' (Fig. 2B), apparently monospecific, with little else associated (e.g., a single anomiid bivalve), between depths of 520 and 546 m. Although we have not yet cut any specimens to reveal the internal features of the brachidium and hinge teeth, these specimens appear closely related to, if not conspecific with, the cyclothyridid *Almerarhynchia kunradensis* Simon, 2003 (Fig. 2A), which is extremely common at some levels within the Kunrade limestone facies in the Kunrade-Benzenrade area, close to Heerlen. The Natuurhistorisch Museum Maastricht collections contain hundreds of well-preserved specimens of this species (H. Senden Collection);

unfortunately, during recovery of this material no notes were taken of spatial distribution of these brachiopods, but sheer numbers available suggest some coquina-like concentrations.

The Kunrade limestone (see recent review of Kroth *et al*., 2024) crops out in the Heerlen-Kunrade-Benzenrade area, in the eastern part of South Limburg (W.M. Felder, 1977, 1978; W.M. Felder & Bosch, 2000). P.J. Felder & Bless (1989) correlated that unit, as developed in its type area, with the Lanaye Member (Gulpen Formation) up to including the base of the Emael Member (Maastricht Formation) in the Maastricht-Eben Emael area. There is a possibility, on ammonite and inoceramid evidence (*Pachydiscus gollevillensis*, *Hoploscaphites pungens* and *Spyridoceramus tegulatus*, in particular), that even equivalents of the basal Nekum Member (Jagt & Jagt-Yazykova, 2018; Jagt *et al*., 2018) are represented.

Figure 1. Representative taxa of correlative value from the Oploo-DB 16 well: **A**. *Gyrolites davreuxi* (depth 790 m). **B.** *Sphenoceramus* sp. (depth 1,102 m). **C.** *Mesostylus faujasi* (depth 597.20-600.70 m). **D**. *Hauericeras pseudogardeni* (depth 998 m).

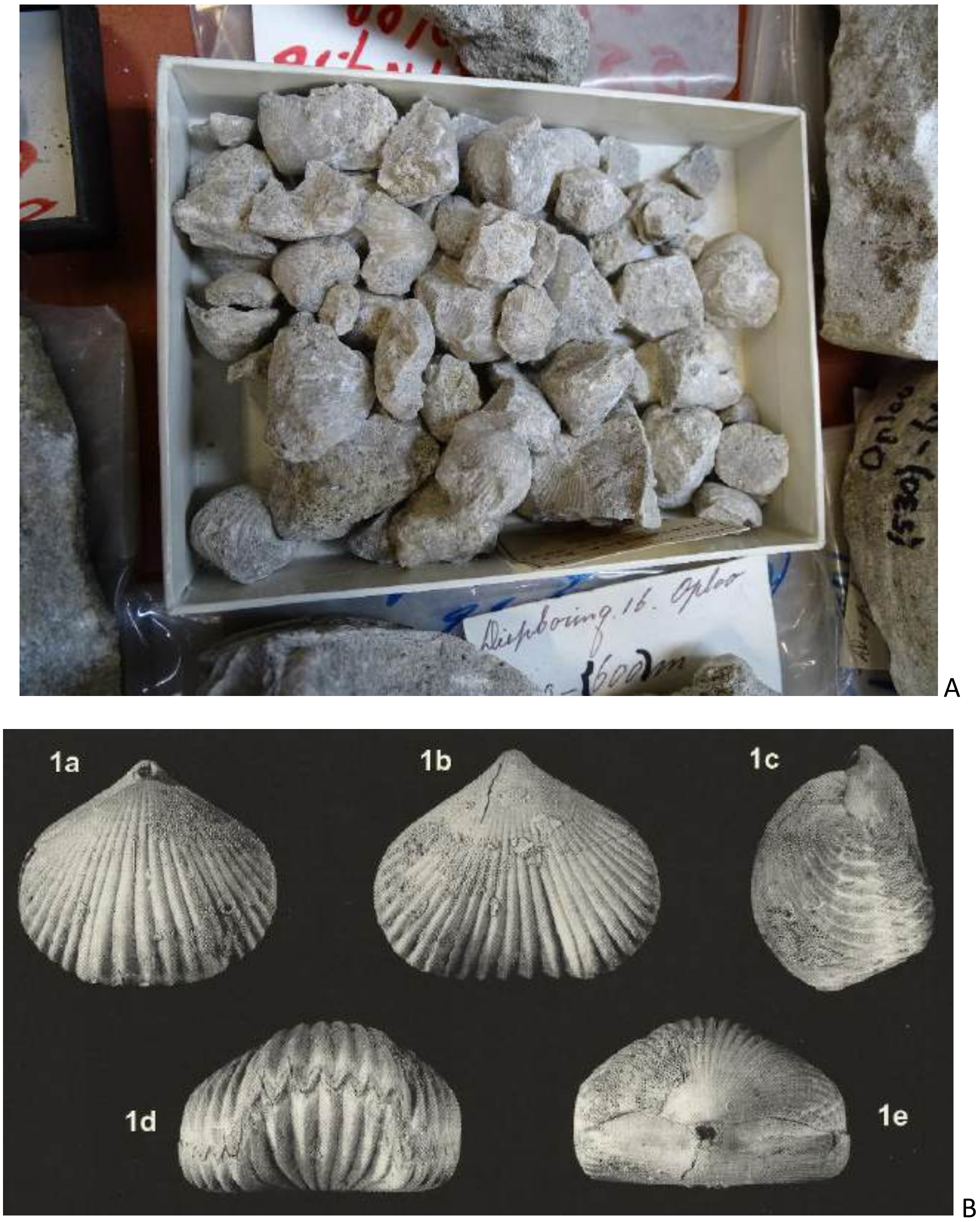

Figure 2. A. Brachiopod coquina interval in the Oploo DB 16 core, depth 520-546 m. **B**. Type specimen of the cyclothyridid *Almerarhynchia kunradensis* Simon, 2003, from the Kunrade 'limestone facies' in the Kunrade area (around 25 mm in greatest width). For details, see Simon (2003).

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The Friedrich Vogel Collection (Naturalis, Leiden) of latest Cretaceous and early Paleocene bivalves reassessed – preliminary observations

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It is widely known that bivalve taxa are ubiquitous in Upper Cretaceous (lower Campanian to uppermost Maastrichtian) siliciclastics and carbonates across the extended type area of the Maastrichtian Stage (south-east Netherlands, north-east Belgium). Both shell and internal/external mould preservation have been recorded. To date, only calcitic pteriomorphs have received ample attention; other groups, with originally aragonitic shells, are much less well known. In recent years, cursory examinations of the latter have already shown that there is a lot of potential for taxonomic assessment, palaeoecological characterisation and considerations of biostratigraphical usefulness (Jagt & Jagt-Yazykova, 2018; Jagt, 2020).

Although bivalves featured prominently in curiosity cabinets in the city of Maastricht ever since the latter part of the eighteenth century (see van Regteren Altena, 1956), the first monographic treatment of the type-Maastrichtian fauna was that by Vogel (1895a; see also Vogel, 1895b). He described existing collections, amassed by Staring's correspondents in Limburg (van de Geyn, 1945), at the 'Rijksmuseum van Geologie en Mineralogie te Leiden' (RGM) (now Naturalis Biodiversity Center, Leiden; Leloux, 2002), providing reliable illustrations (Fig. 1), but apparently did not collect himself. Vogel (1895a) recognised various 'new' species, including the following (in alphabetical order and in original nomenclature):

Anatina millepunctata

Arca geulemensis

Avicula geulemensis [= *Tenuipteria argentea* (Conrad)] (see Dhondt, 1979 ; Jagt & Jagt-Yazykova, 2018)

Cardium lundgreni nov. nom.

Cardium subalternatum

Cucullaea spec. nov. [= *Cucullaea montensis* Vincent]

Dosinia mastrichtiensis [*sic*]

Limopsis kunraediensis

Pectunculus irnichensis

Tellina geulemensis [= *Tellinella geulemensis*]

Trigonia geulemensis [= *Oistotrigonia maestrichtiana* (Briart)] (see Briart, 1888; Jagt *et al*., 2022)

From his data (see also Vogel, 1895b), it has now become apparent that at least some of the material, from 'Kaberg' (Caberg, a north-westerly district of Maastricht) in particular, is not of late Maastrichtian, but of earliest Paleocene age, being correlative with (a portion of) the Geulhem Member (Houthem Formation) of the Geulhem area (see Jagt *et al*., 2013). The matrix is a finer-grained, fairly hard and glauconitic biocalcarenite.

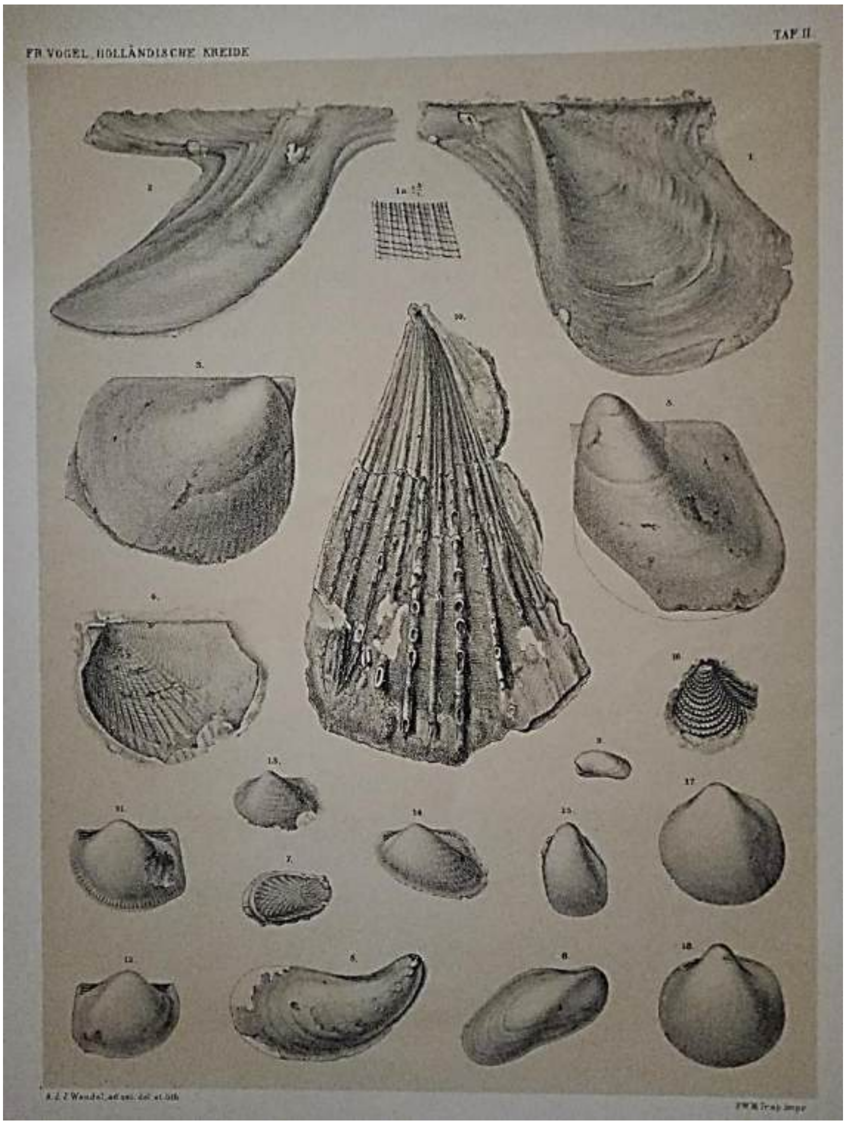

Figure 1. Plate II of Vogel (1895a), with late Maastrichtian and early Paleocene (early and middle Danian) species of bivalve. *Cucullaea* n. sp. (= C. *montensis*) (figs 11, 12) and *Cardium lundgreni* (figs 17, 18), both from Maastricht-Caberg, are definitely of early Paleocene age; sibling taxa occur in the underlying Nekum and Meerssen members of the Maastricht Formation.

Figure 2. Photographs of original material (Vogel, 1895a). **A**. *Cardium subalternatum*, holotype (RGM.13574), in a flint nodule typical of the Nekum Member (Maastricht Formation). **B, C**. *Cardium lundgreni*, holotype (RGM.13575), in a greyish, fairly fine-grained and glauconitic biocalcarenite, typical of the Geulhem Member (Houthem Formation, lower Paleocene), plus plaster cast showing ornament.

We have started a revision of Vogel's (1985a) collection; this includes also an update of the stratigraphical range of the various late Maastrichtian species, based on our own observations at various localities in southern Limburg and contiguous areas during the last 25 years. It is our hope that we can also 'pinpoint' the Irnich fauna that featured in Vogel's dissertation (Vogel, 1892), and either find a match in the Maastricht or Kunrade formations, or consider this fauna to be utterly distinct. In addition, the 'Caberg' assemblage (e.g., Fig. 2B, C) needs to be compared in detail with material from various levels of the Geulhem Member, as well as with assemblages from the Meerssen Member, IVf-7, of earliest Danian age (Jagt *et al*., 2013).

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How on earth did they do it? Recovery of the first mosasaurs in the Maastrichtian type area in the latter half of the eighteenth century

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The first skeletal remains of what later became known as mosasaurs (Mosasauridae, Squamata) ever to have been documented pertained to a fragmentary skull, found in an underground gallery under Sint-Pietersberg (Mount Saint Peter), south of Maastricht, in 1764. Two years later, this appears to have been recovered by Lieutenant Jean Baptiste Drouin; in 1784 it was procured for Teylers Museum in Haarlem by Martinus van Marum, director of that museum. A few years later, in 1790, van Marum published a description of this specimen (Teylers Museum, TM 7424) and considered it to constitute a species of whale (*Pisces cetacei*).

Figure 1. The Teylers Museum specimen of *Mosasaurus hoffmanni*, as published in the late eighteeth century (left) and on current display (right).

In October 1778 (see Homburg, 2015), another, more complete specimen was found (Rompen, 1995; Bardet & Jagt, 1996; Pieters *et al*., 2011; Hovens, 2020; Jagt, 2021; Jagt *et al*., 2024); this was to become the type specimen of *Mosasaurus hoffmanni* (Fig. 2). The exact stratigraphical provenance of the holotype is known: just below the Kanne Horizon within the Nekum Member of the Maastricht Formation (P.J. Felder & Jagt, 1998), a level that was also widely exposed at various quarries in the wider vicinity of Maastricht (W.M. Felder & Bosch, 1998, 2000) and yielded other mosasaur finds, albeit no articulated material.

Figure 2. Top: Faujas Saint Fond's (1798-1803) rendition of the discovery of the second mosasaur skull at the Sint-Pietersberg underground galleries, with five workmen ('blokbrekers') involved in the transportation. **Bottom**: Modern blokbrekers at work (Wikipedia).

Quarry workmen thus played a crucial role in the recognition and recovery of both historical specimens of *Mosasaurus hoffmanni.* But how did they go about it? Having no prior knowledge of the size and nature of the skeletal remains they had encountered, it is mind boggling to see that, without leaving any trace of their large saws, they were able to lift the skulls from the subterranean galleries. This becomes even more puzzling when the width of the pillar-like blocks (Fig. 2 bottom) that were quarried, is considered.

During the past few months we have been discussing this matter with various colleagues, but no definitive reply has been forthcoming. Our current views will be briefly outlined in this talk.

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The *pungens* conundrum (Ammonoidea, Scaphitidae) – late Maastrichtian, the Netherlands*

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* *In commemoration of Herbert Summesberger (1939-2023)*

As far as abundance and spatial distribution of heteromorph ammonites from the extended Maastrichtian type area is concerned, scaphitids come second after representatives of the family Baculitidae Gill. To date, three genera and six species of scaphitid have been recorded from the Maastricht and Kunrade formations (Jagt & Jagt-Yazykova, 2019). One species, *Hoploscaphites pungens* (Binkhorst van den Binkhorst, 1862), was long held to be confined to the 'Kunrade limestone facies' as exposed in the eastern part of the Dutch province of Limburg (see e.g., de Grossouvre, 1908; Kennedy, 1987). In the meantime, it has also been recorded from various levels within the Maastricht Formation, to the west of the River Maas (Meuse) (Jagt & Kuypers, 1994; Jagt & Eysermans, 2012). Rare silicified material is known from the basal Gronsveld Member at the former ENCI-HeidelbergCement Group quarry (Maastricht), while an acme has been documented from the basal Nekum Member (above the Laumont Horizon). From this level both micro- and macroconchs have been collected; the latter are much rarer. The highest occurrence of *H. pungens* is in the top 0.5 m of the Nekum Member/basal Meerssen Member, with records from the former ENCI (Maastricht), Curfs (Geulhem) and 't Rooth (Bemelen) quarries.

When compared to micro- and macroconchs of *Hoploscaphites constrictus* (J. Sowerby), inclusive of subspecies *johnjagti* Machalski, a peculiar feature in the majority of microconchs of *H. pungens* has been noted. There is, on both sides of the shell when preservation of internal moulds allows this to be determined, a clear cylindrical swelling, or bulge, sitting in the centre of the body chamber, high on the flank and roughly with the same curvature as the venter. In width, this measures around 30 to almost 50 per cent of the width of the body chamber; there is no 'clear' beginning, nor end of the swelling; it effaces gradually. In some specimens it is clearly visible (e.g., Figs 1A, 2A-C), while in others, or on the reverse side of some (e.g., Fig. 2D), it is less conspicuous and only seen under low-angle light, if at all. Kennedy (1987) illustrated a range of topotypical microconchs from Kunrade in historical collections. His photographs clearly show comparable swellings in the body chambers of various individuals, such as:

Plate 32, figures 24, 25

Plate 34, figure 18

Plate 35, figures 6, 8, 9 and 11.

None of the handful of macroconchs of *H. pungens* available to us shows this feature. Jagt & Jagt-Yazykova (2019, p. 17) opined that this bulge might be an expression of a feature of the male anatomy, well behind the mouth parts (buccal frame, with radula and aptychi; see Kennedy *et al*., 2002; Kruta *et al*., 2011). Maybe reproductive organs were involved?

As noted above, this feature is not seen in any of the numerous microconchs of the *constrictus* group available to us, nor have we been able to find a match in other, more or less coeval populations of *Hoploscaphites* spp., of pristine preservation, in North America (Landman *et al*., 2013, 2015, 2019, 2020).

In spite of recent advances in our knowledge of scaphitid ammonites, and their buccal frames in particular, allowing us to reconstruct their mode of life in more detail (see Landman *et al*., 2012; Smith *et al*., 2021), there is still something to be learnt about these magnificent animals.

Figure 1. Microconchs of *Hoploscaphites pungens* (Binkhorst van den Binkhorst, 1862). **A**. NHMM 003529 (length 70 mm), Kunrade, Kunrade Formation (also illustrated by Kennedy, 1987, pl. 35, figs 10, 11), with clearly visible cylindrical bulge in the back of the body chamber. **B**. NHMM JJ 14691, former ENCI-HeidelbergCement Group quarry, Maastricht, Maastricht Formation, basal Nekum Member; bulge barely visible. Scale bar in centimetres and millimetres.

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Figure 2. *Hoploscaphites pungens* (Binkhorst van den Binkhorst, 1862), microconchs, internal mould and silicone rubber cast of external mould, respectively. **A, B**. NHMM RZ 02357 (length 51 mm); Maastricht Formation, basal Meerssen Member, former ‘t Rooth quarry, Bemelen. **C, D**. NHMM van Rijsselt Collection, unregistered (length 48 mm); Maastricht Formation, uppermost Nekum Member, former Curfs quarry, Geulhem. Cylindrical swelling well visible on one side (Fig. 2C), but less conspicuous on the other (Fig. 2D).

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A geochemical revisit of the expanded Cretaceous-Paleogene (K/Pg) boundary section in the Maastrichtian type area

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The most recent of the 'Big Five' mass extinctions of the Phanerozoic occurred at the Cretaceous-Paleogene (K/Pg) boundary, ~66 million years (Myr) ago. The global K/Pg boundary interval is correlated with the Chicxulub meteorite impact event on the Yucatán Peninsula in Mexico, dated at 66.043 ± 0.011 Myr ago. However, deciphering the exact timing and mechanisms of the processes that were responsible for the abrupt extinction of 75 per cent of species on Earth, including the iconic non-avian dinosaurs, remains a field that needs more detailed study. A small number of expanded K/Pg boundary sites, both within the Chicxulub impact crater and in terrestrial and marine environments at more distal locations, have recently revealed unprecedented new insights into the direct aftermath of the Chicxulub impact event (e.g., Gulick *et al.*, 2019).

More high-resolution sedimentological, geochemical and palaeontological analyses of expanded K/Pg sites around the globe might further unravel the effects of the dynamic impact-cratering processes on the short-term palaeoenvironmental and climatic changes during the earliest Paleogene. An interesting candidate for this is the type-Maastrichtian area, in the border region of north-eastern Belgium and the south-eastern part of the Netherlands, which yields a >100-m-thick sequence of shallow-marine sedimentary rocks. We have revisited and resampled the Geulhemmerberg K/Pg site, close to Geulhem, which preserves a unique series of calcarenites, shell hashes and clays in underground galleries. This site is situated near Valkenburg aan de Geul, to the east of the River Maas (Meuse) (e.g., Smit & Brinkhuis, 1996).

The aims of the present study are twofold. Firstly, we aim to place the Geulhemmerberg K/Pg section in a long-term palaeoenvironmental proxy record of the type-Maastrichtian, covering a (near-)continuous marine sedimentation over the last *c*. 1 Myr of the Cretaceous. This timescale covers the onset of Deccan Traps volcanism in India and therefore we will be able to differentiate the environmental effects of Deccan volcanic activity and of the Chicxulub impact on this shallow=marine ecosystem across the K/Pg boundary. Secondly, we apply high-resolution geochemical techniques on the Geulhemmerberg K/Pg stratigraphy to obtain novel insights into the distribution of potential impact ejecta, the response of the marine biosphere to climate perturbations and the overall timing of this likely storm-driven deposit (Smit & Brinkhuis, 1996)

With regard to this first goal, the present study represents the top section of a *c*. 115-m-thick composite stratigraphical framework that has been constructed as part of the Maastrichtian Geoheritage Project (Vellekoop *et al*., 2022) and covers also the Hallembaye (now Kreco) and former ENCI quarries (Fig. 1). Revisiting the Geulhemmerberg K/Pg site has resulted in a sample set obtained at 5-cm-stratigraphical resolution for the 7.5 metres below the basal K/Pg shell hash, belonging to the local stratigraphical units IVf-3 to IVf-7 of the Meerssen Member of the Maastricht Formation. At Geulhemmerberg, the base of the hardground at -4 m (relative to the K/Pg boundary) is linked to the base of subunit IVf-5, which can be correlated to a similar interval in the nearby Curfs and former ENCI quarries. We have performed stable carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) isotope analyses on carbonate powders, together with bulk micro-X-ray fluorescence (µXRF) elemental analyses (following Vellekoop *et al*., 2022). The µXRF data reveal an abrupt drop in $CaCO_3$ content at the K/Pg boundary interval compared to the rest of the >100-m-thick sequence. In addition, the $\delta^{13}C$ signal shows a slight decreasing trend towards the top, but a clear negative anomaly at the boundary seems to be missing (Fig. 1).

The second aim of the present study centres around high-resolution analyses of the base of the *c*. 1-m-thick IVf-7 interval, based on 25 µm resolution µXRF element mappings and point-linescans of continuous sediment blocks, following the methodology described in Kaskes *et al*. (2021). The profiles based on this first pilot-study show distinct variations in e.g., Fe content across the various clay and shell hash horizons (Fig. 2), but no clear enrichments are seen in e.g., Cr and Ni. The absence of a clear Cr signal is in line with the absence of an iridium anomaly at this shallow-marine setting, in contrast to distal deep-marine K/Pg boundary sites (Smit & Brinkhuis, 1996). Future work will focus on the geochemical mapping of burrow structures to identify potential impact ejecta components, and on a more thorough major and trace element comparison between the multiple clay layers in the Geulhemmerberg section, in order to understand better the sequence of events in the aftermath of the Chicxulub impact within this shallow-marine palaeoenvironment.

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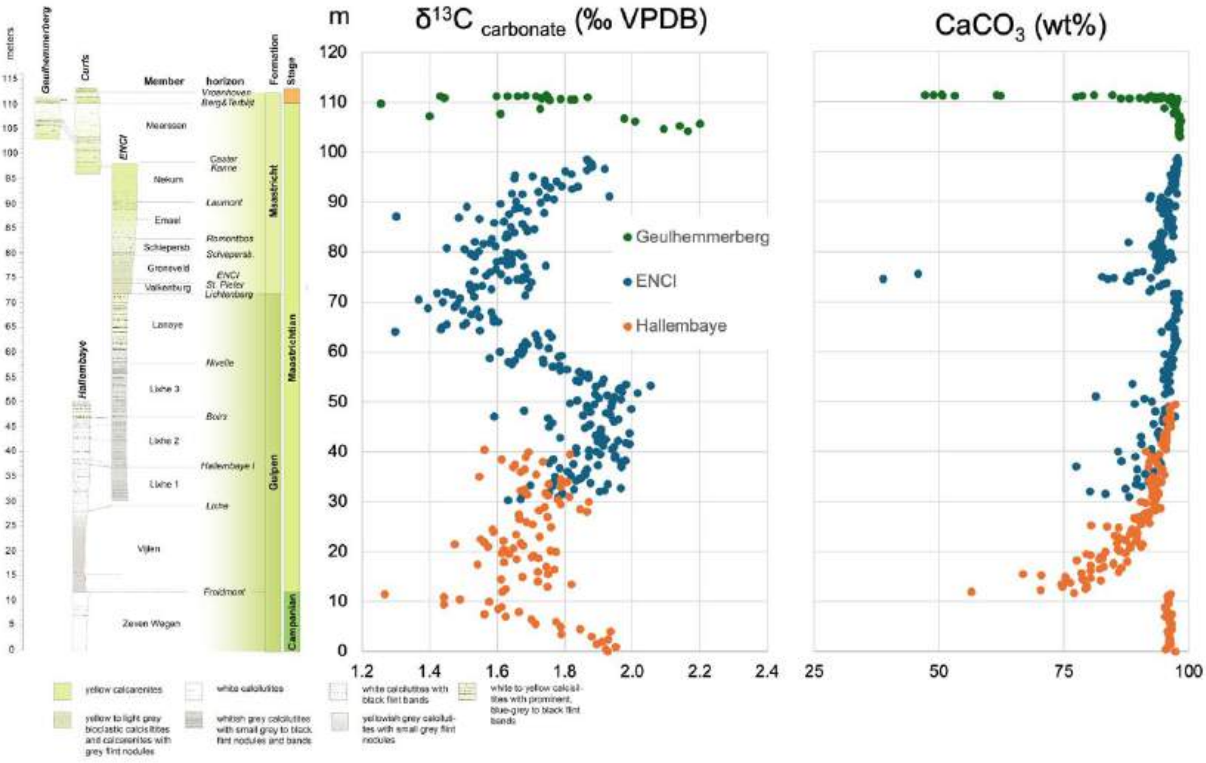

Figure 1. Updated stratigraphical framework of the type-Maastrichtian, based on Vellekoop *et al*. (2022), showing the Geulhemmerberg K/Pg site at the top, and carbon isotope and $CaCO_3$ records.

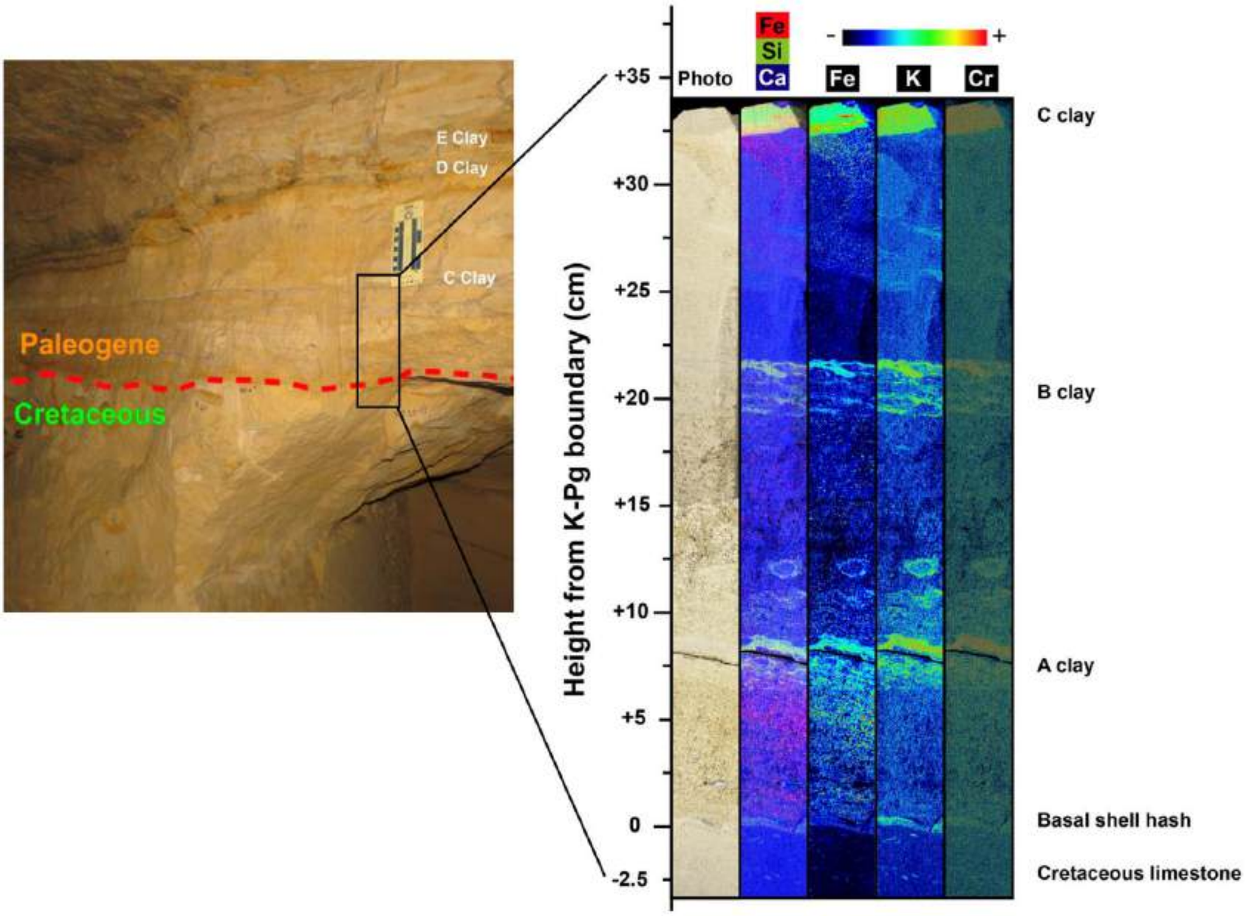

Figure 2. Overview of the Geulhemmerberg K/Pg site focusing on the basal 33 cm of the IVf-7 unit (uppermost Meerssen Member, Maastricht Formation), covering the basal shell hash, and the A-C clay layers. The µXRF maps visualise the distribution of Fe, Si, Ca, K and Cr.

Belemnella (Coleoidea, Belemnitellidae) from Altembroeck (north-east Belgium) revisited

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For the identification of belemnites of the genus *Belemnella* two approaches have been introduced, the so-called classic approach of Schulz (1979) and the Kohonen neural network approach of Remin (2012). Noteworthy, the latter did not use the Lsn- and AV-parameters of Schulz (1979), which are both essential for Schulz's species concept.

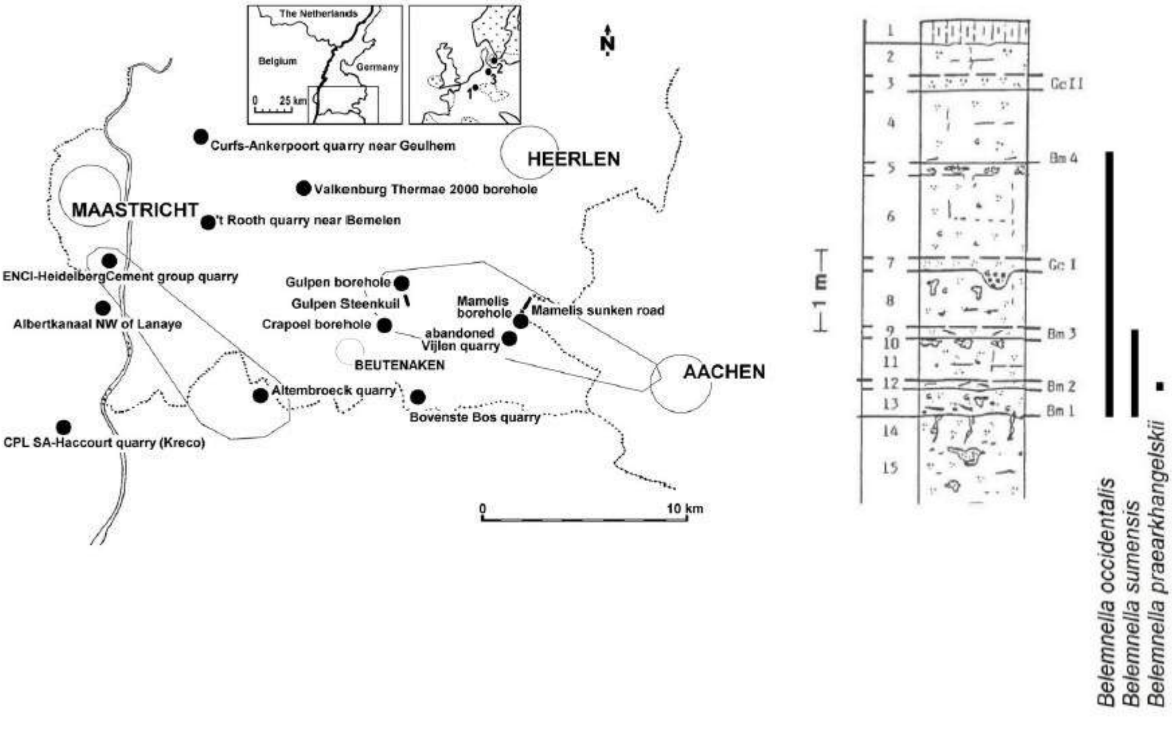

Figure 1. The type area of the Maastrichtian Stage and the Altembroeck section (outcrop 62C-159), with belemnite species recorded. The marked areas between Aachen and Gulpen and between Altembroeck and Lanaye indicate the approximate extension of channel systems, in which the Vijlen Member is most completely preserved.

For the present study, the belemnite material collected from unit 4 of the Vijlen Member at Altembroeck (Fig. 1) has been restudied. Keutgen (1997) identified in this material only two species, *Belemnella sumensis* Jeletzky and *Belemnella* cf. *praearkhangelskii* Naidin, applying

Schulz's 1979 concept. In the current approach, the self-organising Kohonen algorithm implemented in the XLSTAT 2023.1.1 BASIC+ program was applied, taking into account the following parameters: length from apex to protoconch (LAP), dorsoventral diameter at protoconch (DVDP), Schatzky distance (SD), alveolar angle (AA) and fissure angle (FA) (for definitions, see Remin, 2012). In addition, a differently calculated standardised length (SL) was applied. The first step for the calculation of SL is the calculation of the Birkelund index (BI = LAP/DVDP) for each specimen. In a second step, BI was plotted *vs*. DVDP and these data were fit to a logarithmic equation, which expresses the relationship in the case of the genera *Belemnella* and *Neobelemnella* (Keutgen & Keutgen, 2020). Because Schulz (1979) standardised the length of the genus *Belemnella* to a DVDP of 13.5 mm, the BI of each specimen was recalculated for this (DVDP = 13.5 mm) using the logarithmic equation. From thIs BI-value, SL was then calculated as BI x 13.5 mm. Prior to the Kohonen analysis, data for LAP, DVDP, SD, AA, FA and SL were standardised. The topological maps consisted of 5 x 5 output neurons. Further options selected for the analysis were the iteration steps (500,000), teaching parameter decreasing from 0.05 to 0.01, a hexagonal topology and the "bubble" neighbourhood function.

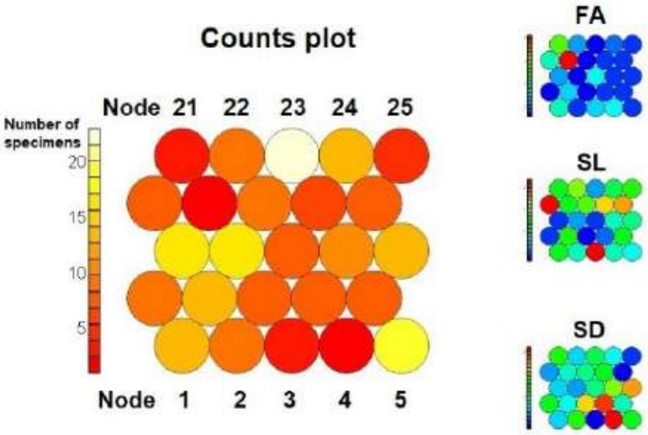

Figure 2. Topological map of the belemnite population from Altembroeck, showing the counts plot and the mean values of fissure angles (FA), standardised lengths (SL) and Schatzky distances (SD). For these three values, colours indicate the height of the mean value of the corresponding node (blue: small value, red: large value).

	LAP [mm]	DVDP [mm]	SD [mm]	AA [°]	FA [°]	SL [mm]	AV [%]	Lsn [mm]
Mean	73.83	15.23	0.83	12.00	28.00	68.94	19.5	69.7
SD	4.48	1.10	0.29	0.00	2.65	1.34	2.44	
Min	71.0	14.5	0.5	12.0	25.0	68.1	16.97	
Max	79.0	16.5	1.0	12.0	30.0	70.5	21.83	

Table 1. Mean values, standard deviation (SD) and minimum (Min) and maximum values (Max) of *B. praearkhangelskii* from level Bm2 at Altembroeck (N = 3).

In addition to material from Altembroeck, the holotypes of *B. sumensis*, *B. occidentalis* Birkelund and *B. cimbrica* Birkelund were integrated here, using the Lsn values given by Schulz (1979) as an approximation of SL. The holotypes appeared in the nodes 24, 10 and 14, respectively. The Kohonen analysis of the 239 specimens produced four nodes with larger SL (3, 16, 19, 20) and smaller SD (exception node 19). FAs were generally small, with the exception of node 17. Node 3 consisted of three large specimens, which are interpreted as *B. praearkhangelskii*. Their mean values are summarised in Table 1.

	LAP [mm]	DVDP [mm]	SD [mm]	AA [°]	FA [°]	Lsn [mm]
Mean	74.31	14.4	0.92	15.57	18.72	72.2
SD	4.87	1.35	0.95	1.44	4.88	
Min	65.50	12.12	0	13.86	11.81	
Max	82.29	16.6	3.01	19	26.26	

Table 2. Mean values, standard deviation (SD) and minimum (Min) and maximum values (Max) of *B. praearkhangelskii* from Hrebenne after Remin (2018; N = 9).

A comparison with *B. praearkhangelskii* from Hrebenne (Remin, 2018) has revealed that that species is large and slender, with a small SD. Remarkably, the FA of the Altembroeck specimens seems to be slightly larger than in those from Hrebenne, but the observed range is similar, so that the three specimens from Altembroeck can be referred to that species. Lsn was calculated from the mean values of LAP and DVDP applying the formula of Schulz (1979). They are rather similar, indicating a slender species.

	LAP [mm]	DVDP [mm]	SD [mm]	AA [°]	FA [°]	SL [mm]	AV [%]	Lsn [mm]
Mean	57.48	10.65	1.30	14.41	23.45	66.31	14.56	64.3
SD	4.15	1.25	0.61	1.40	10.92	4.37	6.13	
Min	48.0	8.6	0.5	12.0	8.0	58.1	4.5	
Max	65.5	13.0	2.5	18.0	50.0	73.6	28.0	

Table 3. Mean values, standard deviation (SD) and minimum (Min) and maximum values (Max) of *B. sumensis* from level Bm2 at Altembroeck (N = 22).

The second species is present in the nodes 16, 19 and 20. However, a detailed analysis has revealed that not all of the specimens of node 19 belong to this species because of their large Schatzky distances (see also Fig. 2). Because the holotype of *B. sumensis* plots in node 24 and the belemnites in node 25 were characterised by small SDs as well (Fig. 2), the belemnites of nodes 24 and 25 were examined in order to determine if they could belong to the second species. In the case of node 24, two of the 12 specimens qualified for this group, in the other specimens SL was too small. In the case of node 25, two of the four specimens qualified for the same reason. The specimens of this group are referred to as *B. sumensis* and the mean values are summarised in Table 3.

A comparison of *B. sumensis* from Hrebenne (Remin, 2018) and Altembroeck indicates the close similarities between both populations. The mean FA of the Altembroeck population is slightly smaller, but the observed range of FA is larger.

	LAP [mm]	DVDP [mm]	SD [mm]	AA [°]	FA [°]	Lsn [mm]
Mean	59.53	11.50	1.40	15.74	31.40	64.3
SD	8.31	2.43	0.98	0.76	6.36	
Min	40.46	5.31	0.00	14.00	24.00	
Max	70.22	14.01	3.53	16.61	42.05	

Table 4. Mean values, standard deviation (SD) and minimum (Min) and maximum values (Max) of *B. sumensis* from Hrebenne after Remin (2018; N = 11).

The majority of specimens from Altembroeck belong to a species not present at Hrebenne and here referred to as *B. occidentalis*. The mean values are summarised in Table 5.

	LAP [mm]	DVDP [mm]	SD [mm]	AA [°]	FA [°]	SL [mm]	AV [%]	Lsn [mm]
Mean	51.72	12.24	2.29	15.70	20.67	54.43	5.43	54.7
SD	6.25	1.97	0.90	1.21	8.79	4.46	5.88	
Min	36.5	7.2	0.5	12.0	7.0	42.1	-9.4	
Max	68.0	17.0	4.5	20.0	62.0	64.9	23.5	

Table 5. Mean values, standard deviation (SD) and minimum (Min) and maximum values (Max) of *B. occidentalis* from level Bm2 at Altembroeck (N = 210).

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Late Cretaceous marine tetrapods from the collections of the Alabama Museum of Natural History

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Alabama has an extensive Late Cretaceous fossil record, primarily found in the central part of this state in the south-eastern USA. As the shoreline retreated from the Mississippi Embayment during this part of the Cretaceous, marine strata were deposited. These sedimentary rocks are assigned primarily to the Eutaw, Mooreville, Demopolis, Ripley and Prairie Bluff formations, ranging in age from late Coniacian to late Maastrichtian. Extensive collecting in these units by staff of the Alabama Museum of Natural History (ALMNH) and avocational palaeontologists over the last century has resulted in a large collection of marine tetrapods comprising primarily mosasaurs and turtles, as well as some plesiosaur and crocodilian material. The ALMNH collection remains understudied, and the goal of this abstract is to increase the awareness of this collection.

For mosasaurs, more than 1,000 records are in the Arctos database (https://arctos.database.museum/almnh_paleo). Nearly all specimens originate from Alabama. The size of this collection makes it one of the largest mosasaur collections in North America. It includes adult and various juvenile specimens and consists of individual bones and teeth to near-complete specimens. One remarkably complete specimen is an unstudied individual of *Clidastes* (ALMNH:Paleo:4920) from the Mooreville Chalk Formation measuring ~3.3 m in length. Other mosasaur specimens represented by relatively many bones including cranial material are two individuals of *Mosasaurus hoffmanni* (ALMNH:Paleo:1036 and 2271), a specimen of *Tylosaurus proriger* (ALMNH:Paleo:3079) and two of *Clidastes propython* (ALMNH:Paleo:4787 and 4601). Both specimens of *M. hoffmanni* may have reached a length of over 12 m. Holotype specimens of mosasaurs in the collection include *Clidastes moorevillensis* Shannon, 1975 (ALMNH:Paleo:5402), *Selmasaurus russelli* Wright & Shannon, 1988 (ALMNH:Paleo:5405) and *Ectenosaurus shannoni* Kiernan & Ebersole, 2023 (ALMNH:Paleo:5452). Mosasaur genera reported in the collection database are *Clidastes*, *Ectenosaurus*, *Eonatator/Halisaurus*, *Globidens*, *Latoplatecarpus*, *Mosasaurus*, *Platecarpus*, *Plioplatecarpus*, *Selmasaurus* and *Tylosaurus*, with *Clidastes* being the most common genus.

Late Cretaceous turtles are also well represented by ~700 records, again consisting of individual bones to individuals with most bones present. Two turtle holotypes are housed in the ALMNH type room: *Peritresius martini* Gentry, Parham, Ehret & Ebersole, 2018 (ALMNH:Paleo:6191) and the freshwater *Appalachemys ebersolei* Gentry, Kiernan & Parham, 2023 (ALMNH:Paleo:670). Cretaceous genera of Testudines present in the collection database are *Adocus, Agomphus, Apalone, Appalachemys, Bothremys, Calcarichelys, Chedighaii, Chelosphargis, Ctenochelys, Lophochelys, Peritresius, Prionochelys, Protostega,* ?*Thinochelys* and *Toxochelys.*

For the ~40 records of plesiosaurs, most material is identified as Elasmosauridae without further determination. A few records have been assigned to *Cimoliasaurus* and *Alzadasaurus*. For the ~40 records of Cretaceous Crocodilia, the genera *Deinosuchus*, *Leidyosuchus* and *Eothoracosaurus* have been identified. One remarkable specimen is represented by >150 postcranial bones, assigned to *Deinosuchus schwimmeri* (ALMNH:Paleo:1002) (Cossette & Brochu, 2020).

Stratigraphically, most material originates from the lower Campanian Mooreville Chalk Formation, in part because the University of Alabama owns a large (132.5 acres or 53.6 hectares) field site called Harrell Station Paleontological Site in central Alabama where mosasaur and turtle remains are regularly encountered.

We welcome proposals for scientific study or other uses of specimens in the ALMNH collection.

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What do we tell visitors? The ‘mosasaur story’ at the Natural History Museum of Maastricht

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On a yearly basis, the Natural History Museum of Maastricht welcomes an average number of visitors of 31,000. As a volunteer I do 60 tours *per annum* with around 7 people each time, but individual visitors are also informed about our collections and specimens on display. In the past, I have also contributed to the preparation of mosasaurs ‘Carlo’ (collected in September 2012) and ‘Lars’ (collected in April-June 2025), in the museum’s Science Lab.

What is it that we tell our visitors? The main subject is, of course, the story of ‘our’ mosasaurs: the five species represented in our collections and the main characteristics of the generalised Meuse lizard. We distinguish three main goals in our story: we wish to generate astonishment, outline the power of evolution to our visitors and inform them about advanced 3D software that offers novel opportunities to palaeontologists.

In addition, I inform visitors about a number of underlying items such as general geology (using the museum’s 3D globe), the history of palaeontology, the Chicxulub asteroid that led to the extinction of numerous species, including mosasaurs, and the occurrence of flint in our upper Maastrichtian levels.

The entrance hall of the museum holds a replica (Fig. 1) of the second mosasaur skull to be unearthed near Maastricht. The original was discovered in October 1778 in one of the subterranean galleries of the Sint-Pietersberg (Saint Peter’s Mountain), south of the city. By the end of 1794 the French revolutionary army had occupied our province, and the city of Maastricht – the skull was seized and put on transport to Paris. I tell visitors that the community of Maastricht has recently sent an official request to the French government for the original skull to be returned to Maastricht. But, I also tell them that, in the long run, the looting of the skull had a positive effect.

One of the most astonishing features of mosasaurs to visitors is the sclerotic ring in the eye socket. Visitors learn about a 66-million-year-old diaphragm; I tell them about the general significance of this ring of bony plates. The power of evolution will be illustrated to our guests in this way. Most visitors appear to be aware of novel techniques such as CT scanning and 3D applications in general, but they are surprised when they hear about the opportunities that 3D software has been offering palaeontologists. To illustrate this I refer to CT scans of the frontal part of the upper and lower jaws of ‘Carlo’, a specimen recovered from the upper Lixhe 3 Member (Gulpen Formation). These scans indicate that ‘Carlo’ did survive a wound in its nose, but probably succumbed to the inflammation in its jaw.

Figure 1. Replica of the holotype of *Mosasaurus hoffmannii* from the subterranean galleries of Sint-Pietersberg, recovered in October 1778.

Figure 2. 3D print of the skull of the holotype of *Asteriornis maastrichtensis* (natural size) from the lower Maastricht Formation (upper Maastrichtian), next to a stuffed individual of an extant partridge for illustration of the reconstructed size of the fossil bird.

One of the other items featuring in my museum tour is the microscanning facilities at the University of Cambridge (courtesy of Dr Daniel J. Field); visitors will see the 3D print of the

Asteriornis skull (Fig. 2). I will tell them about the relationship between this small skull and the impact of the Yucatán comet in the Gulf of Mexico.

And, finally, visitors may marvel at the sizeable skull of mosasaur ‘Bèr’, the holotype of *Prognathodon saturator* and the museum’s newest addition, the Mosasaur Experience, learn about the origins of flint and view the preparation work in our Science Lab.

The aim of this talk is to have an exchange of ideas and views with you about the added value of my tour: many of you are well versed in interaction with the public and know how to get the message across!

A taxonomic revision of sabellid and serpulid polychaete tube worms from the Maastrichtian chalk of Denmark — preliminary observations

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This preliminary report on a revision of sabellid and serpulid tube worms from the Maastrichtian Møns Klint Formation in Denmark is based on material in the collections of Geomuseum Faxe (abbrevation: OESM). Most specimens were collected in outcrops; only a few were picked from processed sediment samples. The material originates from the following localities (Fig. 1): Stevns Klint in south-eastern Sjaelland (227 specimens), Rørdal quarry at Aalborg, northern Jylland (nine specimens) and the cliffs of Møn (10 specimens). Our research builds upon the detailed taxonomic study of Late Cretaceous/early Paleocene serpulids and sabellids from Denmark by Brünnich Nielsen (1931), as well as other papers in which Late Cretaceous polychaetes from Denmark are referred to and/or illustrated, such as Gravesen & Jakobsen (2012, 2017), Hansen & Surlyk (2014) and Gravesen (2020). Our preliminary revision has documented 13 polychaete species in the Geomuseum Faxe collections, belonging to two families in the order Sabellida, namely Sabellidae (with a single species, *Glomerula serpentina*) and Serpulidae (serpulids), which comprises 12 species: *Filogranula cincta*, *Cementula sphaerica*, *Spiraserpula versipellis*, *Orthoconorca turricula*, *Neovermilia ampullacea*, *Nogrobs* (*Tetraditrupa*) *canteriata*, *Pentaditrupa subtorquata*, *Pyrgopolon* (*P.*) *hagenowii*, *Pyrgopolon* (*P.*) *cicatricatus*, *Pyrgopolon* (*Septenaria*) *macropus*, *Bipygmaeus pygmaeus*, *Neomicrorbis crenatostriatus crenatostriatus* and *Neomicrorbis crenatostriatus subrugosus*. A few additional species have been mentioned in the literature, and several smaller species may also be expected to be found when sediment samples are screened in more detail. For example, *Glomerula lombricus*, which is not represented in the collections of the Geomuseum Faxe, does occur in the Maastrichtian of Denmark, but its small tubes are easily overlooked at outcrop.

Our research shows that:

1. The local trilobate narrowing of the tube lumen is commoner in *Glomerula serpentina* (Fig. 2B) from the Maastrichtian of Denmark than in Maastrichtian-aged material of *Glomerula* from the Netherlands and Belgium described by Jäger (2005, 2012), but about equally common as in northern Germany. The first appearance of trilobate lumina within

the genus dates back to the Lower Cretaceous. This feature seems to be an expression of genuine phylogenetic progress, presumably enabling the animal to fix itself inside its tube as protection against being drawn out of it by a predator (Jäger, 2005; Sklenář *et al*., 2013).
2a. *Glomerula serpentina* which forms a "network of nodes" or "carpet of nodes" with larger connecting tubes (Fig. 2C) indicates an adaptation for living on soft substrates (Seilacher *et al*., 2008; Sklenář *et al*., 2013).
2b. Figure 2P shows a characteristic feature of *G. serpentina* when this species lived on chalk ooze, as originally described, illustrated and reconstructed by Müller (1964): a straight vertical tube portion was damaged at its anterior end. After that, the tube formed a very narrow curve and turned spirally downwards all around its straight vertical stump, so that the tube resembles a slender screw with the straight vertical stump hidden in the centre.
3. The five-keeled species originally described as *Ditrupula triminghamiensis* (see Brünnich Nielsen, 1931, pl. 1, figs 7, 8) is synonymous with *Pentaditrupa subtorquata* (Fig. 2T).
4. The strongly and regularly curved seven-keeled tubes (Fig. 2H-K) of *Ditrupula hagenowii* (of Brünnich Nielsen, 1931) may rather be assigned to the subgenus *Pyrgopolon* (*Pyrgopolon*); interestingly, these specimens are closely similar to *Serpula heptagona* (of von Hagenow, 1840) from the lower Maastrichtian of Rügen, which is considered a subjective synonym of *Pyrgopolon* (*Septenaria*) *macropus*.
5. The long, gently curved and circular (in cross section) tubes originally named *Ditrupula cicatricata* by Brünnich Nielsen (1931) are now referred to as *Pyrgopolon* (*Septenaria*) *cicatricatus* (Fig. 2L, M).
6. The seven-keeled *Pyrgopolon* (*Septenaria*) *macropus* (Fig. 2N, N1) shows well-developed "tabulae" in the tube lumen, as already described by Müller (1963, 1964) and Nestler (1963) for material from Rügen.

Most serpulids are encrusters of a range of substrates, as shown by examples in Figure 2: *Filogranula cincta* (Fig. 2Q, R) encrusting a saleniid echinoid (Fig. 2Q) and a cidaroid spine; *Neovermilia ampullacea* (Fig. 2E-G) fixed to a test fragment of *Echinocorys* and an echinoid spine and *Spiraserpula versipellis* attached to a molluscan valve (Fig. 2U). However, a few species are adapted to life on soft substrates, e.g., *Pentaditrupa subtorquata* (Fig. 2T), *Pyrgopolon* (*P.*) *hagenowii* (Fig. 2H-K) and *Nogrobs* (*Tetraditrupa*) *canteriata* (Fig. 2S). These species possess keels and regularly curved tubes, constituting an adaptation (snowshoe strategy) to avoid sinking into soft substrates (according to Seilacher *et al*., 2008).

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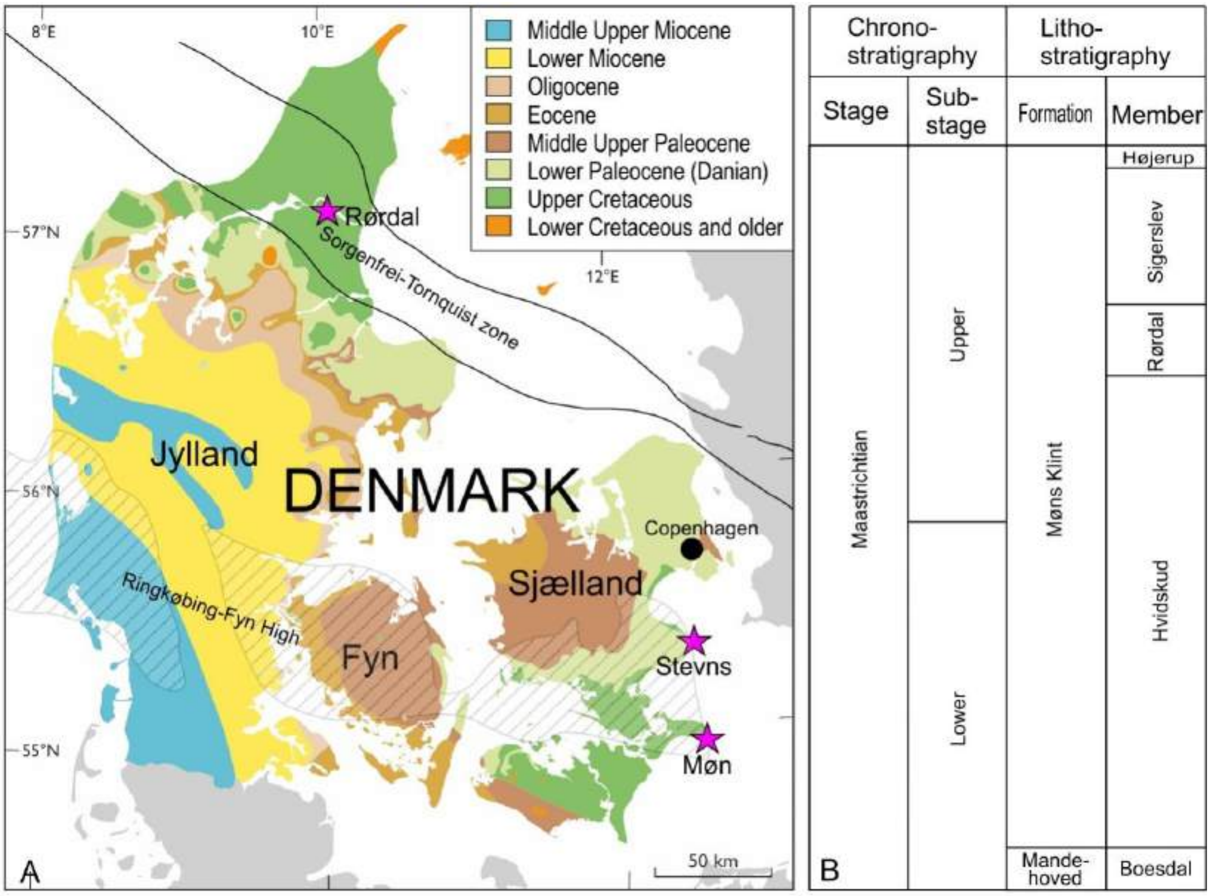

Figure 1A. The localities Rørdal, Møn and Stevns, all marked by purple asterisks. **B.** Local chrono- and lithostratigraphy (modified from Clemmensen & Thomsen, 2005).

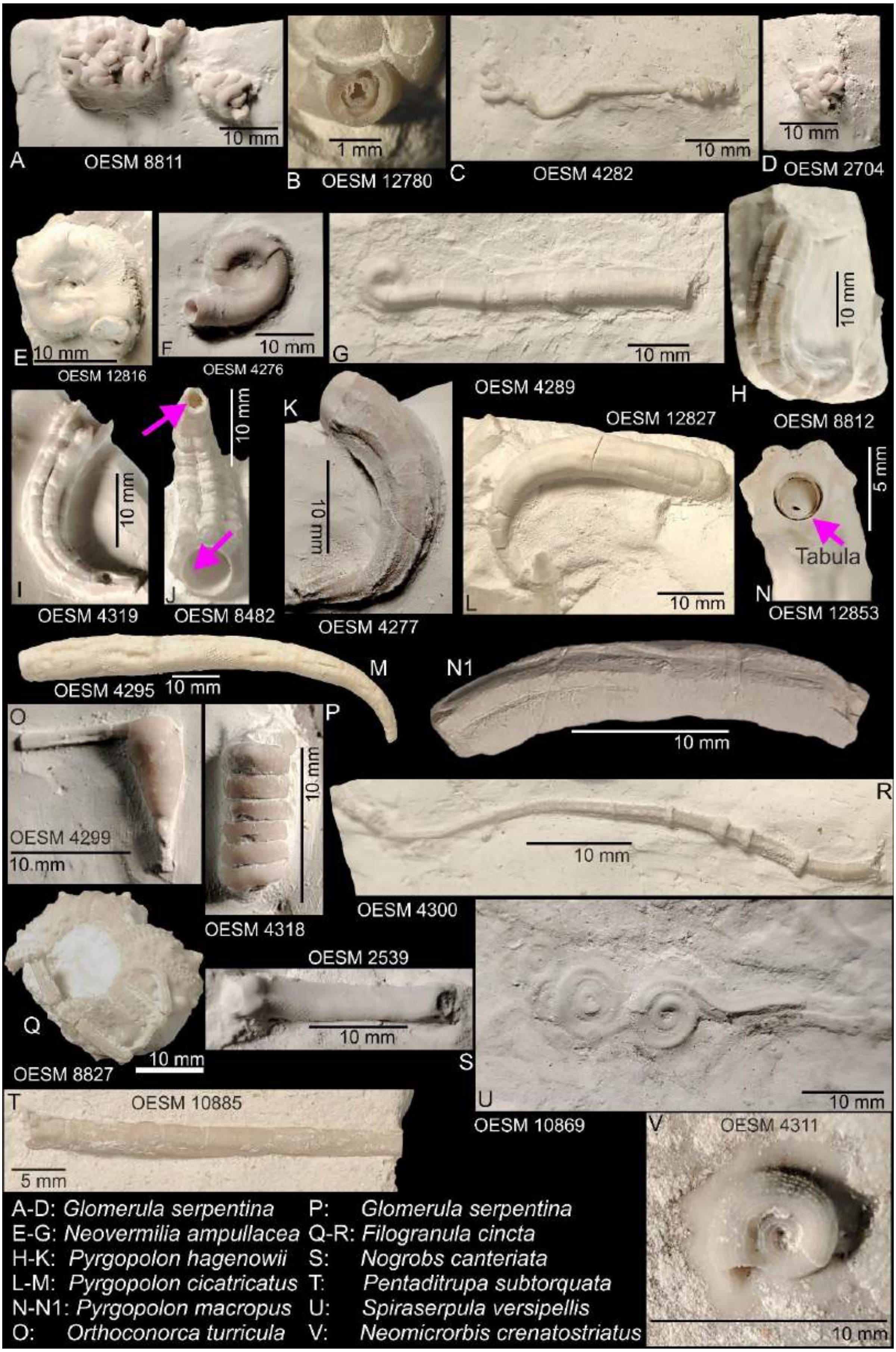

Figure 2. Sabellids and serpulids from the Maastrichtian of Denmark (OESM collections).

Facies characterisation and stratigraphy of the upper Maastrichtian to lower Danian Maastricht Formation

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The upper Maastrichtian to lower Danian Maastricht Formation of the Chalk Group consists of bioclastic calcarenites and calcirudites deposited in a proximal zone of the Late Cretaceous Chalk Sea, in the Campine Basin and neighbouring Dutch territory, north of the Anglo-Brabant and Rhenish massifs (Fig. 1a). Unlike the typical North Sea chalk, the Maastricht Formation is much coarser and at times contains a significant terrigenous component. The formation crops out in South Limburg, the Netherlands, in the German state of North Rhine-Westphalia, near Aix-la-Chapelle (Aachen) and in the Belgian provinces of Liège and Limburg (Fig. 1b) (Bless *et al.*, 1987; Robaszynski, 2006).

The Maastricht Formation has been informally subdivided into six members: Valkenburg, Gronsveld, Schiepersberg, Emael, Nekum and Meerssen (Fig. 2a) (W.M. Felder, 1975; W.M. Felder & Bosch, 2000). A popular subdivision of the formation into two units, the Maastricht and Kunrade limestones, is often used alongside these members (Francken, 1947; Hofker, 1966; W.M. Felder & Bosch, 2000). The main difference between these two limestones appears to be related to diagenesis: the Maastricht limestone consists of soft calcarenites, whereas the Kunrade limestone contains well-cemented calcarenites that alternate with soft calcarenites. The Maastricht limestone occurs in the west of South Limburg and the Kunrade in the east (Fig. 1c).

Identification of the six members of the Maastricht Formation is not straightforward, usually requiring *a priori* knowledge of the stratigraphy of South Limburg or a characterisation of the fossil content. Most stratigraphical studies thus far have relied on fossil and flint content to subdivide and correlate the Maastricht Formation (e.g., Hofker, 1966; W.M. Felder, 1975, 1977; P.J. Felder *et al.*, 1985; P.J. Felder, 2001). This is due to a lack of clear and distinguishing lithostratigraphical criteria. The lack of a lithostratigraphical framework based on modern facies studies hampers stratigraphical correlation between outcrops and, more importantly, boreholes. A facies characterisation and facies-based lithostratigraphical framework of the Maastricht Formation in South Limburg is particularly urgent because groundwater is abstracted from aquifers in the formation and geological models currently in place fail to predict facies heterogeneity and, consequently, aquifer properties.

We have studied eight outcrops of the Maastricht Formation across South Limburg (Fig. 1c) and carried out a (micro-)facies analysis of the outcrops. Here, we show that the Maastricht Formation, as defined now, can be subdivided into three lithofacies and five microfacies. The lithofacies reflect the traditional subdivision of the formation into a Maastricht limestone and a Kunrade limestone. Our results suggest that the current *informal* subdivision of the Maastricht Formation into six members (and seven horizons) is untenable. The formation is best subdivided into a lower member and an upper one, which is a subdivision that was also proposed by W.M. Felder (1975) (Fig. 2b). The Kunrade limestone should be afforded the status of formation.

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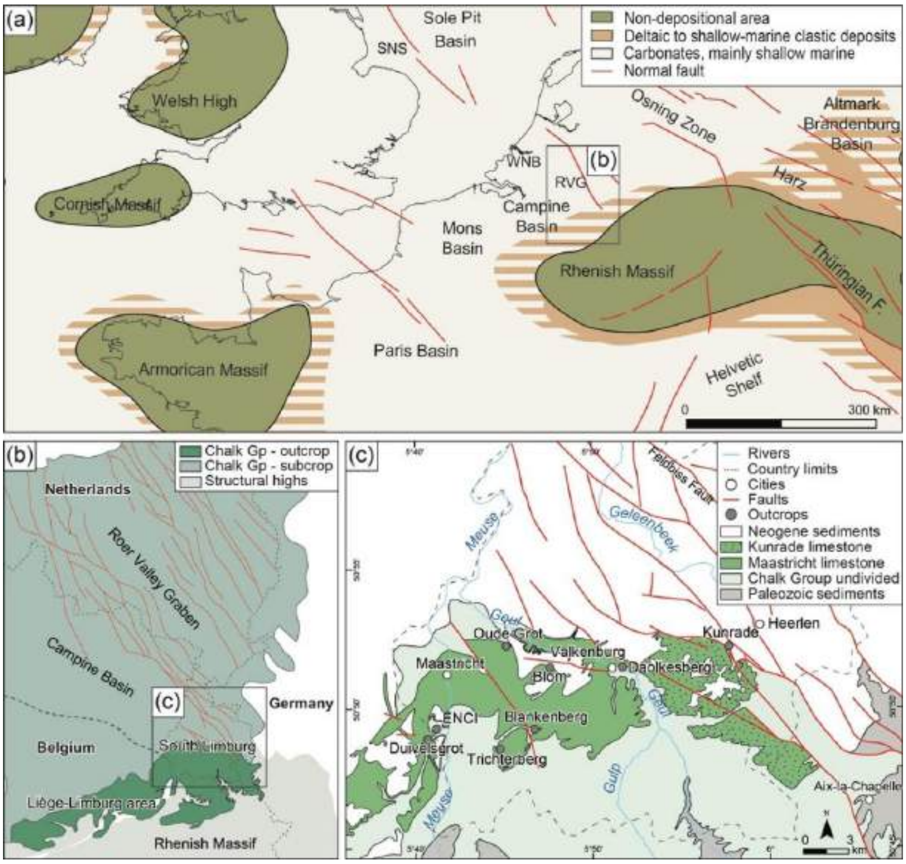

Figure 1. (a) Cenomanian to Danian palaeogeographical map of the Chalk Sea of northwest Europe (modified from Vejbaek *et al*., 2010, after Ziegler, 1982). *Abbreviations*: SNS – Southern North Sea; WNB – West Netherlands Basin; RVG – Roer Valley Graben. **(b)** The Upper Cretaceous of South Limburg is an extension of the subsurface stratigraphy of the Campine Basin of Belgium. The outcrops of South Limburg extend to the provinces of Liège and Limburg in Belgium and the German state of North Rhine-Westphalia, near Aix-la-Chapelle. **(c)** Simplified geological map of South Limburg with emphasis on the distribution of the Maastricht Formation. The Maastricht Formation has traditionally been subdivided into a Maastricht limestone in the west and a Kunrade limestone in the east.

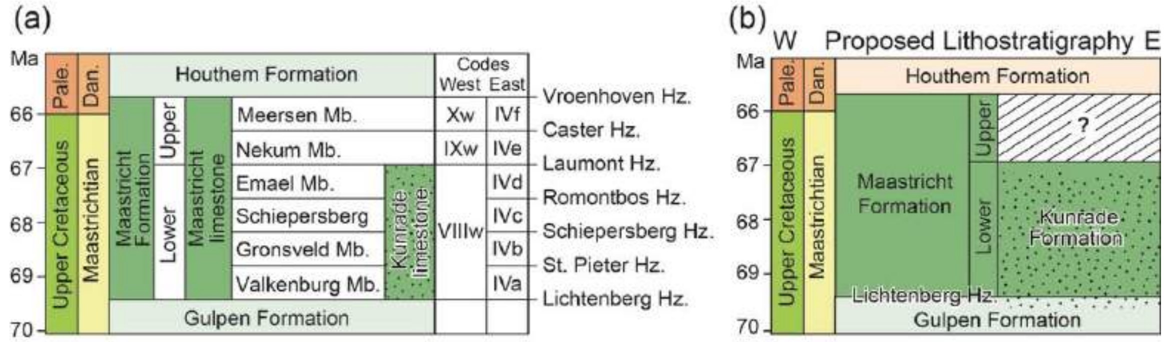

Figure 2. (a) Stratigraphical diagram of the Maastricht Formation, based on W.M. Felder (1975) and W.M. Felder & Bosch (2000). The stratigraphical codes are relative to the River Maas (Meuse). **(b)** Simplified stratigraphical diagram. Here, we propose abandoning the subdivision of the Maastricht Formation into six members proposed by W.M. Felder (1975) and to formalise the subdivision of the formation into a lower member and an upper, which was also proposed by W.M. Felder (1975). The upper member of the Maastricht Formation has no lateral equivalent in the east. The contact between the Maastricht Formation and the underlying Gulpen Formation has been referred to as the Lichtenberg Horizon, which can be traced in boreholes and outcrops.

Ammonites at Cretaceous-Paleogene sites in North America: abundance and short-term survivorship

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In the search for Cretaceous-Paleogene (K/Pg) sections with ammonites in North America, my colleagues and I have documented more than a dozen sites. Most of them are on the inner-middle shelf at depths of less than 100 m and occur along the Atlantic and Gulf Coastal plains (New Jersey, Missouri, Alabama, Mississippi, Arkansas and Texas; see Fig. 1). In this talk, I will review several of the most important sites.

In Monmouth County (New Jersey), the K/Pg interval is represented by the Tinton Formation below and the Hornerstown Formation above. The top of the Tinton Formation contains a rich unit (the *Pinna* Layer), with abundant ammonites (*Discoscaphites*, *Eubaculites*, *Sphenodiscus* and *Pachydiscus*), overlain by a thinner, much more depauperate unit (Burrowed Unit) with only a few fragments of *Eubaculites* and *Discoscaphites*, as well as several isolated ammonite jaws. A weak iridium anomaly (500-600 pg/g) is present at the base of the *Pinna* Layer. The most parsimonious explanation is that the *Pinna* Layer was deposited during the latest Maastrichtian, followed by an event deposit (the Burrowed Unit) containing ammonites that may have survived for a brief interval of time (a few days to hundreds of years) after the impact. In this interpretation, the iridium spike would have been displaced downwards from its original position at the top of the *Pinna* Layer via chemical remobilisation (Landman *et al.*, 2007, 2012).

In Tippah County (northern Mississippi), the K/Pg interval spans the Owl Creek Formation and lower Paleocene Clayton Formation (Larina *et al.*, 2016). The Owl Creek Formation represents the uppermost Maastrichtian *Discoscaphites iris* Zone, the highest ammonite zone on the Atlantic and Gulf Coastal plains. The Owl Creek Formation is rich in ammonites, especially *Eubaculites* and *Discoscaphites*, in addition to occasional specimens of *Sphenodiscus*. The ammonites are abundant throughout the section and do not show any evidence of diminution due to supposed environmental degradation. The base of the Clayton Formation consists of a heavily weathered, laminated unit, which may represent a post-impact event bed.

At a nearby site (4th St.) in Union County (Mississippi), the base of the Danian Clayton Formation consists of a thin layer (15-30 cm thick) of poorly sorted quartz sand containing ammonites (*Discoscaphites*, *Eubaculites*) intermixed with other macrofossils and Chicxulub impact spherules (Witts *et al.*, 2018). This admixture suggests rapid deposition immediately following impact. Many of the ammonite shells are filled with spherules, implying that the ammonites were alive at the time or were empty shells sitting on the sea floor.

Recent field work has uncovered another site near Starkville (Oktibbeha County, Mississippi), which preserves an unusually complete post-impact record (Sosa-Montes de Oca, in review; Garb *et al.*, in prep.). The upper Maastrichtian Prairie Bluff Formation is overlain by multiple event deposits in the Clayton Formation. The deposits occur in down-dropped blocks, which were probably produced by earthquake activity at the time of impact. They include two spherule-rich beds containing reworked phosphatised ammonites (*Eubaculites* and *Discoscaphites*) and foraminifera (*Guembelitria*). Conformably overlying the spherule beds is a heavily bioturbated unit, completely devoid of spherules ("the Burrowed Unit") and containing foraminifera indicative of the basal Danian Zones P0 and Pα. This unit also contains specimens of the early Danian bivalves *Pycnodonte pulaskensis* and *Cucullaea macrodonta*. In addition, several specimens of *Eubaculites carinatus* occur 40-60 cm above the top of the upper spherule bed and several ammonite jaws (attributed to *Eubaculites* and *Discoscaphites*) occur as high as 1 m above the top of the upper spherule bed and may represent individuals that survived for a short time after impact (ten to hundreds of years).

On the western end of the Gulf Coastal Plain along the Brazos River (Falls County, Texas), the stratigraphical succession consists of the Corsicana and Kincaid formations (Kennedy *et al.*, 2001; Witts *et al.*, 2021; Irizarry *et al.*, 2023). Three genera of ammonites are abundant in the Corsicana Formation (*Discoscaphites, Eubaculites* and *Sphenodiscus*). In addition, ammonite jaws (attributed to *Discoscaphites* and *Eubaculites*) and juvenile specimens are also present, suggesting a living population at the site. The Corsicana Formation represents the uppermost Maastrichtian *Discoscaphites iris* Zone. It is capped by two event deposits consisting of a mudstone-clast-bearing unit with rare impact ejecta, representing a cohesive debris flow produced by seismic activity, and an ejecta-spherule-rich coarse sandstone unit produced by a tsunami or shelf collapse. Both event deposits contain specimens of all three ammonite genera, which may have been alive at the time of impact.

The Tanis site in south-western North Dakota is a fluvial rather than an open-marine site (DePalma *et al.*, 2019). It consists of two seiche deposits that were probably produced by seismic activity at the time of impact. Ammonites (*Sphenodiscus* and *Hoploscaphites*) are present in these deposits. Examination of the sedimentary matrix inside the phragmocones and body chambers of the ammonites in comparison with the surrounding matrix suggest that the ammonites were living at the time and were transported into the site along with other debris.

In summary, these K/Pg sections are characterised by 1) an abundance of ammonites extending to the top of the K/Pg section, attesting to the robust health of the ammonites at the time; 2) "event deposits" reflecting high-energy processes immediately post-impact and 3) the presence of ammonites in the event deposits and immediately above, which may represent individuals that were alive at the time and even survived for a short period afterwards.

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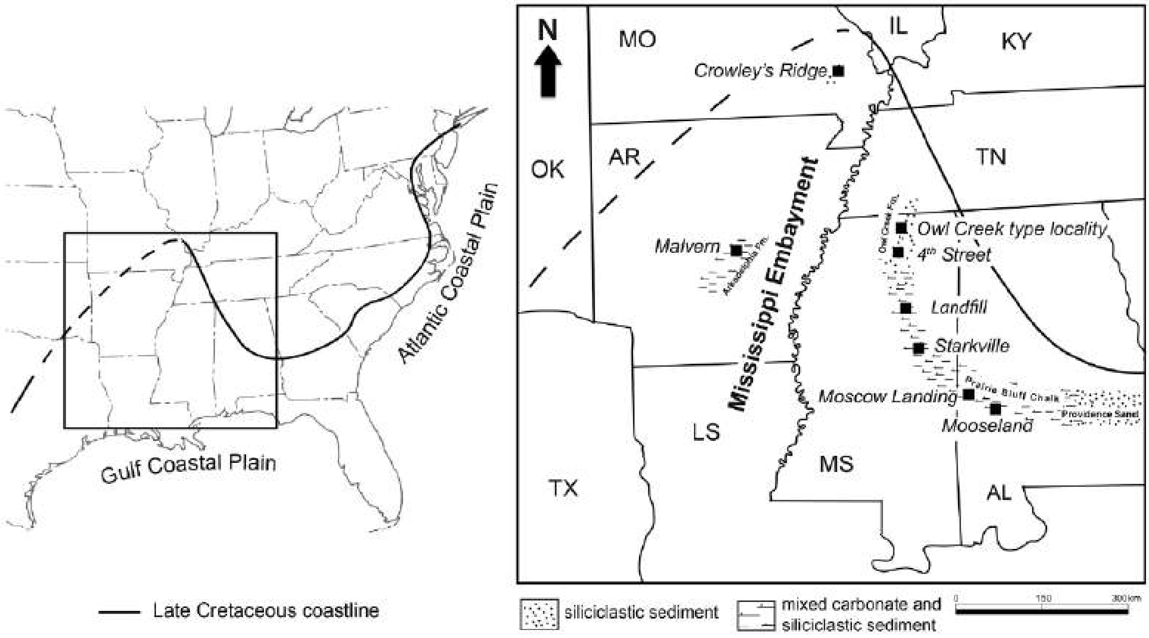

Figure 1. Palaeogeographical map showing the position of the shoreline of the Gulf and Atlantic Coastal plains at the end of the Cretaceous with the cited localities (from Larina *et al.*, 2016). The Tanis site (North Dakota) is not shown.

Soft-tissue fossils – implications for the life and habits of ancient marine reptiles

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The fossil record is capable of exceptional preservation and occasionally labile and decay-prone organs and tissues, such as skin and scales, are preserved as mineralised remains with a high degree of morphological fidelity. These rare findings yield information on features that are generally not available to the scientific community, and are thus instrumental for increasing our understanding of, e.g., evolutionary innovations, modes of locomotion, the degree of adaptation and biology of extinct animals.

In addition to soft-tissue replacement structures, the methodological advances and sophisticated new tools of molecular biology and analytical biochemistry have provided access to another source of geobiologically relevant information: primary organic compounds associated with exceptionally preserved fossils. Examination of ancient biomolecules provides, among other things, a potentially independent means of testing morphology-based phylogenetic hypotheses, thereby strengthening the objectivity of the field of palaeontology.

Here, I review current knowledge on soft-tissue structures and primary biomolecules obtained from mosasaur and ichthyosaur fossils, and show how this novel information can be used to elucidate traits that contributed to two outstanding radiations of giant marine reptiles during the Mesozoic.

The Danish Danian ammonites

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The ammonites are a text-book example of victims of the end-Cretaceous mass extinction. However, data amassed lately suggest that some ammonite populations from the Netherlands, Denmark and New Jersey (USA) briefly survived the Cretaceous–Paleogene (K–Pg; Maastrichtian–Danian) mass extinction event (Machalski *et al*., 2009; Landman *et al*., 2014, 2015). Yet, the hypothesis on short-term ammonite survival into the Danian is still regarded as controversial by some workers (e.g., Ward *et al*., 2016). The aim of our report is to provide additional support for the survival hypothesis based on new specimens collected by ourselves in 2009 and 2013, under the guidance of the late Claus Heinberg, from lowermost Danian levels exposed along Stevns Klint, north-eastern Denmark.

Stratigraphy at Stevns Klint. The Maastrichtian–Danian succession is accessible at several locations along the coastal cliff of Stevns Klint (Fig. 1A). The litho- and chronostratigraphy and facies of this world-famous K–Pg succession were described in detail by Surlyk *et al*. (2006); part of the succession is here shown in Figures 1B and C. In summary, the small basins between crests of the bryozoan bioherms in the uppermost Maastrichtian chalk (Højerup Member) are filled in with the lowermost Danian iridium-bearing Fish Clay (Fiskeler Member), which is overlain by the lowermost Danian Cerithium Limestone Member. Both the Cerithium Limestone (further on abbreviated CL) basins and the intervening tops of the Maastrichtian bioherms are truncated by a planar, intra-Danian hardground with abundant burrows and glauconite mineralisation (Surlyk *et al*., 2006). The hardground surface is overlain by another set of bioherms, composed of later Danian bryozoan limestones (Korsnæb Member). At their base, these limestones occasionally contain glauconitised and phosphatised pebbles and fossils (also ammonites) derived from the underlying strata (Machalski & Heinberg, 2005).

Newly collected material. The specimens studied stem from two locations at Stevns Klint, namely from the large, now disused, Sigerslev chalk quarry (Eskesti) and from a coastal outcrop at Rødvig (Fig. 1A). At Sigerslev, our fieldwork concentrated on a single CL basin located at the top of the quarry along its western face (Fig. 1B). We recovered five ammonites in mouldic preservation from the CL in this basin. These include three specimens of *Baculites* cf. *vertebralis*, and two specimens of *Hoploscaphites* cf. *constrictus johnjagti*. Two additional ammonite specimens, assigned to *Baculites* sp. and *H*. cf. *constrictus* *johnjagti*, come from neighbouring basins at Sigerslev. At this locality, the CL has a pseudo-nodular texture due to presence of innumerable post-CL burrows, stylolites and dissolution seams. This certainly contributed to the fragmentary preservation of the specimens. The best-preserved baculitid came from the very top of the CL, and is filled with calcisphere-rich matrix typical of this unit (Fig. 2A, B). A fragmentary mould of *Baculites* sp. (Fig. 2C) was collected from the lower portion of CL at Rødvig, from a basin located *c*. 200 m north-east of the access to the beach.

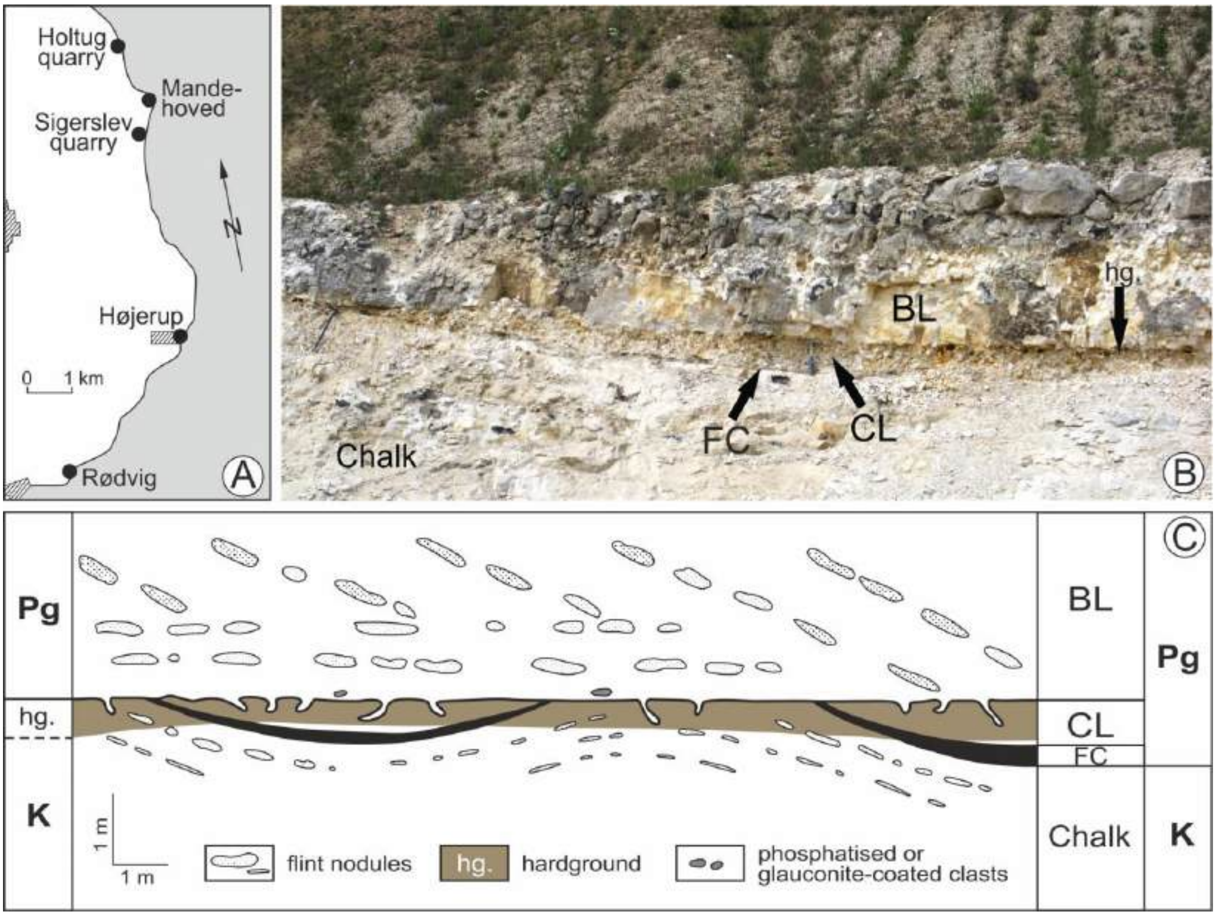

Figure 1. A. Location of the outcrops that have yielded the Danish Danian ammonites (modified from Heinberg, 2005, fig. 3). **B**. Field photograph of a Cerithium Limestone basin at Sigerslev, hammer with blue handle marks position of the specimen in Fig. 2A. **C**. Stratigraphy of the Cretaceous–Paleogene boundary interval at Stevns Klint (modified from Machalski & Heinberg, 2005, fig. 1). *Abbreviations*: FC – Fish Clay, CL – Cerithium Limestone, BL – Bryozoan Limestone.

Discussion and conclusions. Machalski & Heinberg (2005) presented several lines of evidence for the short-term ammonite survival into the Danian based on 11 specimens from the CL outcrops at Højerup, Sigerslev (Eskesti), Mandehoved and Holtug. These ammonites were recovered mainly as a by-product of the CL bulk sampling in search for minute bivalves and gastropods (Heinberg, 2005). Our present collection comprises specimens identified in the field with determined position in relation to the K–Pg boundary. The specimens from Sigerslev, seven in total, were collected during one and a half day by six people, which suggests that ammonites are not as rare in the CL as is commonly assumed. The most important argument put forward by Machalski & Heinberg (2005) in favour of the survival hypothesis was that the CL fauna is almost totally devoid of low-magnesium calcitic shells (e.g., pectinid and ostreid bivalves, microbrachiopods) which occur *en masse* in the Maastrichtian chalk. If the CL ammonite specimens had been reworked from the crests of the Maastrichtian bioherms, as proposed by, e.g., Birkelund (1993), they should have been accompanied by a large number of calcitic fossils, which is not the case, as we have also noted at Sigerslev. The CL ammonites are now known from the entire range of outcrops along the cliffs at Stevns Klint (Fig. 1A). Planktic foraminiferal data have demonstrated the diachroneity of the CL, which becomes progressively younger northwards, from the *Parvularugoglobigerina eugubina* Zone in the south to the *Parasubbotina pseudobulloides* Subzone in the north (Heinberg, 2005; Rasmussen *et al*., 2005). This suggests that the survivors thrived in the study area for a relatively long period of time during the early Danian, their populations falling victim to environmental changes related to the formation of the hardground truncating the CL basins.

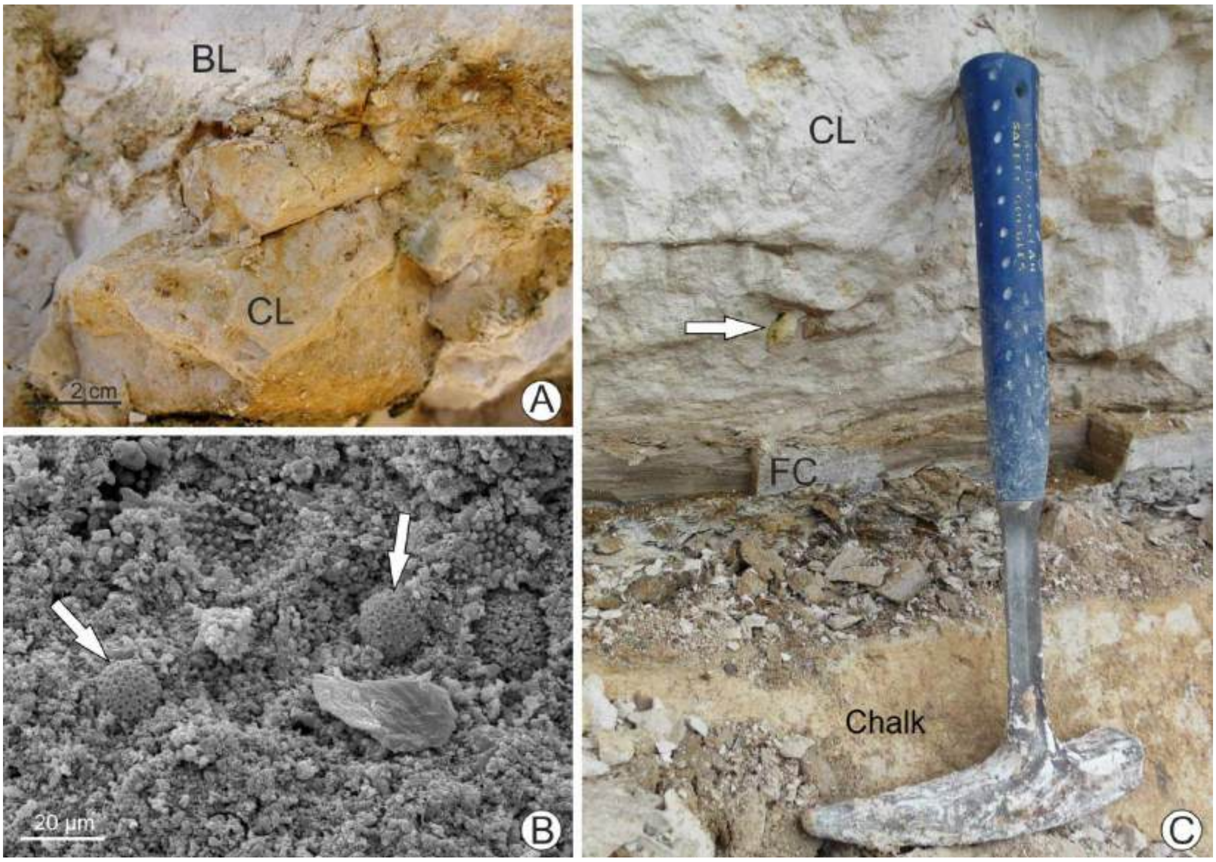

Figure 2. A. *Baculites* cf. *vertebralis* from the top Cerithium Limestone at Sigerslev. **B**. Scanning Electron Microscope (SEM) photograph of a calcisphere-rich matrix infilling the specimen figured in A; note cysts of *Operculodinella operculata* (arrowed). **C**. *Baculites* sp. (arrowed) from the lower Cerithium Limestone at Rødvig. Abbreviations as in Figure 1.

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The oldest occurrence of a selmasaurin plioplatecarpine mosasaur from the Coniacian of Kansas, USA

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Here we report a new mosasaur specimen recently donated to the Sternberg Museum of Natural History (FHSM VP-23317) from the Coniacian of Kansas, possessing characters which allow assignment to the plioplatecarpine tribe Selmasaurini (Longrich *et al.,* 2024). Presence of a canal running through the basicranium allows confident placement in the Plioplatecarpinae. Crown morphology, tooth implantation and the height of the medial parapet of dentaries, allows assignment to the tribe Selmasaurini. The maxilla has eleven teeth, the dentary twelve and the pterygoid eight. Although the bone surfaces are highly bioeroded, the shape of frontal margins is strikingly similar to *Selmasaurus johnsoni*. The position and morphology of the scar (presumably for the *M. depressor mandibulae*) on the posterior surface of the suprastapedial process of the quadrate, and a deep sulcus on the posteromedial shaft of the quadrate, are similar to the condition seen in *S. johnsoni*. However, it is not clear that the suprastapedial and infrastapedial processes contact. Preliminary phylogenetic analysis recovers the new specimen as the sister taxon to all other selmasaurin plioplatecarpines. However, due to the poor preservation and lack of knowledge of many aspects of its morphology, we conservatively leave the specimen in open nomenclature as *Selmasaurus* aff. *johnsoni*.

Mosasaurs of the subfamily Plioplatecarpinae are represented by hundreds of specimens in institutional collections, but most of those are members of the tribe Plioplatecarpini (*sensu* Longrich *et al.,* 2024). Conversely, members of the tribe Selmasaurini are rare and represented by a small number of specimens, including some of the most unusual and enigmatic mosasaurs known. The genus *Goronyosaurus* was erected by Azzaroli *et al.* (1972) to include a partial skull and postcrania from the Maastrichtian of Nigeria, which they referred to the species *G. nigeriensis*, a taxon originally erected by Swinton (1930) as *Mosasaurus nigeriensis.* Wright & Shannon (1988) described *Selmasaurus russelli* from the lower Campanian of Alabama, and in a short note added in proofs, Lingham-Soliar (1988) noted the affinities of *Goronyosaurus* and *Selmasaurus*. Two decades later, Polcyn & Everhart (2008) described a second species of *Selmasaurus* (*S. johnsoni*) from the lower Santonian of Kansas. A taxon first described by Arambourg 1952 as *“Platecarpus ptychodon”* on the basis of isolated teeth and caudal vertebrae, was described and named *Gavialimimus almaghribensis* by Strong *et al*. (2020). This unusual longirostrine mosasaur from the Maastrichtian of Morocco was recovered in their phylogenetic analysis as a selmasaurin plioplatecarpine, a relationship first noted by Polcyn *et al.* (2016). Most recently, Longrich *et al.* (2024) erected the genus *Khinjaria* from the Maastrichtian of Morocco, a taxon quite closely related to *Goronyosaurus*. Compared to the relatively conservative plioplatecarpin plioplatecarpines, selmasaurins exhibit a broad array of feeding adaptations and skull shapes. Although representative taxa of both tribes are present by the early Santonian, significant morphological differences between plioplatecarpin and selmasaurin plioplatecarpines at that time, suggest a much earlier split.

The specimen reported here was recovered in late 2014 by a Triebold Paleontology Inc. field crew in northernmost Lane County, Kansas, and has only recently been prepared, scanned and donated to the Sternberg Museum of Natural History at Fort Hays State University, Hays, Kansas. The locality that produced the specimen is a relatively featureless flat, but approximately 100 metres to the north are good exposures of the Smoky Hill Chalk in which Hattin's (1982) marker units 3-5 are readily identifiable. This interval is below the first occurrence of the inoceramid bivalve *Cladoceramus undulatoplicatus,* which falls in Hattin's Marker Unit 6, and which also marks the Coniacian-Santonian boundary. The close proximity of the exposures and minimal strike and dip, allows placement of the locality near the bottom of Hattin's (1982) Marker Unit 3. The excavation site is low in the alternating chalk/shaly chalk series that is diagnostic of that unit. This interval is within the Lower Shale Unit of Walaszczyk & Cobban (2006), a unit spanning the middle Coniacian and the lower part of the upper Coniacian or approximately 88 Ma, making this the oldest selmasaurin plioplatecarpine thus far reported.

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A calculation of acceleration capabilities of *Mosasaurus hoffmanni*

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In a recent episode of 'Prehistoric Planet 2', it was claimed that *Mosasaurus hoffmanni* exhibited remarkable acceleration capabilities, reaching around 13,4 $m\ s^{-2}$. To investigate this claim, an upscaled model of *Prognathodon kianda* may be used to measure the volume of the tail section used for propulsion. Our measurements have resulted in a volume of 1,00 m^3 ± 0,25 for a body length of 17 metres.

This volume by the percentage of the tail that consists of muscle could be multiplied by volume, assumed to be similar to modern crocodiles and alligators, with a value of p = 0,70 ± 0,10. Considering the density of muscle, the average muscle mass can be calculated to have been approximately 744,8 kg. Using the tail beat frequency calculated based on an assumed muscle stress of 300 $kN\ m^{-2}$, the muscle power output may be determined. By multiplying this power output by muscle mass, the work the muscles deliver over the first second is obtained. After accounting for drag, which is estimated using the drag coefficient calculated from the length and width, the resulting force may be derived. Using the total body mass, speed may be calculated. Since the acceleration is measured over one second, the acceleration is equal to the speed after one second.

The results show an acceleration rate of around 5,14 $m\ s^{-2}$ ± 1,01. This informs us that *Mosasaurus hoffmanni* was not an ambush predator, indicating a possibly different hunting strategy. When compared to similar animals such as killer whales, the latter possess a much higher acceleration rate. This low acceleration rate in *Mosasaurus hoffmanni* implies that the species may have encountered disadvantages during hunting. As an explanation, *Mosasaurus hoffmanni* could have hunted on different kinds of prey to avoid having to accelerate the whole body but rather used similar hunting techniques as killer whales or sharks. This relatively slow acceleration suggests that ambush predation might not have been the only hunting strategy for *Mosasaurus hoffmanni*. Given that a C-start manoeuvre is unlikely for *Mosasaurus hoffmanni*, it is possible that mosasaurs preferred hunting relatively slow prey over potentially C-start-using fish.

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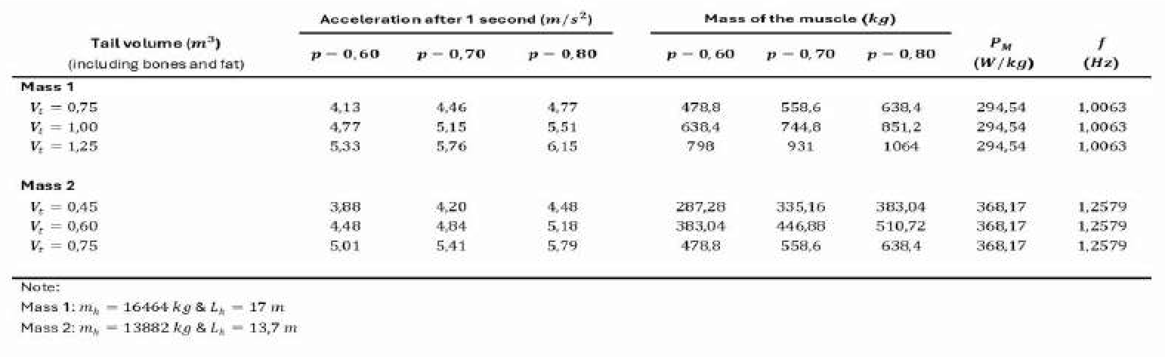

Tail volume (m^3) (including bones and fat)	Acceleration after 1 second (m/s^2)			Mass of the muscle (kg)			P_M (W/kg)	f (Hz)
	$p = 0{,}60$	$p = 0{,}70$	$p = 0{,}80$	$p = 0{,}60$	$p = 0{,}70$	$p = 0{,}80$		
Mass 1								
$V_t = 0{,}75$	4,13	4,46	4,77	478,8	558,6	638,4	294,54	1,0063
$V_t = 1{,}00$	4,77	5,15	5,51	638,4	744,8	851,2	294,54	1,0063
$V_t = 1{,}25$	5,33	5,76	6,15	798	931	1064	294,54	1,0063
Mass 2								
$V_t = 0{,}45$	3,88	4,20	4,48	287,28	335,16	383,04	368,17	1,2579
$V_t = 0{,}60$	4,48	4,84	5,18	383,04	446,88	510,72	368,17	1,2579
$V_t = 0{,}75$	5,01	5,41	5,79	478,8	558,6	638,4	368,17	1,2579

Note:
Mass 1: $m_b = 16464\ kg$ & $L_b = 17\ m$
Mass 2: $m_b = 13882\ kg$ & $L_b = 13{,}7\ m$

Figure 1. *Mosasaurus hoffmanni* – acceleration rate at different tail volumes and muscle masses. The uppermost three values for the tail volume are measured using a mass of 16464 kg and a body length of 17 m obtained from an upscaled version of *Prognathodon kianda*. The last three are obtained using the mass and length proposed by Potekhin & Sukhih (2020).

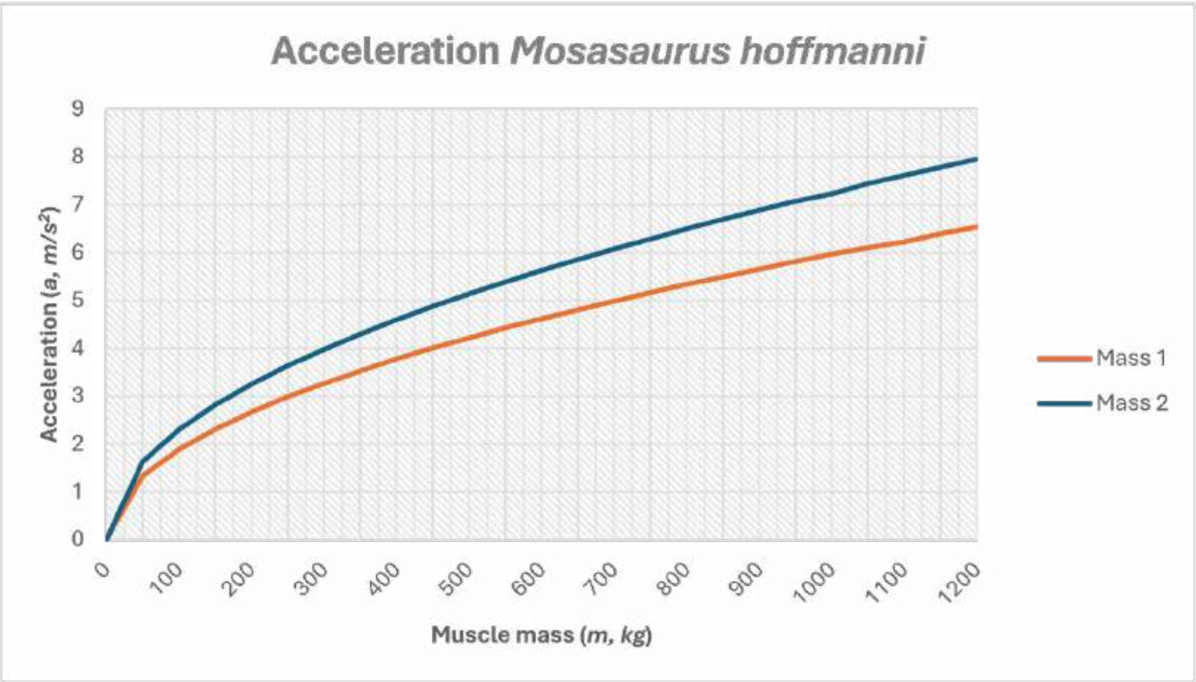

Figure 2. Acceleration *a* as a function of muscle mass *m* for *Mosasaurus hoffmanni*. Mass 1 (16,464 kg) in orange and mass 2 (13,882 kg) in blue.

Osteological correlates for a dorsal fin in plesiosaurs?

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Classic cases of convergent evolution across numerous lineages of vertebrates are exemplified in their secondary adaptations for life in the sea. All free-swimming organisms are subjected to the same constraints imposed by the surrounding water, and thus evolve analogous structures for locomotion and stabilisation (Renesto *et al*., 2020; Fish, 2023). Sharks, marine reptiles (ichthyosaurs and perhaps also mosasaurs) and whales all evolved a dorsal fin to control roll and stabilise the body (Lingham-Soliar, 2005; Renesto *et al*., 2020; Okamura *et al*., 2021). Adaptations for propulsion and manoeuverability are exemplified by limbs modified into flippers (Fish, 2023) and the evolution of a caudal fluke (Lindgren *et al*., 2013). However, the potential presence of fins, flippers and flukes in marine vertebrate fossils can be difficult to assess due to incomplete or absent soft-tissue remains. Nonetheless, osteological correlates can be used as indirect evidence for such structures, including tail flukes (Lindgren *et al*., 2007, 2013; Young *et al*., 2010; Sachs *et al*., 2019) and perhaps also dorsal fins (Konishi *et al*., 2023). It is noteworthy that while ichthyosaurs (and potentially also mosasaurs) evolved a dorsal fin, a comparable control structure is missing in plesiosaurs. There is only one partial body outline of a plesiosaur documented in the scientific literature, and this specimen is unfortunately preserved with only the ventral-half of the body exposed (Frey *et al*., 2017). Thus, for now, the potential presence of a dorsal fin in plesiosaurs can only be inferred from indirect (osteological) clues.

In many delphinoids (dolphins and porpoises), the inclination of the neural arches and spines in the torso show a distinct change from being posteriorly to anteriorly oriented (Buchholtz & Schur, 2004; Konishi *et al*., 2023), a directional shift that occurs directly underneath the dorsal fin (Konishi *et al*., 2023). This arrangement is reminiscent of the caudal neural spines in mosasaur tails, where the dorsal lobe of the crescentic fin is located. The posterior to anterior shift in the orientation of the neural arches in delphinids (dolphins) has been attributed to increased stiffness of the body anterior to the tail (Buchholtz & Schur, 2004; Marchesi *et al*., 2020). However, the seemingly consistent presence of a dorsal fin above this transition warrants further investigation.

To test for the presence of osteological correlates for a dorsal fin, different delphinoid species in the largest collection of cetaceans in the world — the Smithsonian Institution —

were investigated. Species with and without a dorsal fin were studied to determine if neural arch/spine orientation along the vertebral column could be used as a means to infer the presence of such a control structure. Additionally, scarring and/or distinct bone texture on the torso neural spines was examined as a possible indicator for a dorsal fin. The findings were then compared against osteological patterns observed in the vertebral column of various plesiosaurs.

In the delphinoid skeletons studied (20 in total), the posterior to anterior shift in the neural arch/spine arrangement for the lumbar vertebrae was present in 80 per cent of the species with a dorsal fin. However, the killer whale (*Orcinus orca*), Burmeister's porpoise (*Phocoena spinipinnis*), dwarf sperm whale (*Kogia sima*) and La Plata dolphin (*Pontoporia blainvillei*) lacked an anterior orientation of the neural arches/spines despite having a dorsal fin. Moreover, the neural arches/spines of the finless dolphin, *Lissodelphis borealis*, are all inclined posteriorly with no sudden inflection anteriorly, thus differing from most other delphinoids (Fig. 1A-D). Likewise, the neural spines in the trunk of the finless porpoise (*Neophocoena phocaenoides*) are all oriented posteriorly. Notably though, in all investigated taxa where there is an anterior shift in the orientation of the lumbar neural arches/spines there is also an accompanying dorsal fin.

A rough bone texture along the distal neural spines in the lumbar region was only apparent in the Indian humpback dolphin (*Sousa plumbea*), while other delphinoids with a dorsal fin lacked such osteological traces. Therefore, scarring was not found to be a reliable indirect indicator for a dorsal fin.

The microcleidid plesiosaurs *Seeleyosaurus guilelmiimperatoris* and specimen MH 8 (Urwelt-Museum Hauff; *Microcleidus brachypterygius*; *sensu* Benson *et al*., 2012) (Fig. 1E) exhibit a change in the orientation of the neural arches in the posterior dorsal vertebrae that is virtually identical to that in the studied delphinoids with a dorsal fin. Accordingly, we interpret this arrangement as potential indirect evidence of a dorsal fin. Given the impressive 130-million-year evolutionary history of Plesiosauria, we find it likely that a dorsal fin, or some other type of external ornamentation(s), was present in derived forms, especially given the prevalence of such a feature in extant marine amniotes. In addition to a stiffening function, the anteriorly shifted neural arches/spines could have served as the structural support for a dorsal fin in microcleidid plesiosaurians.

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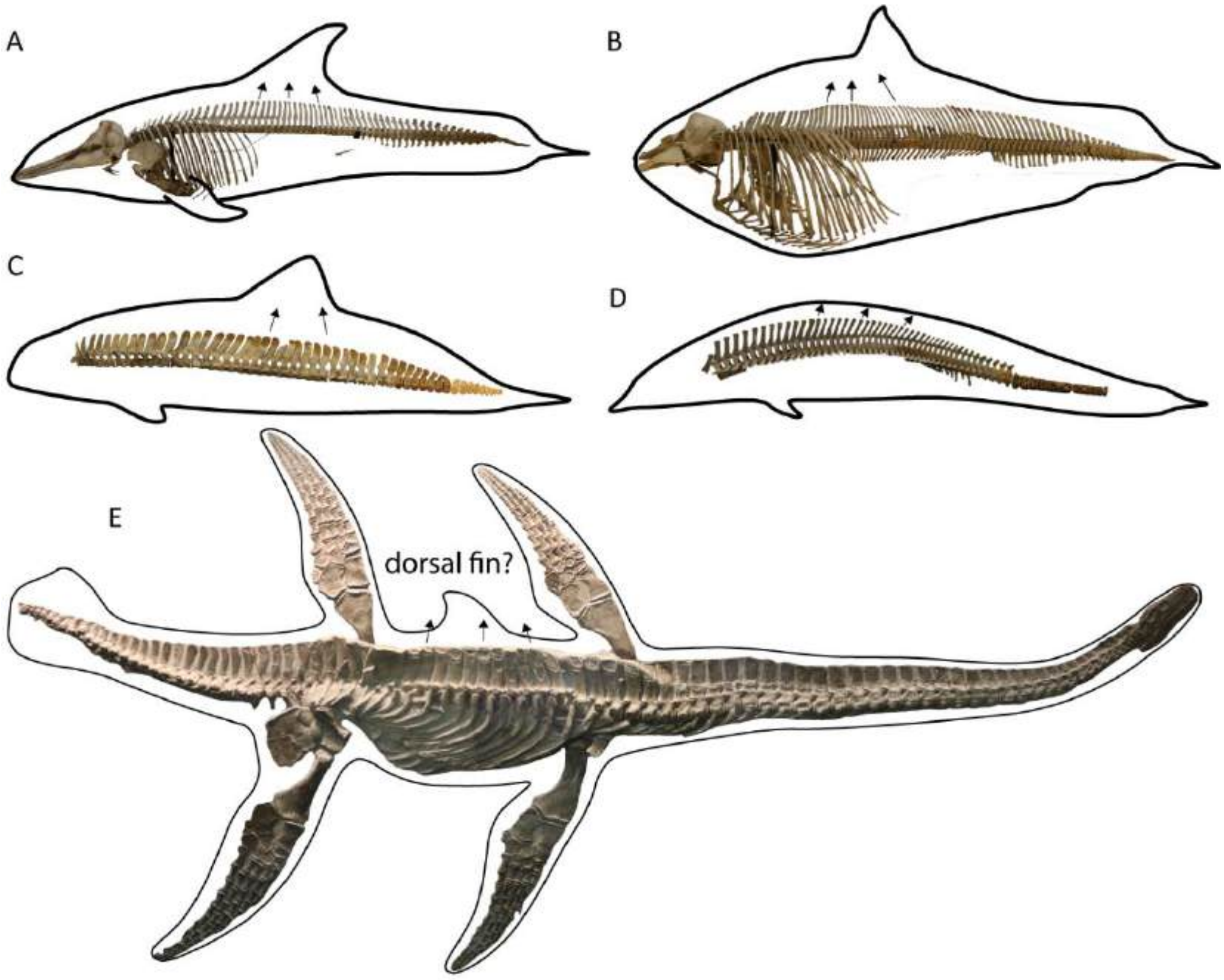

Figure 1. Skeletons of selected extant delphinoids and a microcleidid plesiosaurian from the Lower Jurassic Posidonienschiefer Formation of southern Germany. Silhouettes are drawn to visualise body shape, including the presence or absence of a dorsal fin. Arrows are drawn to indicate the orientation of the lumbar neural arches/spines in the delphinoids and dorsal neural arches in the plesiosaur. **A**. *Lagenorhynchops acutus*; **B**. *Phocoenoides dalli*; **C**. *Phocoena dioptrica*; **D**. *Lissodelphis borealis*; **E**. *Microcleidus brachypterygius* (MH 8). Note the presence of a dorsal fin in all delphinoids with an anterior redirection of the neural arches, while in the finless dolphin (D), these protuberances are uniformly inclined posteriorly.

A Maastrichtian sequence near Włoszczowa (southern Holy Cross Mountains, Poland) – preliminary data

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The Miechów Synclinorium in southern Poland is widely known for its richly fossiliferous Albian to Maastrichtian strata, but its northern part, the so-called Włoszczowa Trough (Fig. 1; see Pożaryski, 1966), is markedly understudied in comparison. During field work in recent years, several temporary outcroups exposing Campanian and Maastrichtian deposits have been sampled, mainly by one of us (DW). The biostratigraphically most important macrofossil taxa include inoceramid bivalves, ammonites and belemnites. Associated faunal elements comprise common sponges, predominantly hexactinellids, as well as nautilids, non-inoceramid bivalves, echinoids, gastropods, brachiopods and bryozoans. Trace fossils have also been recovered (Szymutko, 2019).

Figure 1. The Włoszczowa Trough highlighted on a map of Poland. Map by Qqerim under CC BY-SA 4.0; https://commons.wikimedia.org/wiki/File:342.14_Niecka_W%C5%82oszczowska.png

These finds enable a preliminary dating of the strata sampled and broad-based comments on palaeoenvironmental conditions at those localities. Our identification of early Maastrichtian-aged levels at some sites in the Włoszczowa area is supported by the occurrence of the ammonites *Pachydiscus* cf. *neubergicus* (von Hauer), *Acanthoscaphites tridens* (Kner) (Fig. 2A) and *Baculites knorrianus* (Desmarest), the bivalves *Trochoceramus* sp. (Fig. 2B) and “*Inoceramus*” aff. *redbirdensis*, the belemnite *Belemnitella pulchra* Schulz, and some other taxa typical of the Maastrichtian.

Figure 2. Stratigraphically important fossils from the Włoszczowa area. **Left.** *Acanthoscaphites tridens* (Kner) (microconch) from locality no. 2 (specimen UO-ZP-AS-5). **Right.** *Trochoceramus* sp. from locality no. 9 (specimen UO-ZP-AS-29). Scale bar in centimetres and millimetres.

In the Middle Vistula River valley, *Pachydiscus neubergicus* is represented by two subspecies according to Błaszkiewicz (1980): *P. neubergicus raricostatus* in the *Belemnella lanceolata lanceolata* Zone and *P. neubergicus neubergicus* in the *Belemnella occidentalis* Zone. The stratigraphical range of the former is not well established, and should be more conservatively ascribed to the *B. lanceolata lanceolata-B. occidentalis* zones (compare Machalski, 2012). The specimen from Włoszczowa eludes taxonomic assignment at the subspecies level on account of its rather poor preservation. Generally speaking, *Pachydiscus neubergicus* is a very important taxon for defining Campanian/Maastrichtian boundary globally, but it has a convoluted taxonomic history (K. Waindzoch, work under way). According to Machalski (2012), the species characterises the lowest ammonite zone of the Maastrichtian.

As far as inoceramids are concerned, only one definite representative and several possible relatives of “*Inoceramus*” *redbirdensis* were noted by Walaszczyk (2004) in the Middle Vistula River sections. These specimens mark the lower Maastrichtian

“*Inoceramus*”*redbirdensis* Zone, below the first occurrence (FO) of *Acanthoscaphites tridens* (sensu stricto) in the Lviv and Hrebenne areas (see below). In our collection, there are also several specimens of ‘trochoceramids’. Dating the first appearance of *Trochoceramus* in relation to the Campanian/Maastrichtian boundary is problematic, but specimens known from the Middle Vistula River localities all seem to be early Maastrichtian in age, with the FO of *Trochoceramus* approximating the boundary (for a discussion, reference is made to Walaszczyk *et al*., 1996).

In the Lviv area (western Ukraine), it seems that *Hoploscaphites quadrispinosus* was replaced anagenetically by *Acanthoscaphites tridens* (sensu stricto) in the lower Maastrichtian *Endocostea typica* Zone (Machalski & Malchyk, 2016). It follows that *A. tridens* sensu stricto from the Włoszczowa area would be no older than the *Belemnella occidentalis* Zone in belemnite terms. On the Polish side of the border (Hrebenne), *Acanthoscaphites tridens* sensu stricto and *Baculites knorrianus* commonly co-occur, both in the *Belemnella sumensis* Zone (Kin, 2010), strengthening the late early Maastrichtian age for the occurrences of the taxa mentioned in the Włoszczowa area. Of several belemnites in our collection, only one has been identifed at the specific level: *Belemnitella pulchra* is a typical (early) Maastrichtian form.

As fas as correlation with the extended type area of the Maastrichtian Stage (south-west Netherlands and north-east Belgium) is concerned, the following may be stated. *Acanthoscaphites tridens* is well known from the lower Vijlen Member (Gulpen Formation), and interval 4 in particular, with records from Altembroeck (Voer, Belgium) and the Aachen area in Germany (Jagt *et al*., 1999; Jagt & Jagt-Yazykova, 2019). *Baculites knorrianus* has also been demonstrated for the Vijlen Member, but both inoceramid taxa recorded from Włoszczowa are unknown. Other species, including ‘tegulated’ forms, are known (Walaszczyk *et al.*, 2010; Jagt *et al*., 2018).

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New perspectives on sea turtles from the Cretaceous to the Neogene

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"Sea turtles" are an assemblage of fossil and extant testudinates with uncertain interrelationships, including Protostegidae, Chelonioidea, Sandowniidae, Thalassochelydia and Bothremydidae. They document secondary transitions to the marine realm (e.g., Motani, 2009; Bardet *et al*., 2014; Motani & Vermeij, 2021) and include the last surviving fully marine amniote clade from the Cretaceous-Paleogene extinction (e.g., Hutchison & Archibald, 1986; Benson *et al*., 2010; Parham & Pyenson, 2010; Evers & Benson, 2019).

Fossil sea turtles have received little attention and their early morphological evolution is therefore poorly understood. Indeed, hundreds of fossils still await primary evaluation or secondary redescription, while the group as a whole is in need of taxonomic revision. We here present new work on fossil sea turtles targeting to improve our understanding of this fascinating group.

We first present the results of the redescription of *Nichollsemys baieri* from the Campanian of Alberta, Canada (Brinkman *et al*., 2006), based on a µ-CT scan of the holotype skull, which is notable for being preserved without crushing. Morphological analysis of this specimen documents similarities with *Toxochelys latiremis* while highlighting the early acquisition of derived characters in stem chelonioids.

We also present work in progress on the redescription of the holotype complete shell of the enigmatic, but nearly forgotten taxon *Glyptochelone suyckerbuykii* (Ubaghs, 1879) from the uppermost Maastrichtian of southern Limburg (Netherlands), as well as a smaller new species from the uppermost Campanian Chalk of Spiennes (southern Belgium; see de Lapparent de Broin *et al*., 2018, fig. 11.i). Both of these taxa from the second half of the Upper Cretaceous display a spectacular ornamental pattern, therefore we will also discuss here the diversification of ornamented chelonioids during this period. In order to shed new light on the alpha-taxonomy of fossil sea turtles, we also provide early results regarding our taxonomic revision of cryptodiran lineages of sea turtles (Protostegidae, Chelonioidea, Sandowniidae and Thalassochelydia), ranging from the Cretaceous to the Recent.

This work in progress is being done to target the establishment of an updated database on marine cryptodires, allowing macroevolutionary and diversity studies of these groups in the future.

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Eric Simon (1948-2018): his contributions to the knowledge of Campanian-Maastrichtian (Late Cretaceous) brachiopods

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Eric Simon was born in Grivegnée (province of Liège, Belgium) on December 23, 1948. He obtained his PhD degree in 1978 at the Free University of Brussels (Laboratory of Plant Ecology and Biogeochemistry), working on heavy metal (Pb, Zn, Cd) tolerance in plant populations. Until his retirement in 2013, he taught biochemistry and microbiology at higher education institutions. From 1989, he also worked as an associate researcher at the Palaeontology Department of the Royal Belgian Institute of Natural Sciences (Brussels). He gained expertise in Cretaceous and Recent brachiopods, and his contributions to the field are widely recognised. Eric's research interest focused on ontogeny, evolution, ecology and palaeoecology, morphological analyses and taxonomic problems. He was deeply concerned about improving the perception of biological characteristics in the field of palaeontology. Eric passed away suddenly at Wavre on February 11, 2018.

Eric reignited interest in the study of brachiopods from the Upper Cretaceous of the Mons Basin (southern Belgium) and the Liège-Maastricht-Aachen area (Belgium, the Netherlands and Germany). This field of research had previously experienced a decline since its pioneering work in the nineteenth century. Eric also contributed to the development of the study of micromorph species from chalk facies in these regions. When reading his numerous publications on Cretaceous and Recent brachiopods, the reader is captivated by the exhaustive descriptions and quality of photographic illustrations. Eric complained about the lack of descriptions and pictures in the literature, which is why he spent whole days at the SEM or in the photographic lab of the Royal Belgian Institute of Natural Sciences to document his material photographically as best he could. His paper dedicated to *Terebratulina chrysalis* (von Schlotheim) is exemplary, containing a complete illustration of all stages of growth of this emblematic Maastrichtian terebratulide brachiopod (Simon, 2011).

In 1990, he began to sample the Ciply-Malogne Phosphatic Chalk Formation methodically and published his first article on the early Maastrichtian brachiopod fauna of the Mons Basin (Van Damme quarry at Ciply, La Malogne underground quarry at Cuesmes) two years later, which was followed by a series of others on the Late Cretaceous brachiopods of the same basin (Simon, 1992, 1994, 1996, 1998b, 2000, 2004a; MacKinnon *et al*., 1998; Simon & Owen, 2001; Sklenář & Simon, 2009; Simon & Motchurova-Dekova, 2010). Meanwhile, Eric's interest focused on the brachiopods of the Cretaceous succession of the Liège-Maastricht area (Simon, 1993, 1995, 1998a), which were first mentioned by Faujas Saint-Fond (1798-1803; 1802-1804), and contributed to the study of those from Kazakhstan (Dhondt *et al*., 1996). He joined the so-called ‘Vijlen Groep’, a group of professional and amateur palaeontologists and geologists, who co-operated to advance understanding of the (bio)statigraphy of the different members of the upper Campanian to upper Maastrichtian Gulpen Formation (Keutgen & Jagt, 1998).

Figure 1. Eric Simon in the field sampling his beloved Upper Cretaceous (left) and new data extracted from micro-CT imaging (centre and right) of paratype IRSNB 10937 (Simon, 2004a, pl. 2, fig. 5), a large (87.7 mm in length), gerontic individual of the terebratulide *Cyranoia bosqueti* Simon, 2004a, from the upper Maastrichtian Saint-Symphorien Formation of Ciply (Mons Basin, Belgium) and screenshots of a 3D-surface mesh of the entire specimen, supplemented with those of a mesh of the brachidium which is fairly well preserved.

Since the early 2000s, up to the day he died, Eric largely directed his research efforts to the brachiopod faunas from the Gulpen and Maastricht formations (Simon, 2003, 2004a, b, 2005, 2007a,b, 2011; Jagt & Simon, 2004; Jagt et al., 2007; Sklenář & Simon, 2009; Simon & Mottequin, 2018), but also investigated Recent brachiopods, notably those from the Indonesian Archipelago (e.g., Simon & Hoffmann, 2013) and from a submarine cave of Mayotte (France), partial results of which were published posthumously (Simon et al., 2019). Eric's sudden death put an end to the study of Maastrichtian brachiopods from Belgium and the Netherlands, which was far from over.

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On the desirability to designate a lectotype for the Late Cretaceous turtle *Allopleuron hofmanni* (Gray, 1831) from the Maastrichtian type area

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"*Habent sua fata fossilia ...*"

Paraphrasing the classical Afro-Roman grammarian Terentianus Maurus (about AD 200), Rüschkamp (1925, p. 125) noted that at the end of the first quarter of the twentieth century still no extensive monograph had been published on the latest Cretaceous turtle *Allopleuron hofmanni* from the Maastrichtian type area, which is all the more remarkable because already in 1862, a fairly complete specimen had been found.

In 1913 this specimen (NHMM 000001)[1] was moved to the Natuurhistorisch Museum Maastricht (Mulder, 2003, and references therein). Nowadays there is consensus amongst vertebrate palaeontologists who engage in fossil turtle research, about what *Allopleuron hofmanni* in fact is (e.g., Mulder, 2003; Gentry *et al*., 2018). Nevertheless, Rüschkamp's paraphrase turns out to be even more appropriate than he could have imagined.
When Gray introduced the name *Chelonia Hofmanni* in 1831, he did not describe or define this fossil turtle, nor designate a type specimen. In his *Synopsis Reptilium* (p. 54) he devoted three lines to the subject, only referring to pages and figures or tables in the works of Faujas Saint-Fond (1798-1803) and Cuvier (1824). Gray's enumeration includes a reference to "Elk Horns", as described, pictured and erroneously interpreted by Faujas Saint-Fond (1799, pls xv, xvi). Cuvier (1824, pl. 14, fig. 3; see Fig. 1 here) understood that the sediment blocks with fragmentary bone material (the "Elk Horns"), pictured in plates xv and xvi by Faujas Saint Fond, as well as the block pictured in plate x, belonged together, because they actually fit. When combined, these blocks reveal several turtle bones, amongst them a fragmentary hyo- or hypoplastron. Contrary to the plastron referred to as *Allopleuron hofmanni* (Fig. 2), the fragmentary plastral element illustrated by Cuvier (1824, pl. 14, fig. 3; see Fig. 1 here) has a spade-like appearance with short and blunt "fingers". As such, it shows a much closer resemblance with the hyo- and hypoplastra of Late Cretaceous protostegid turtles (see e.g., Hay, 1908, figs 250, 262).

This shows that Gray's enumeration raises a nomenclatorial problem, because it means that technically, the name *Allopleuron hofmanni* would be applicable to two different species of extinct turtle.

Therefore, as matters stand, one could argue that *Allopleuron hofmanni* is a *nomen dubium*. However, in view of the unambiguousness of the fossil material generally considered to be assignable to *Allopleuron hofmanni*, and naturally because of the lack of a type specimen, it is proposed here to designate lectotype specimen IRScNB 3901 (Mulder, 2003, pl. 52). This individual comprises a fragmentary skull and a near-complete postcranium, except for the peripherals. It is the only specimen that has made a reconstruction of the complete *Allopleuron* plastron possible (Mulder, 2003, pl. 34; see Fig. 2 here). I also wish to designate a paralectotype, namely specimen NHMM 009017. This is a slightly distorted, but complete skull, with the associated lower jaw, enabling a reconstruction of the dermatocranial elements (Mulder, 2003, pls 8, 9, 12, 13, 17 and 18).

Note

[1] Abbreviations of repositories: IRScNB – Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; MNHNP – Muséum National d'Histoire Naturelle, Paris, France; NHMM – Natuurhistorisch Museum Maastricht, Maastricht, the Netherlands.

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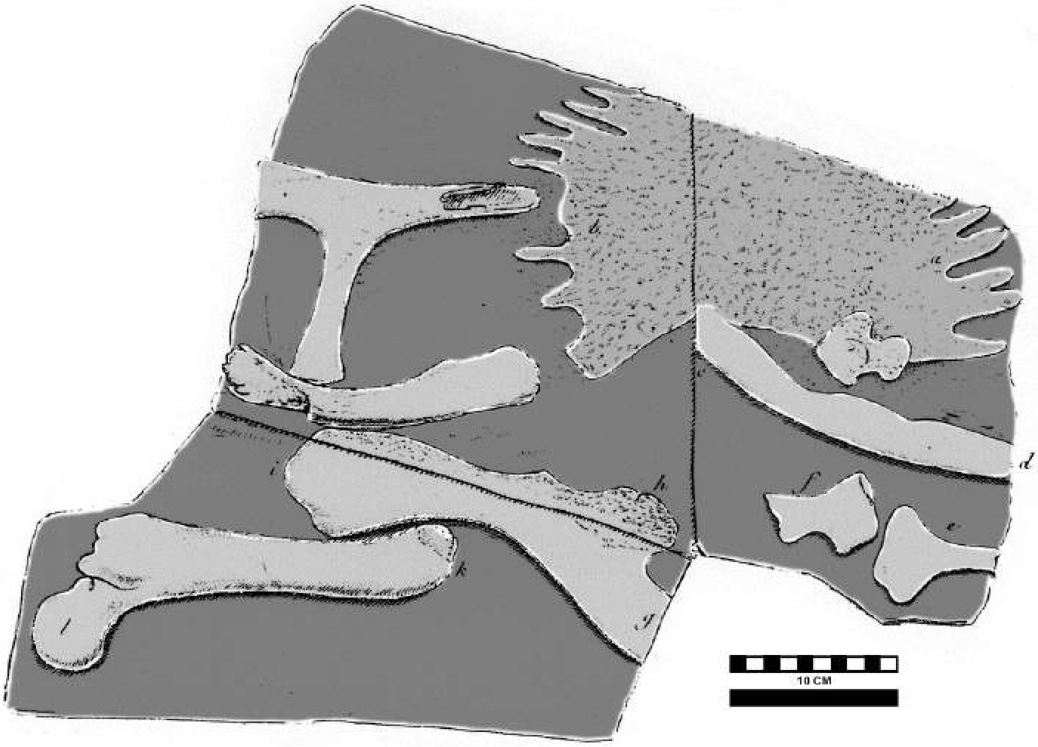

Figure 1. Three connecting sediment blocks with turtle bones comprising plastral, pectoral, peripheral and limb fragments; Maastricht Formation (Nekum Member inferred), upper Maastrichtian, Sint-Pietersberg area, Maastricht (MNHNP collections). Over time, the humerus apparently became lost (modified from Cuvier, 1824, pl. 14, fig. 3). The plastral fragment is indicated by the letters 'a' and 'b', the lost humerus by the letters 'g', 'h' and 'j'.

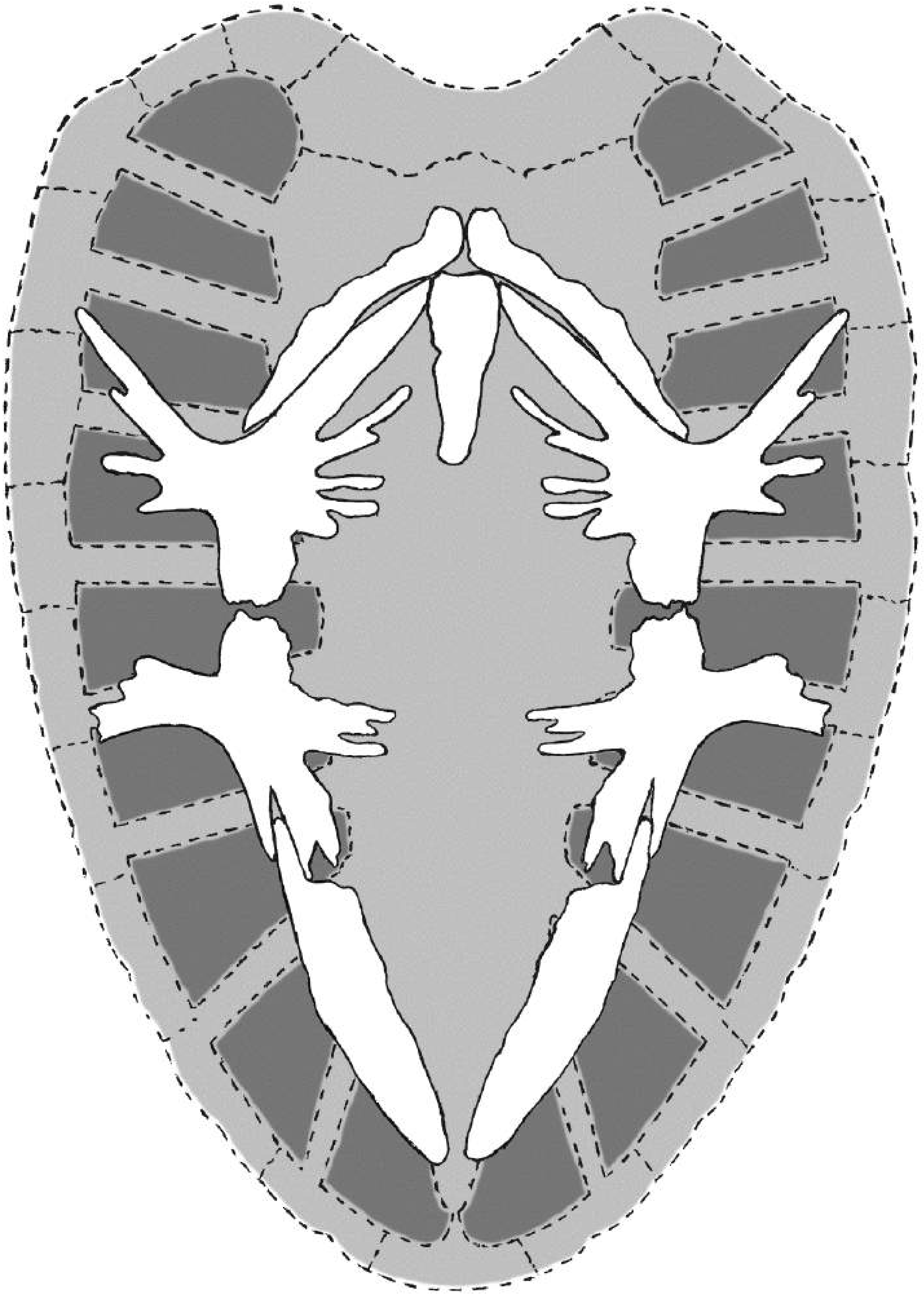

Fig. 2. Reconstruction of the plastron of *Allopleuron hofmanni* in anatomical position relative to the carapace in ventral view. Dotted lines indicate carapace outline, interperipheral sutures and intercostal fenestrae (adapted from Mulder, 2003, pl. 34). Carapace length approximately 150 cm.

The Bulgarian fossil record of Mosasauridae

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Mosasaurids (mosasaurs) are an iconic clade of diverse, faunivorous marine squamates, which existed during the last 32 million years of the Cretaceous. Herein, I briefly review the Bulgarian record of these fascinating animals, focusing on taxonomic content, fossil-bearing formations and localities and scientific collections which hold relevant material.

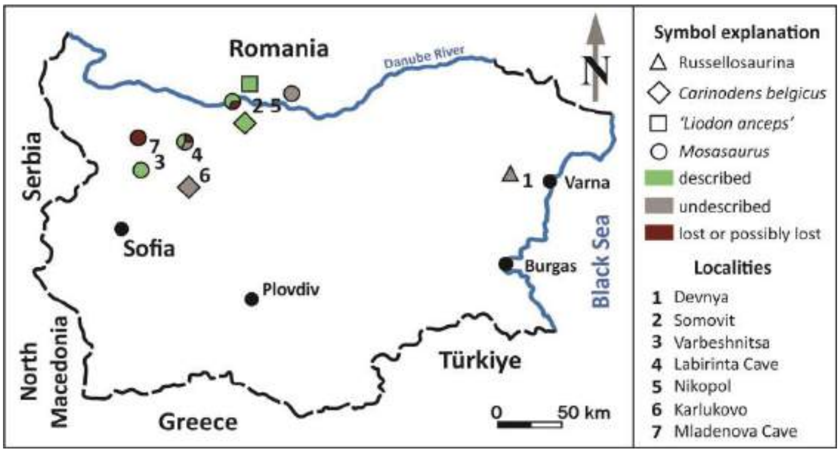

Figure 1. A list of confirmed mosasaur-bearing localities from Bulgaria.

On the basis of published data and personal communication with professionals and amateurs involved with unpublished specimens, a list of seven confirmed localities yielding mosasaur remains has been compiled (Fig. 1). The fossil-bearing rocks belong to two shallow-marine units: the upper Turonian-lower Santonian Dobrin Dol (= Dobrinski dol) Formation (Yolkichev, 1988) and the upper Maastrichtian Kaylaka (= Kajlâka) Formation (Yolkichev, 1986). Except for an isolated tooth from a condensed phosphate bed of Turonian age near the town of Devnya (D. Dimitrov, pers. comm.), all mosasaur material stems from the upper Maastrichtian limestones of the Kaylaka Formation. In the 1970s, Nikolay Spassov recognised two mosasaur teeth in a lot of *Ursus spelaeus* material collected from Mladenova Cave, but these appear to be lost (N. Spassov, pers. comm.; see below). Because the original notes on these specimens are preserved (pers. obs.), the existence of fossils and the validity of Mladenova Cave as a fossil locality are herein accepted. The presence of mosasaur fossils in the Kaylaka Formation limestones near the villages of Kreta, Riben and Komarevo and the Kaylaka locality near the city of Pleven mentioned by Ivanov (2008) and Boev (2017) could not be confirmed.

At least four mosasaurid taxa are present in Bulgaria (Fig. 2). The genus *Mosasaurus* is best represented with numerous teeth, a jaw fragment and a partial skeleton (Tzankov, 1939; Nikolov & Westphal, 1976; Jagt *et al.*, 2006). At least some of these probably belong to *M. hoffmannii* (Jagt *et al.*, 2006). Tzankov (1939) assigned two teeth from Somovit to the dubious taxon *'Liodon anceps'* (Schulp *et al.*, 2008). These clearly differ from *Mosasaurus* teeth and warrant taxonomic revision (Fig. 2b, c). Until recently, the relatively rare durophagous species *Carinodens belgicus* was known from a single tooth crown (Fig. 2a) (Tzankov, 1939). Another crown attributable to this species, which was found in 2020 by the collector Georgi Hristov in the area of Karlukovo, resides in the private collection of Dimitar Dimitrov (Fig. 2o). In the same private collection sits an isolated mosasaur tooth of late Turonian age from the area of Devnya (Fig. 2p; D. Dimitrov, pers. comm.). Its age makes it of particular interest; hence a short description is provided here. The specimen is a marginal tooth with an apicobasal height of ~18.5 mm. The crown is conical, slightly compressed labiolingually, with a more convex lingual side, and an oval cross-section basally. The lingual side bears more distinctive striae. The tooth is bicarinate, with both carinae being unserrated and weakly developed in general. Morphologically, on the basis of published descriptions, the specimen appears to be similar to the teeth of yaguarasaurins and to *Romeosaurus sorbini* in particular (Palci *et al.*, 2013; Street & Caldwell, 2014; Sachs *et al.*, 2018). Pending deposition in public collection and proper description, this tooth might be the first record of the Russellosaurina from Bulgaria.

The Museum of Paleontology and Historical Geology at Sofia University (MPHG) holds the material described by Tzankov (1939), as well as the partial skeleton from Varbeshnitsa (Nikolov & Westphal, 1976), while the National Museum of Natural History at the Bulgarian Academy of Sciences (NMNHS) keeps the three teeth described by Nikolov & Westphal (1976), along with the material from Labirinta Cave (Jagt *et al.*, 2006) and some undescribed specimens, including a tooth found in the area of Nikopol (NMNHS F31533 – see Fig. 2m; N. Spassov, pers. comm.).

The two collections are curated well; however, some problems with the material may be noted. First, although they were described in 1939, Tzankov's specimens were given MPHG catalogue numbers only in 2023 for the purposes of the present study and are presented here for the first time (see Fig. 2). Additionally, the partial skeleton from Varbeshnitsa has been left unprotected for decades and without any designation within the exhibit of MPHG, and has been damaged - the second anteriormost vertebra is now missing, probably broken or stolen, and the four posteriormost centra are partially broken (Fig. 2j). Regarding the NMNHS collection, two specimens from Labirinta Cave (NMNHS F31525 and F21526), catalogued as '*Mosasaurus* tooth fragments', were supposedly loaned for research in November 2008. A check up with the colleague who is thought to have worked on them revealed that this is not actually the case (J.W.M. Jagt, pers. comm., 2024), and currently it is not known what happened to these specimens. Additionally, specimen NMNHS F30056, a partial *Mosasaurus* tooth crown, which is catalogued as one of the two teeth from Mladenova Cave, has turned out to be part of the Varbeshnitsa's specimen NMNHS 452/1 (Fig. 2h), which for some reason was not described or illustrated by Nikolov & Westphal (1976). Both the reason behind this confusion and the current whereabouts of the Mladenova Cave's teeth are unknown.

In January 1998, a tooth crown identified as *Mosasaurus* sp. was catalogued in the collections of the Regional History Museum-Pleven (RHMP), Bulgaria, under specimen number RHMP 1226 (Fig. 2n; Grancharov *et al.*, 1999), only to disappear shortly thereafter (Rumyanka Baleva, pers. comm.). In addition to the above-mentioned specimens in D.

Dimitrov's private collection, anecdotal data suggest that several other mosasaur specimens from the uppermost Cretaceous of the country reside in private collections. However, professional palaeontologists have no clue as to their current whereabouts, nature and geographical and stratigraphical provenance.

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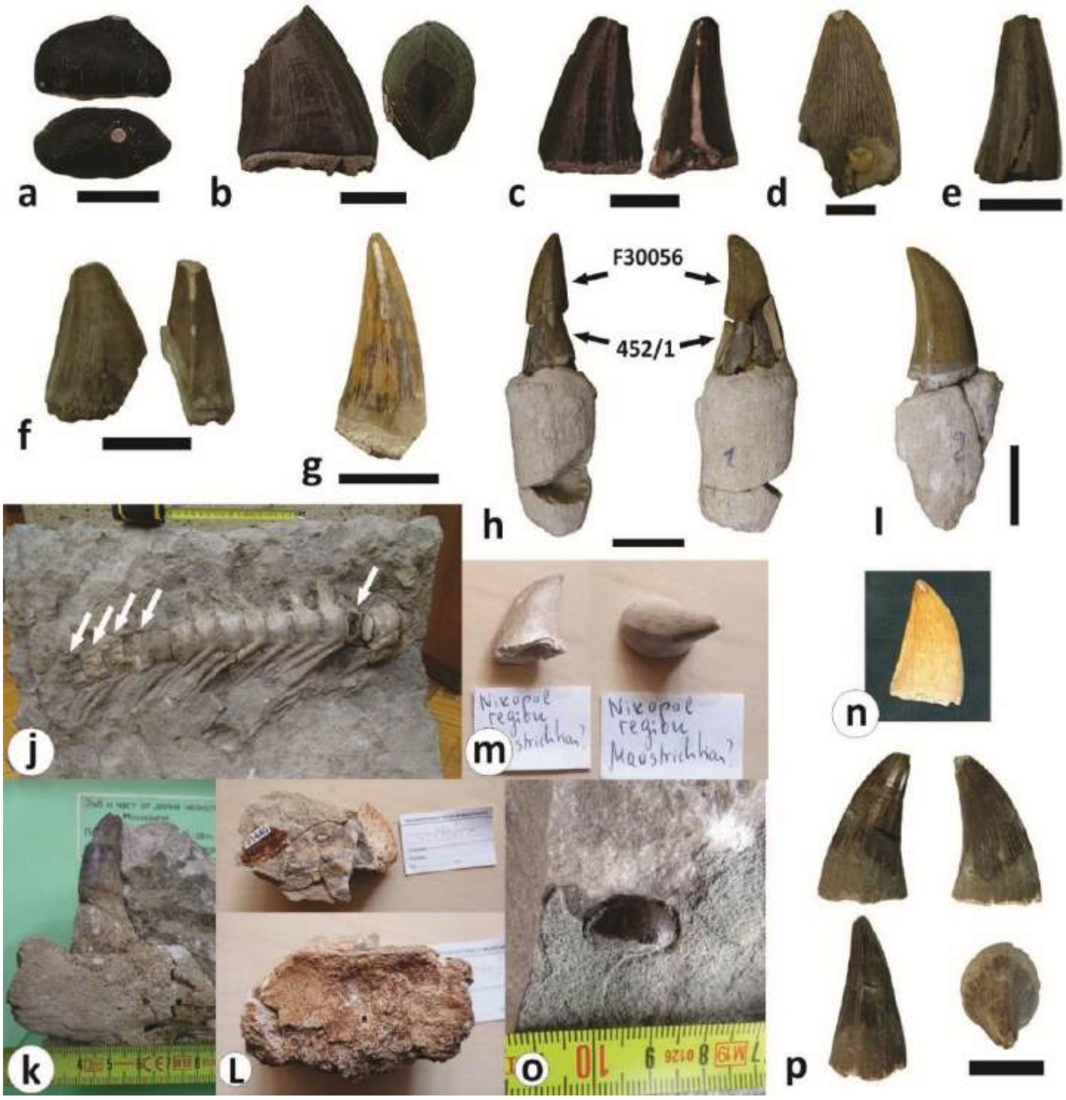

Figure 2. Mosasaur fossil material found in Bulgaria. a – *Carinodens belgicus*: U.S. $K_2$1808; b, c – *'Liodon anceps'*: U.S. $K_2$1809 and U.S. $K_2$1810; d-j – *Mosasaurus*: U.S. $K_2$1811, U.S. $K_2$1812, U.S. $K_2$1813, NMNHS 451, NMNHS 452/1 (with NMNHS F30056, catalogued as coming from Mladenova Cave), NMNHS 452/2, and U.S. $K_2$1814 (arrows indicating damaged areas); k – *Mosasaurus* cf. *hoffmannii*: NMNHS F11897-1; l, m – ?*Mosasaurus*: NMNHS F31440, NMNHS F31533 and RHMP 1226 (photo from Grancharov *et al.*, 1999; used with permission); o – *Carinodens belgicus*; p – ?Russellosaurina. Scale bars equal 10 mm (a-f, p) and 30 mm (g-i).

Dinoflagellate cyst biostratigraphy of the upper Campanian-lower Maastrichtian interval in the Oslen Krivodol reference section, north-west Bulgaria

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Recent studies of dinoflagellate cyst successions from the upper Campanian and lower Maastrichtian in the Oslen Krivodol reference section (north-west Bulgaria) have enabled the establishment of a new biostratigraphical dinocyst zonation of this interval in this part of the country. The rich and continuous dinoflagellate cyst assemblages include several biostratigraphically critical taxa with high correlation potential for the Campanian - Maastrichtian boundary (CMB) interval. Their ranges correspond well to those documented in other Tethyan successions, including the GSSP section at Tercis les Bains (France) for the base of the Maastrichtian Stage. Apart from dinocyst bioevents previously recognised as significant for the CMB (i.e., the last occurrences [LO] of *Corradinisphaeridium horridum, Raetiaedinium truncigerum, R. evittigratia, Samlandia mayi* and *S. carnarvonensis*), the importance of some other events, such as the last occurrences of *Odontochitina costata, O. porifera, Corradinisphaeridium horridum, Achomosphaera fenestra*, and the first occurrences (FO)of *Cerodinium diebelii* and *Microdinium carpentierae* is pointed out.

The recently described Oslen Krivodol section is situated in the western Fore-Balkan area, a part of the Central Balkan-Fore-Balkan Zone in the northern segment of the Balkan Orogen in Bulgaria. The upper Campanian-Maastrichtian succession starts with green to greenish glauconitic limestones to calcareous sandstones of the Darmantsi Formation. The succeeding Kunino Formation is represented by thin- to medium-bedded limestones, clayey and nodular limestones, overlain by nodular limestones, typically rich in flint nodules of the Mezdra Formation (Dochev *et al*., 2023). In our ongoing research, these sedimentary rocks were studied for dinoflagellate cysts, calcareous nannofossils and inoceramid bivalves, and belemnite rostra were used for strontium isotope stratigraphy. The nannofossil bioevent for the base of the Maastrichtian, the LO of *Uniplanarius trifidus*, was documented at 3.25 m in the Oslen-Krivodol reference section (Fig. 1). Strontium isotope stratigraphy indicated the CMB at a value of 0.707728 ±0.000004, at 3.15 m above the base of the section (Wagreich *et al*., 2023). Inoceramid data were used to characterise the lower Maastrichtian part of the succession (Dochev *et al*., 2023).

The dinoflagellate cyst record, based on a calibrated and dense sample set, shows a comparatively distinctive taxonomic turnover around the Campanian-Maastrichtian boundary interval in the section, with last occurrences of typical Campanian taxa and their replacement by Maastrichtian forms. The framework of the dinocyst zonal scheme is based on these key dinocyst events and the stratigraphical ranges of selected taxa with high correlation potential for Campanian -Maastrichtian stratigraphy and the boundary interval. The dinocyst scheme comprises the zones of *Areoligera coronata* and *Cerodinium diebelii,* in ascending order, and illustrates the sharp transition between the Campanian and Maastrichtian assemblages.

***Areoligera coronata* Zone.** The base of this zone is marked by the FO of *Areoligera coronata* as defined originally by Kirsch (1991). This species is regularly present and common within the zone. The characteristic zonal association includes *Odontochitina costata, O. porifera, O. operculata, Corradinisphaeridium horridum, Achomosphaera fenestra, A. ramulifera, Chatangiella ditissima, C. tripartita, Raetiaedinium truncigerum, Cannosphaeropsis utinensis, Oligosphaeridium complex, Cassiculosphaeridia reticulata, Samlandia mayi, Dinogymnium acuminatum* and *D. denticulatum*. The characteristic species *Odontochitina costata, O. porifera, O. operculata, Corradinisphaeridium horridum, Achomosphaera fenestra* and *Palaeohystrichophora infusorioides* have their last occurrence (LO) within the zone. *Chatangiella ditissima, C. tripartita* and *Coronifera oceanica* also have their last common occurrence close to the upper boundary of the zone. The zone spans the interval from the base up to 3.10 m (OS-10) in the section and marks the upper Campanian according to correlations with the dinocyst zones of Kirsch (1991), Roncaglia & Corradini (1997) and Schiøler & Wilson (2001).

***Cerodinium diebelii* Zone.** The FO of *Cerodinium diebelii* defines the base of this zone at 3.10 m in the section. The characteristic zonal association includes *Cerodinium diebelii, C. speciosum, Alterbidinium acutulum, Hystrichodinium pulcherrimum, Microdinium carpentierae, Isabelidinium cooksoniae, I. korojonense, Cannosphaeropsis utinensis, Glaphyrocysta expansa, Florentinia maye* and *Areoligera medussetiformis.* The species *Samlandia mayi* and *Raetiaedinium truncigerum* have their last occurrences in the lower part of the zone. The zone spans the interval from 3.10 m to the topmost sample in the Oslen- Krivodol section (OS-10 to OS-17) and marks the lower Maastrichtian according to correlations with the dinocyst zones of Kirsch (1991), Roncaglia & Corradini (1997) and Schiøler & Wilson (2001).

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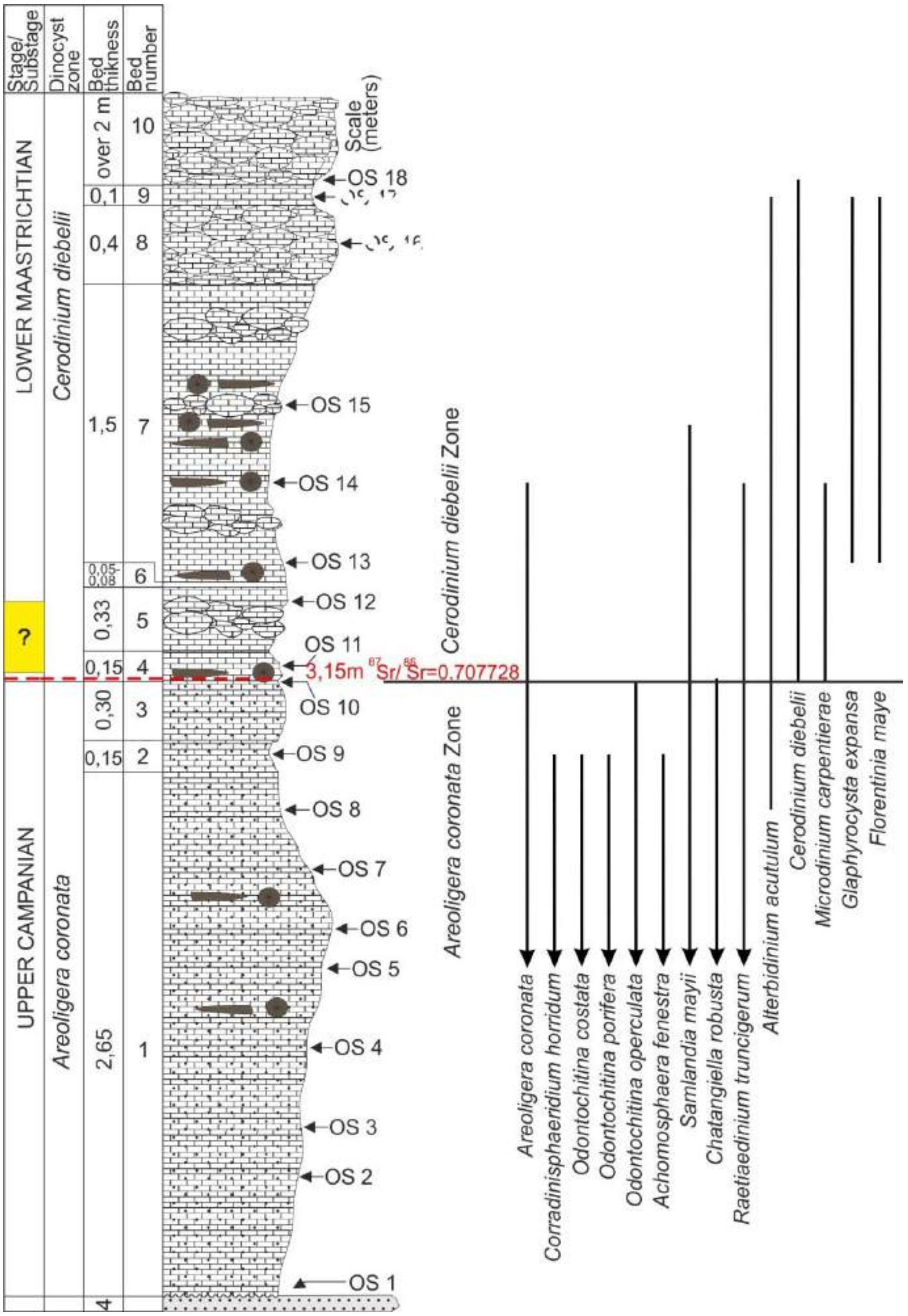

Figure 1. Dinoflagellate cyst zones and ranges in the Oslen Krivodol reference section.

Putting an ocean where one had not previously existed: an update on the marine amniote record of Angola

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Tectonic rifting of Africa from South America began by 131 Ma, resulting in an attenuated Gondwana stretched between the two nascent continents and containing fluvial and lacustrine sedimentary environments. The protracted, but connected, rifting of Africa and South America allowed communication of flood plain and terrestrial biota, including fishes, crocodylians and piscivorous dinosaurs between what is now Africa and South America during the Early Cretaceous. Marine flooding and more open ocean conditions were initiated in the central South Atlantic by the late Aptian (~113 Ma), interrupting the terrestrial biome. With the opening of the Equatorial Atlantic Gateway by ~90 Ma (Turonian), intermediate and bottom water flowed north to cool global oceans (Jacobs *et al.*, 2024). It was within these later stages that the first marine reptile fauna appears, preserved at the locality of Iembe, Angola. This locality has produced the oldest examples of mosasaurs, elasmosaurid plesiosaurs and sea turtles from the central South Atlantic (Mateus *et al.*, 2019). Long considered early Turonian (~90 Ma) in age, new biostratigraphical dating for the fossil-bearing horizon, suggests it is no older than middle Coniacian (~87 Ma).

The mosasaurs from Iembe are most closely related to contemporaneous North American forms. A new phylogenetic analysis, based on an expanded character-taxon matrix, recovers *Angolasaurus* as the sister taxon of all other selmasaurin plioplatecarpines, which are rare and only known from North America prior to the Campanian (~84 Ma). A new specimen of *Tylosaurus iembeensis* is recovered as the sister taxon to all other species of *Tylosaurus*, retaining plesiomorphic characters not seen in North American forms. The eucryptodiran sister taxon of *Angolachelys* is from the Aptian (~122 Ma) of the western Eurasian plate (Mateus *et al.*, 2009), while the elasmosaurid plesiosaurs are of unknown affinities (Marx *et al.*, in press). The Santonian and lower Campanian record in Angola is sparse, but a single locality near Sumbe has produced some associated large tylosaurine vertebrae, and a polycotylid plesiosaur femur.

There is a rich upper Campanian and Maastrichtian record of marine amniotes, best documented from the locality of Bentiaba, which includes the lower Maastrichtian (~72 Ma) Bench 19 Bonebed, and mid- to late Maastrichtian (~70-66 Ma) fossils higher in the section. This area has produced at least nine mosasaur, four sea turtle and two plesiosaur taxa, the majority of which are known from the lower part of the section, from the Bench 19 Bonebed. Recent reports on Bentiaba fossils include a description of the cranial anatomy of

Cariocorax mukulu by Marx *et al.* (2021) in which multiple character-taxon matrices were used, recovering an early-branching or intermediate position of *Cardiocorax* within the Elasmosauridae. Most recently reported from Bench 19 at Bentiaba is a small plotosaurin mosasaurine, *Bentiabasaurus jacobsi* (Polcyn *et al*., 2023), the holotype of which was recovered from the stomach contents of an individual of *Prognathodon kianda*. The new phylogenetic analysis recovered *Bentiabsaurus* along with *Jormungandr walhallaensis* (see Zietlow *et al*., 2023) as basal branching plotosaurins. Here we report on new data on *Prognathodon kianda, Gavialimimus* sp. and a new unnamed halisaurine from the locality, which helps resolve phylogenetic relationships within their respective clades.

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Glimpses into the early evolution of mosasaurs

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Our understanding of the first ten million years of mosasaur evolution is based on a very small number of specimens, most of which are fragmentary, or preserved in such a way that makes detailed assessments of their anatomy and relationships difficult. For decades, the prevailing view of mosasaur evolution was a simple path of acquired marine adaptations leading from a terrestrial varanoid ancestor to derived mosasaurs, through facultatively amphibious "aigialosaurs" and primitive marine forms such as halisaurines, as intermediates (e.g., DeBraga & Carroll, 1993). This model was challenged by the discovery in the lower middle Turonian (~93 Ma) of Texas of the basal branching mosasaurine, *Dallasaurus* (Bell & Polcyn, 2005), showing that convergent acquisition of marine adaptations in the limbs of mosasaurs occurred independently in more than one major (e.g., subfamily-level) clade. The co-occurrence of *Russellosaurus* (Polcyn & Bell, 2005), a taxon now considered to be a basal branching plioplatecarpine (Polcyn *et al*., 2023) with *Dallasaurus*, in the same area and from the same horizons, demonstrated the early divergence of those subfamilies. The discovery of *Sarabosaurus* (Polcyn *et al*., 2023) from the lower Turonian Tropic Shale of Utah, and reassessment of the relationships of *Tethysaurus* (Bardet *et al*., 2003), have pushed the origin of plioplatecarpines to the lower Turonian or earlier, implying deep branching for the other subfamilies as well. Nonetheless, for most pre-Coniacian taxa, details of limb structure and various aspects of cranial anatomy have been elusive, confounding our understanding of their phylogenetic relationships and timing of the acquisition of secondarily derived marine adaptations.

In this contribution, I report two new mosasaur specimens from the lower middle Turonian of Texas (~93 Ma). Although preparation is still underway, a preliminary assessment of their relationships can be made. One specimen is a basal branching russellosaurian and possibly more closely related to tylosaurines than to plioplatecarpines (*sensu* Polcyn *et al*., 2023). Although incomplete and disarticulated, it preserves much of the skull, some vertebrae and ribs. The skull exhibits a unique combination of characters including a narrow, elongate frontal, a prominent premaxillary rostrum and corresponding edentulous anterior dentaries. The quadrate alar rim is thick anterodorsally but narrows anteroventrally, the posteroventral ascending rim is present but not well developed, and the so-called infrastapedial process is present but not large, the suprastapedial process has parallel sides and the distal terminus narrows and is slightly medially directed. The second specimen is a taxon allied with *Russellosaurus*, and is mostly articulated and much of the skeleton is present, including well-preserved limbs, girdles (bone and cartilaginous structures) and the tail (both as bone and impressions). It is only slightly larger than the holotype of *Russellosaurus coheni*, but exhibits differences in the skull roof that suggest it may be a new species. The propodial and epipodial elements are relatively elongate with simple flat articulations, the mesopodial elements flat and phalangeal joints are simple, indicating the forelimb was modified as a flipper. The tail is slightly longer than the snout-vent length and has no apparent downturn. Together, these specimens demonstrate additional taxonomic diversity in North American Turonian mosasaurs and will increase our understanding of the anatomy, relationships and evolutionary patterns of russellosaurian mosasaurs.

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A review of Maastrichtian sea cucumbers (Echinodermata, Holothuroidea)

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Since the last celebratory conference, dedicated to the 150th anniversary of the Maastrichtian Stage and organised by the Natuurhistorisch Museum Maastricht in 1999, some progress has been made in the study of Maastrichtian holothurians. In his cumulative dissertation, Reich (2002a) also summarised the state of knowledge on sea cucumbers from the Maastrichtian. Some systematic chapters, based on material from northern Germany, Jasmund/Rügen and the south-central Baltic Sea region, were published at the same time (Reich, 2002b, 2003a-d) or could only be finalised in later years (Reich, 2012). The occurrence of Maastrichtian-aged sea cucumbers was also referred to in several conference talks or short papers (e.g., Reich, 2001a, b, 2017; Reich & Jagt, 2001). And finally, all sea cucumber taxa that were originally described from Maastrichtian sedimentary rocks were listed in overviews by Reich (2013, 2014, 2015).

Otherwise, progress with regard to "Maastrichtian Holothuroidea" can only be assessed as moderate or modest due to a lack of interested scientists and corresponding work.

About 40 sea cucumber species, based on distinctive ossicles and calcareous ring elements, are known from Maastrichtian deposits. The taxa identified to date can be assigned systematically to almost all known major groups of the Paractinopoda (footless sea cucumbers) and Actinopoda (foot-bearing sea cucumbers). In fact, ten taxa belong to the Apodida, three to the Elasipodida, seven to the Holothuriida/Synallactida, nine to the Molpadida and nine to the Dendrochirotida.

These taxa had different body sizes/lengths (i.e., small to medium-sized, with vermiform or cylindrical bodies), life forms, life habits and feeding modes (vagile infaunal, semi-infaunal, epibenthic, nektobenthic deposit or suspension feeders on soft bottoms, secondary hardgrounds). Body fossils, although potentially preservable with the common "flint" fossil deposits, are missing so far. The echinoderm group of the Holothuroidea should also be able to be indirectly identified by trace fossils or special fish otoliths (Carapidae, pearlfishes that have been shown to live symbiotically or parasitically inside various invertebrate hosts, including sea cucumbers).

To summarise the known distribution palaeogeographically, most of the Maastrichtian holothurian reports to date are restricted to Europe (Germany, Denmark, the Netherlands, Belgium, France) with only a few faunas investigated and published so far. Previously unpublished evidence by the author refers to Maastrichtian material from England (Norfolk), Belarus (borehole near Minsk) and the Crimean Peninsula/Black Sea. In addition, there is still a considerable need for additional research, as some colleagues already noted (e.g., Jagt *et al.,* 2018).

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Mosasaur remains from the Puskwaskau Formation (Santonian-lower middle Campanian) of Alberta, Canada

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Due to limited collecting efforts, mosasaurid remains from high palaeolatitude localities are relatively uncommon compared to material from coeval deposits further south. However, a growing number of studies have produced mosasaurid remains from high palaeolatitudes in both the northern and southern hemisphere (Ryabinin, 1937; Russell, 1967; Rinaldi *et al.,* 1978; Olivero *et al.,* 1986; Gasparini & del Valle, 1981, 1984; Martin, 2006; Martin *et al.,* 1999a, b, 2002; Novas *et al.*, 2002; Martin & Fernández, 2007; Konishi, 2012; Reguero *et al.,* 2015; Otero *et al.,* 2017; Grigoriev & Grabovskiy, 2020; O'Gorman *et al.,* 2023).

The Puskwaskau Formation is comprised of a series of marine strata laid down during the Santonian to mid-Campanian in the northern Western Interior Seaway (WIS) of North America (Wall, 1960). During the approximately 35-myr existence of the WIS, it underwent several transgression-regression cycles resulting in major variations in latitudinal extension, width and depth. The Puskwaskau Formation represents the last time period in which the WIS remained open to the Boreal Sea (Hu & Plint, 2009). Situated approximately 55 km north of Grande Prairie, Alberta (Canada), exposures of the Puskwaskau Formation are among the northernmost mosasaur-bearing fossil localities. This site had a palaeolatitude of 62°N during the Late Cretaceous (Van Hinsbergen *et al.*, 2015). Mosasaur remains from the Puskwasaku Formation predominantly consist of fragmentary skeletal elements and teeth (Bell *et al.,* 2014; Garvey, 2020). Here, new material is described and previously noted material is reviewed. *Institutional Abbreviations*: **PJCDM** – Philip J. Currie Dinosaur Museum, Wembley, Alberta, Canada; **TMP** – Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada.

Geographical and stratigraphical setting. The Puskwaskau Formation is composed of muddy sediments laid down in a shallow-marine (<50 m) setting of the northern Western Interior Sea (Wall, 1960). It is composed of five lithostratigraphical members, from oldest to youngest: Dowling (lower Santonian), Thistle (middle-upper Santonian), Hanson (upper Santonian–lower Campanian), Chungo (lower-middle Campanian) and Nomad (middle Campanian) (Stott, 1963, 1967). Other than the sandy Chungo Member, these units are dominated by mudstones and siltstones (Hu & Plint, 2009). The Puskwaskau Formation is stratigraphically correlated with the upper Wapiabi Formation in southern Alberta and the Niobrara Formation in the United States (Hu & Plint, 2009).

Fossils are found in loose concretions along the banks and streambeds of the Smoky River and its surrounding tributaries. The out-of-context nature of the specimens precludes knowledge of precise origin; however, local stratigraphy and associated matrix composition allows for tentative predictions.

PJCDM.2023.4. An isolated plioplatecarpine tooth, bearing a pointed apex, two carinae (crenulations absent), striated enamel, slight posterior and strong medial curvature and a subcircular basal cross-section.

TMP. 1978.011.1269. An intermediate caudal centrum of an indeterminate russellosaurine mosasaur, weakly procoelous and possessing the abraded bases of the neural arch, haemapophyses and transverse processes. Bell *et al.* (2014) referred this specimen to Russellosaurina based on the presence of articular facets on the haemapophyses.

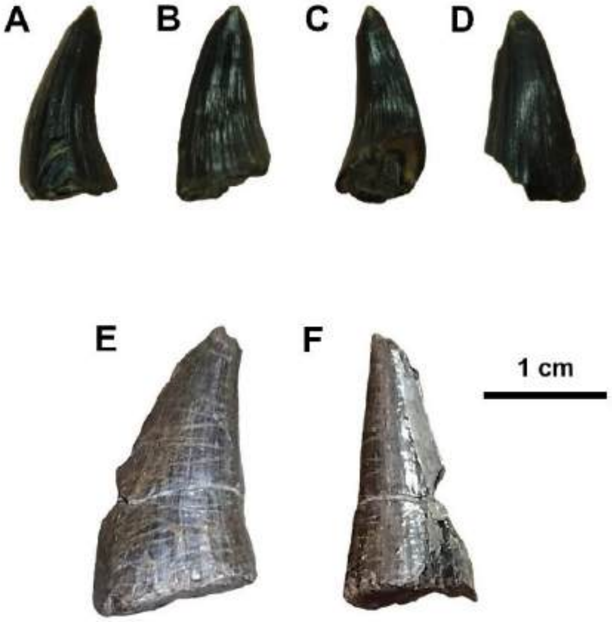

Figure 1. Isolated mosasaurid tooth crowns from the Puskwaskau Formation.. Plioplatecarpine marginal tooth (PJCDM.2023.4) in **A**, anterior view; **B**, lingual view; **C**, posterior view; **D**. labial view. Tylosaurine marginal tooth (TMP 1973.001.2796) in **E**, lingual view; **F**, posterior view.

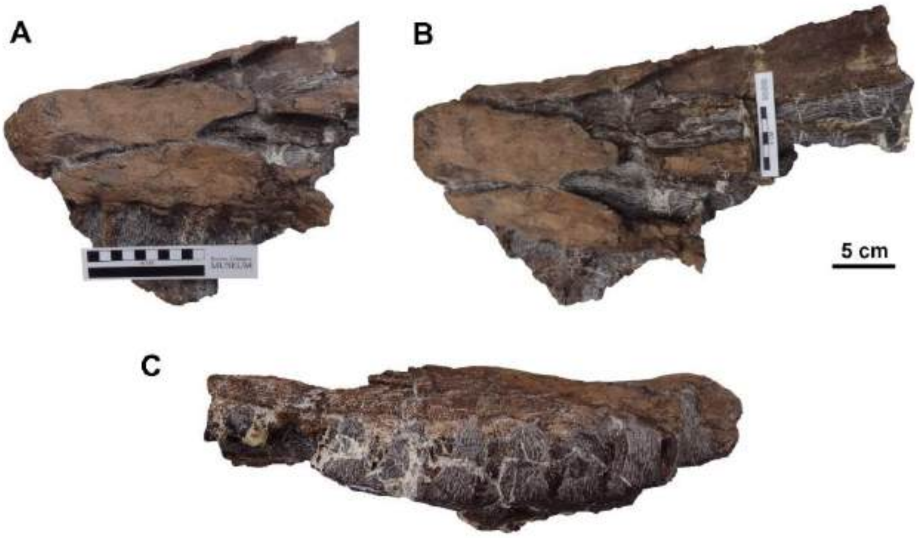

Figure 2. TMP2014.0011.0001, a semi-articulated *Tylosaurus* muzzle in **A**, left lateral view; **B**, dorsal view; **C**, right lateral view.

TMP 1973.001.2796. An isolated tylosaurine tooth crown collected from Bad Heart Creek, preserved on matrix with its lingual and posterior surfaces exposed. The tooth is robust and characterised by an exposed anterior carina (posterior carina hidden in matrix), finely striated enamel, posterior curvature and a subcircular basal cross-section. This tooth was previously identified as plioplatecarpinae indet. by Bell *et al.* (2014) based on purported symmetrical features and the historic precedent that only plioplatecarpines were found at northerly latitudes within North America.

TMP 2014.0011.0001. A tylosaurine anterior muzzle unit from Kakut Creek, consisting of a premaxilla, anterior maxillae, vomers, right septomaxilla, dentary, splenial and marginal teeth. Significant plastic deformation has resulted in numerous fissures in the cortical surface and exposures of cancellous bone. This specimen was informally named *Tylosaurus “borealis”* based on the high aspect ratio of the maxillary tooth crown bases and the presence of downward extensions of maxillary cortical bone over the tooth roots. However, labiolingual tooth compression is paedomorphic in *Tylosaurus* and examination of the downward extensions of maxillary cortical bone finds them to be the upper cementum of the tooth roots. It is here suggested that TMP 2014.0011.0001 is a typical juvenile specimen of *Tylosaurus*, indistinguishable from coeval specimens of *T. proriger.*

Significance of high-latitude mosasaur remains. Mosasaurs from the palaeo-Artic are poorly sampled compared to coeval southern deposits. Thus, the mosasaur remains from the Puskwaskau Formation represent important data points for understanding the northern realm of the WIS. While taxonomic resolution is currently low, the described specimens show that at least two mosasaurid subfamilies, the Plioplatecarpinae and Tylosaurinae, achieved geographical distributions above 60°N.

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Plant fossils from the type Maastrichtian

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Maastrichtian chalks and biocalcarenites in the type area of the Maastrichtian Stage (south-east Netherlands and contiguous areas in north-east Belgium and western Germany) are well known for their very rich and diverse animal macrofossil contents – from bryozoans, corals, rudists, ammonites, nautiloids, belemnites, gastropods, bivalves, echinoids and sharks and rays, to giant turtles and mosasaurs, and even a few rare dinosaur teeth and bones, two new bird taxa and a single tooth of a marsupial.

The occurrence of marine and terrestrial plant macrofossils has been less noticed. Although relatively poor in comparison to the rich sandy/clayey Aken Formation (Santonian), the Gulpen and Maastricht formations inspired Miquel (1853) to a substantial account of the plant fossils known from these marine deposits, including descriptions of several new genera and species. However, for a long time, this remained the only comprehensive study. As a result of renewed interest and an intentional search through the Maastrichtian strata, especially by amateur collectors, a lot of new material has become available in the last two decades, including quite a number of anatomically preserved specimens, either in flint nodules, or silicified in a chalky matrix (Van der Ham *et al.*, 2022, and references therein).

Plant fossils appear to be relatively common in the lower part of the Maastricht Formation (see Fig. 2). This might be due to the currently limited accessibility of higher strata of this unit. Much of the new material has now been studied, but important groups such as dicot leaves and wood, as well as a new sea grass genus (stems), plus a number of ’difficult specimens’ still have to be tackled. So far, nine conifer species have been identified in Maastrichtian strata (Fig. 2). The cone scales of *Araucaria* represent the last known occurrence of the family Araucariaceae in Europe (Fig. 2), while *Brachyphyllum patens* (Fig. 1/3) has tentatively been assigned to the extinct family Cheirolepidiaceae. Anatomically preserved leaves of this conifer contained stomatal hypostromata of *Pteropus brachyphylli*, a close relative of the extant parasite/saprophyte fungus *Phaeocryptopus* (see Van der Ham & Dortangs, 2005). The seagrass leaf taxon *Thalassotaenia debeyi* (Fig. 1/2) probably belongs to the stems named *Thalassocharis bosquetii* (Fig. 1/1). The oldest seagrass stems worldwide are known from the Vaals Formation (lower Campanian) in the extended Maastrichtian type area (*Thalassocharis muelleri*), while the oldest anatomically preserved material (stems and leaves) comes from the upper Maastrichtian.

Mosacaulis spinifer has been classified as a species of unknown affinity, showing a resemblance to such disparate lineages as lycopsids and angiosperms. Its seagrass-like habit, gregarious occurrence, association with genuine seagrass and a diverse marine fauna, as well as the absence of any accompanying terrigenous material, remains of land plants and terrestrial palynomorphs in the deposit from which it was collected in great numbers (upper Meerssen Member), suggest that these plants grew in a fully marine environment. Fossil palm remains recorded from the type Maastrichtian led us on a quest for the holotype – a fruit – of *Palmocarpon cretaceum*. When we finally managed to find it, it turned out to be an Eocene *Nypa burtinii* from the Brussels area (Belgium) (Van der Ham *et al*., 2022).

Taphonomy

Most plants are preserved as either internal moulds (such as *Mosacaulis* and *Thalassocharis*) or imprints (*Mosacaulis*, *Thalassocharis* and *Thalassotaenia*, plus leaves of terrestrial and other plants, twigs of conifers, wood, seeds), or a combination thereof – predominantly in relatively coarse-grained tuffaceous chalk. A special type of preservation is when SiO_2 replaces plant cellulose (Butts, 2014), producing anatomically exquisite fossils of, among others, marine *Thalassocharis* (Fig. 1/1) and terrestrial *Brachyphyllum*, plus other conifers. It even perfectly preserved the fungus *Phaeocryptopus* in a flint nodule. In 1981, Professor Ehrhard Voigt, always very apprehensively on the lookout for new bryozoan species, came across algae preserved by bioimmuration, which he (Voigt, 1981) named *Fosliella inexpectata*. Although we have, so far, collected many examples of bioimmuration, no new plant species have been found bioimmured.

Earlier papers have also mentioned red algae. These usually appear bright white in the type Maastrichtian and may have all sorts of appearances, from bulbous encrustations to discs. In the distant past, they were assigned to species solely on the basis of external appearance, but this has proved very unreliable. To identify them, not only do thin slices of specimens need to be produced, but the type specimens of taxa need to be traced, which might prove difficult.

To date, we have managed to trace most holotypes of nineteenth century publications on the flora from the Maastrichtian type area and described new taxa such as *Mosacaulis* and *Thalassotaenia*. What remains, is a vast catalogue of 'shapes' that, one day, we hope to assign to families, genera or even species. Another question to solve, is how the chaotic mix of terrestrial and marine plants – often in close association – came to be found together in a fully marine environment.

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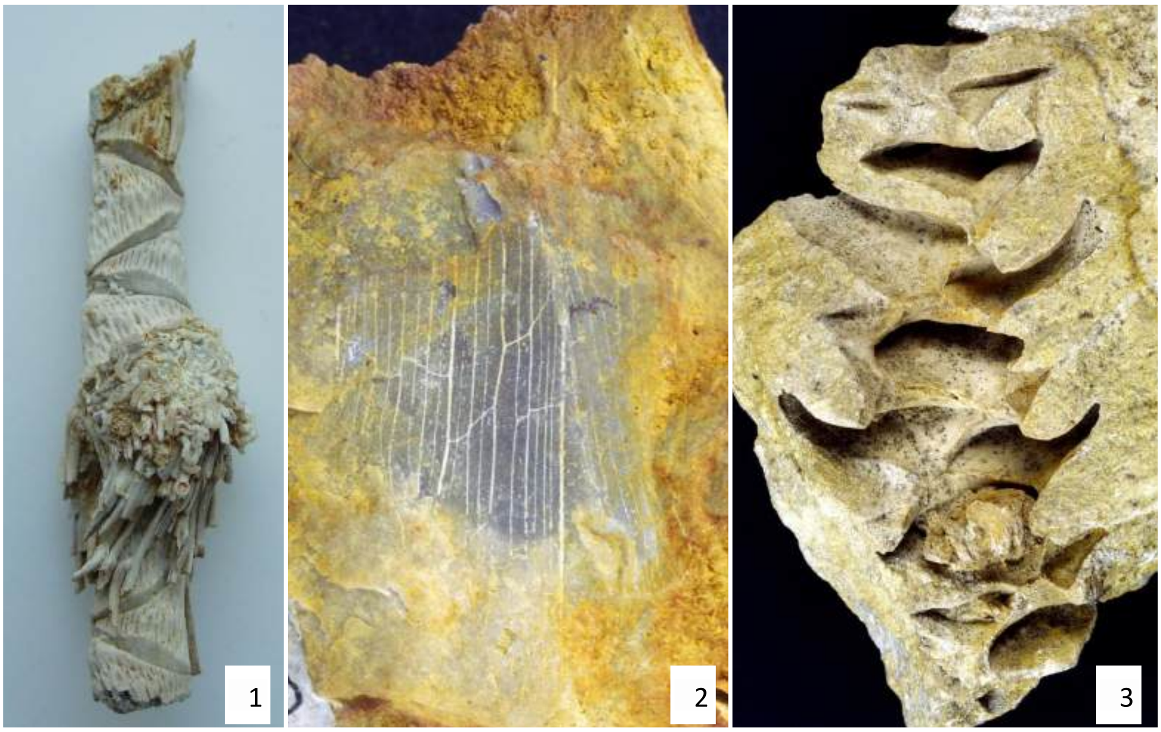

Figure 1. Maastrichtian plant taxa in the collections of the Natuurhistorisch Museum Maastricht (NHMM) and Naturalis, Leiden (RGM); **1**. *Thalassocharis bosquetii* Miquel; silicified stem with roots and epibiont sabellid worm tubes (*Glomerula lombricus*) (NHMM JJ 8575), Gronsveld Member. **2.** *Thalassotaenia debeyi* Van der Ham et Van Konijnenburg-Van Cittert, leaf fragment with 11 veins (middle and both marginal veins relatively thick), alternating fibre strands and cross-veins (NHMM LI 4606), Nekum Member. **3**. *Brachyphyllum patens* (Miquel) Van der Ham et Van Konijnenburg-van Cittert (RGM 21398), Kunrade limestone. Original size 68 mm.

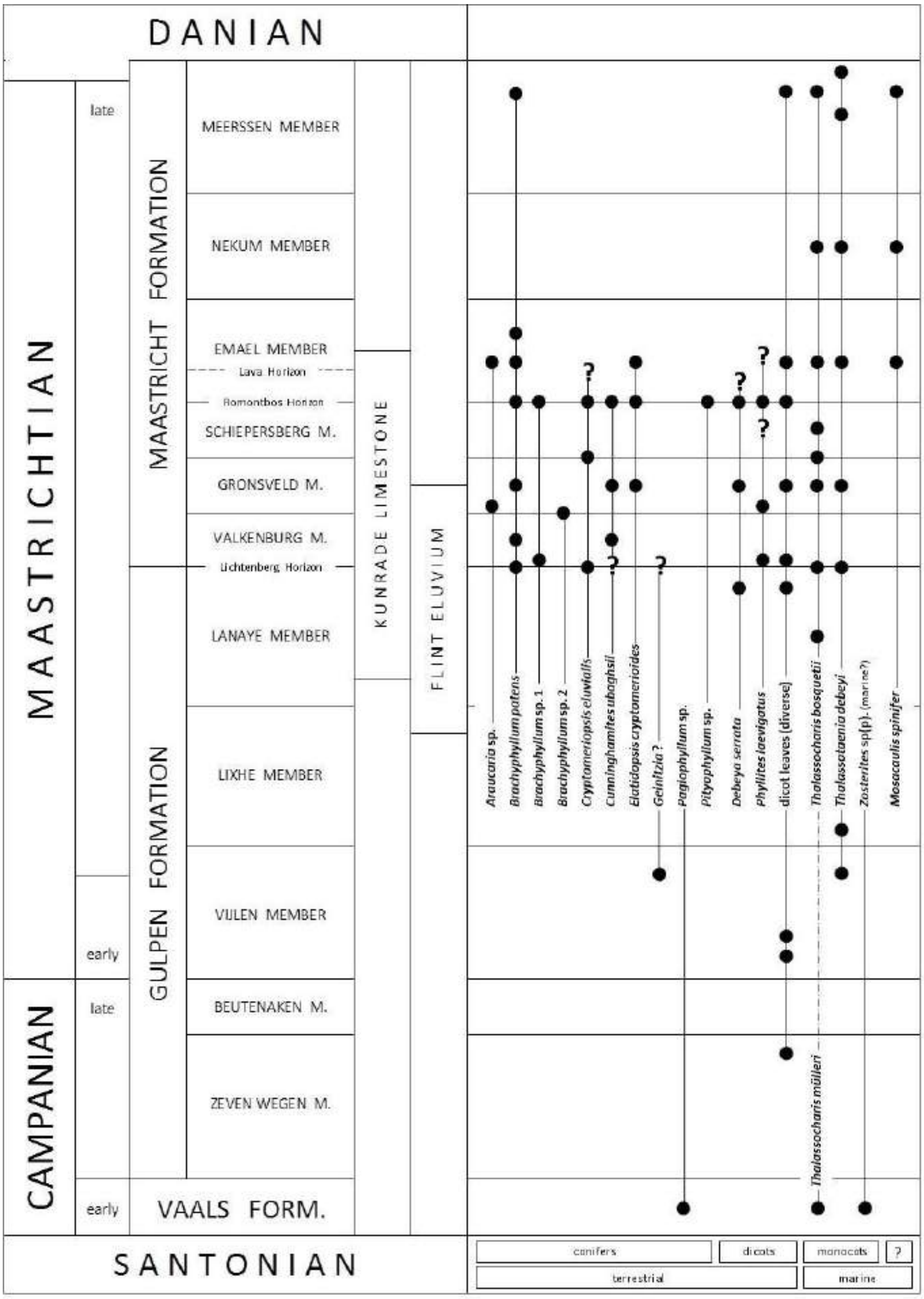

Figure 2. Stratigraphical distribution of Campanian to Danian plant fossils in the Maastrichtian type area.

Keeping the light shining on the truly Maastrichtian dinosaurs, those from Maastricht!

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To begin with, we put great value on indicating right from the start that we are dealing here with non-avian dinosaurs, and that recent descriptions of the oldest neornithine and youngest ornithurine birds from the type Maastrichtian will not be considered further. Maastrichtian strata dated between 69.3 and 66.04 Ma, as exposed in the type area, are renowned for their large marine reptiles such as mosasaurid squamates and chelonioid turtles (Mulder *et al*., 2016). Terrestrial non-avian dinosaurs are rare in these marine strata and as a result of incomplete preservation such taxa remain poorly understood. Almost all previous records have been assigned to specifically indeterminate hadrosaurids or to the dubious taxon '*Orthomerus dolloi*' (see Csiki-Sava *et al*., 2015; Madzia *et al*., 2020), except for a single theropod leg bone, the holotype of *Betasuchus bredai* (Seeley, 1883), which to this day remains poorly known as well (Weishampel *et al*., 1999; Jagt *et al*., 2024).

A fragmentary pubic bone (NHMM LVDC 200), a heavily bored femoral fragment (NHMM 2009 012), a portion of a left femur (NHMM K21.03.950) and the first cranial material (parietal, NHMM K21.03.973) of hadrosaurid origin, all in the Natuurhistorisch Museum Maastricht (NHMM) collections, are novel records for the Maastrichtian type area. For the first time since Seeley's (1883) seminal paper, the find of a theropod bone may be noted: a fragmentary left femur (Fig. 1A-C, D1-4, E). Of these, the parietal and pubic bone are considered to be of taxonomic value. In contrast to occurrences of theropods, the presence of hadrosaurid dinosaurs in mainland Europe, right up into the latest Cretaceous, is well documented. As such it is much more likely that, against all odds, hadrosaurid remains be encountered entombed in marine strata laid down in the "Maastricht Gulf". It is highly plausible that such remains stemmed from floating carcasses that were washed into the shallow sea by rivers from a distant hinterland. Exposure to scavengers and borers (e.g., in NHMM 2009 012), and the high-energy setting in this fairly shallow sea determined the state of preservation of these fragmentary bones.

NHMM K21.03.950 is a partial left femur, representing around 30 per cent of the bone and preserving the proximal part, with the exclusion of the femoral head (Fig. 1D1-4). This specimen was collected at the former Curfs quarry (Geulhem) in June 1963, but the exact level of provenance is not noted on the accompanying label. The black colour of the bone is unusual for vertebrate remains in the Maastricht Formation, and finds a match in carapace remains of the sea turtle *Glyptochelone suyckerbuyki* Ubaghs, 1879, which appears confined to the upper portion of the Meerssen Member at Maastricht and Valkenburg aan de Geul. For now, we assume NHMM K21.03.950 to have originated from this stratigraphical level as well. Overall, this bone is eroded, with burrowing ichnotaxa on the cortex and inside the medullary cavity. The mid-shaft shows a clean, pre-fossilisation fracture that may have resulted from scavenging activities. The lesser trochanter is not preserved, while the fourth trochanter is partially eroded caudally. On the medial side of the trochanter there are two attachment sites for muscle groups. The attachment site for the *m. caudofemoralis longus* extends from the fourth trochanter onto the medial surface of the femoral shaft. A second insertion scar lies more proximomedially and is attributed to the *m. puboischiofemoralis internus*. Its determination is based on the presence of a fourth trochanter and attachment scars of muscle groups. Comparison with the femur of *Appalachiosaurus montgomeriensis* from the Campanian (Carr *et al*., 2005) and of *Dryptosaurus aquilunguis* (Brusatte *et al*., 2011) from the Maastrichtian of North America, suggest it to have come from a tyrannosaurid. A femur from the Maastrichtian of Mongolia, previously described as part of the holotype of the theropod *Bagaraatan* (Osmólska, 1996), has recently been judged not to belong to that species, but to another theropod taxon (Słowiak *et al*., 2024). In comparison, our specimen is smaller and less robust than the right femur of *Betasuchus bredai.* The ridge that leads up to the lesser trochanter in that species is pronounced, giving the bone an anteriocaudally elongated cross section. This ridge is not well marked in NHMM K21.03.950, which is therefore mediolaterally elongated in cross section across the diaphysis. Both bones are of unclear origins, but apparently originated from the highest level of the Maastricht Formation, the Meerssen Member.

We have also studied the internal bone structure and ichnofossils within the bone. The clearly defined bone cortex, with a thickness between 2.3 and 2.9 mm, is consistent with a theropod long bone of this size (Fabbri *et al*., 2022). A large number of trace fossils (pascichnia), left by benthic burrowing organisms in search of digestible organic matter, are concentrated on the outside perimeter of the medullary cavity where fragmentary trabeculae are present (Fig. 1A-C). The presence of these traces is indicative of bioactivity and scavenging after burial in an oxygen-rich sea floor, consistent with the shallow sea model for the ''Maastricht Gulf''.

The find of a parietal bone (Fig. 2A-G) in the De Heer Collection (NHMM) came as a huge surprise. It is complete, but bears the tooth marks of scavengers. CT scanning has revealed the internal structure to be highly organised (Fig. 2G1-3). Fifteen laminae are seen to be stacked dorsoventrally in the central part of the bone. Fossae connect the dorsal surface of the skull with the interior of the braincase. For now, it cannot be linked to any hadrosaurid braincase in the literature.

In conclusion, these newly recognised specimens from the type-Maastrichtian area further expand our understanding of the ''truly Maastrichtian dinosaurs''. Scarce as their remains may be, they do rank amongst the stratigraphically youngest non-avian dinosaurs to have ever lived.

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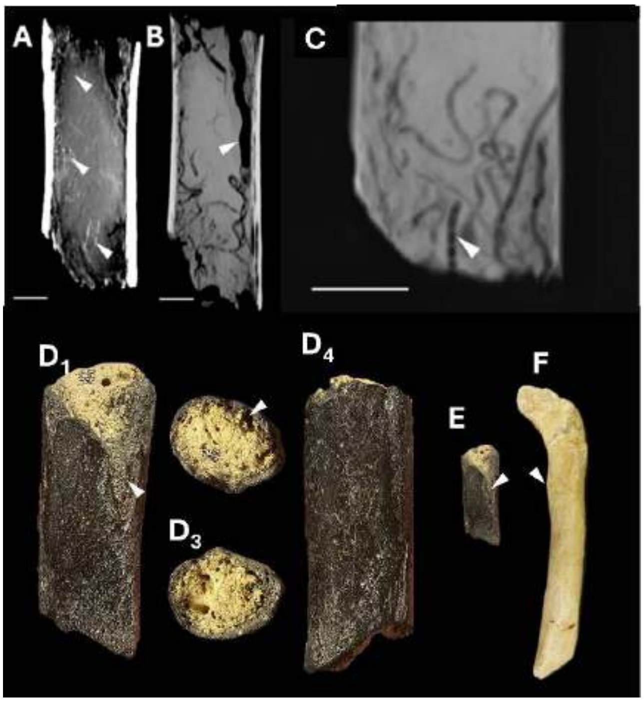

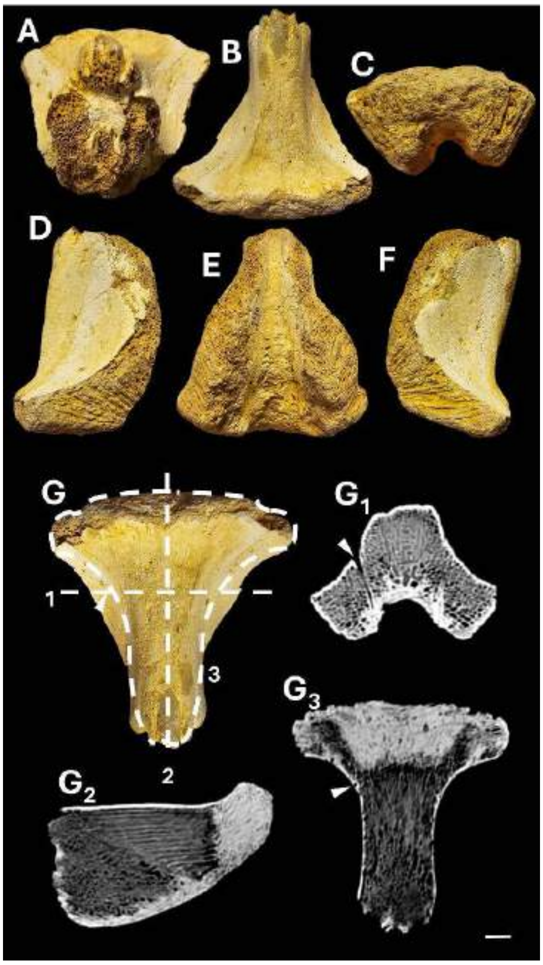

Figure 1 (*left*). CT images of NHMM K21.03.950, a partial left femur of a theropod. **A**. cross section, white arrows indicating trabeculae, most prominent on perimeter of medullary cavity (minimum intensity projection). **B**. cross section (maximum Intensity projection), showing ichnfossil diversity, white arrow indicating large burrow. **C.** closeup of endosteal surface of medullary cavity, showing high concentration of ichnofossils, suggesting high nutritional yield. White arrow indicating ichnogenus *Scalarituba*. **D.** Overview of femur in caudal (D_1), proximal (D_2), distal (D_3) and cranial (D_4) views, arrow indicating large burrowing ichnofossil and comparison of NHMM K21.03.950 (**E**) with the holotype of *Betasuchus bredai* in caudal view (**F**). White arrows indicate fourth trochanter. Scale bars equal 10 mm (A-D) and 50 mm (E, F).

Figure 2 (*right*). Hadrosaur parietal (NHMM K21.03.973) in anterior (**A**), dorsal (**B**), posterior (**C**), right lateral (**D**), ventral (**E**) and left lateral views (**F**). Overview and CT images of hadrosaur parietal. Sections made in frontal (G_1), sagittal (G_2) and transverse planes (G_3). White arrows indicating same foramina in G, G_2 and G_3. Scale bar equals 10 mm.

Biostratigraphy and sequence stratigraphy of the Upper Cretaceous (Maastrichtian) Quiriquina Formation in central Chile

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The Upper Cretaceous Quiriquina Formation crops out around Concepción Bay in central Chile and presents a retrogradational pattern in shoreface environments, which may have resulted from sea level rise (transgression) at the end of early Maastrichtian. Upsection, low-energy offshore facies developed during the late Maastrichtian. Thirty ammonite species, assigned to seventeen genera (Salazar *et al.*, 2010) have been recovered; these represent one of the most diverse assemblages for the uppermost Cretaceous. The presence of *Hypophylloceras* (*Neophylloceras*) *surya*, *Zelandites varuna*, *Pachydiscus* (*P.*) *jacquoti*, *Diplomoceras cylindraceum*, *Baculites anceps, Eubaculites carinatus, Hoploscaphites constrictus* and *Menuites fresvillensis* indicates an early late to late Maastrichtian age for the unit.

Four parasequences have been identified by a retrogradational pattern of depositional facies. Parasequences 1 to 3, determined at Las Tablas, are also recognised in numerous other sections in the area. They correspond to the basal conglomerate (parasequence 1), the yellow cross-bedded sandstone (parasequence 2) and the coquina unit (parasequence 3); they represent shoreface facies of decreasing energy. Parasequence 4 corresponds to a silty sandstone with calcareous sandstone concretions and reflects offshore transitional facies.

Based on the vertical stacking pattern of the four parasequences described above, a single depositional sequence is recognised in the Quiriquina Formation. It consists of a TST, which is characterised by a retrogradational stacking pattern of parasequences 1 to 3. Parasequence 3 contains the maximum flooding surface (mfs). The HST is formed by the retrogradational stacking pattern of parasequences 3 and 4. Parasequences 1 to 3 correspond to shoreface facies and parasequence 4 to offshore transition facies representing maximum water depths in the depositional area.

In consequence, parasequence 1 represents a retrogradational facies pattern in a shoreface high-energy environment. This transgression resulted from sea level rise near the end of the early Maastrichtian. Transgression continued through parasequences 2 to 3 which also reflect shoreface facies, but with gradually decreasing energy levels. During parasequence 4, this retrogradational system (transgression) continued in an offshore transition environment with low energy levels. A strong regression ended marine sedimentation either near the end of the Maastrichtian or cutting down from the Paleocene. The K/Pg boundary is thus incomplete due to erosion and an extended hiatus.

The following three biozones are distinguished (from base to top): *Baculites anceps*, *Eubaculites carinatus* (subdivided into the *Menuites fresvillensis* and *Kitchinites darwini* subzones) and a zone without baculitids (subdivided into the *Hoploscaphites constrictus* biozone and a zone without ammonites). Species richness and abundance of ammonoids are high throughout the Quiriquina Formation but gradually decline in the uppermost 10 metres of the section within the unit of green sandstone-siltstone. No ammonoids appear to be present in the last 5 metres of the unit, indicating that the extinction of ammonites in the region was completed prior to the end of the Maastrichtian. The assemblage shows an Indo-Pacific character, but endemic and cosmopolitan as well as European-Tethyan faunal elements are also present.

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Mosasaurus 3D: scanning, digital reconstruction and 3D-printing of a large *Prognathodon* skeleton for museum display

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The past decade has seen considerable progress in both 3D surface scanning technology as well as additive and subtractive 3D printing. Both technologies have become much more accessible, more affordable, faster and yield higher-quality results, making inroads in the consumer market, the citizen scientists' community and 'Maker movement' alike. These advances have an impact in many different fields, and vertebrate palaeontology is no exception.

In this short contribution, we shall highlight an example of how these technological developments have made a difference in building a life-sized skeletal model of the holotype of *Prognathodon saturator*, a large globidensine mosasaur from Lanaye Member (Gulpen Formation) in the Maastrichtian type area. At the time of submitting thise abstract, the first skeleton is being 3D-printed; this was put on display at the Natuurhistorisch Museum Maastricht in early August 2024, in a special exhibition entitled 'Mosasaurus Experience.'

The type specimen of *Prognathodon saturator* (NHMM 1998 141, nicknamed 'Bèr') was discovered in August 1998, put on display at the Maastricht museum in 2002 and formally named in the same year (Dortangs *et al*., 2002), followed by an in-depth description in Schulp (2006). The holotype consists of an almost complete skull, which lacks only the greater part of the premaxilla and the anterior part of the dentaries. Post-cranial elements preserved include most of the cervical series, part of the dorsals and ribs, a scapula-coracoid, as well as a few isolated caudal and limb elements. Most of the tail, sacral elements and limbs are missing. In view of the fact that the specimen is embedded in limestone, with various elements shifted from their original anatomical position, it is challenging from a museum perspective to convey fully the anatomy, size and appearance of the animal to a wider audience.

With support of the Dutch Mondriaan Fonds, through a grant in their programme for international museum collaboration, inspired by the growing experience in 3D scanning and printing at the national natural history at Leiden (Naturalis Biodiversity Center), and with help of the discovery of a similar-sized macrophagous *Prognathodon* specimen in Namibe province in Angola, we had the opportunity to bring this together in a project aimed at putting a full skeletal reconstruction of *Prognathodon* on display both in Angola and the Netherlands.

The new discovery in Angola comes from the upper Maastrichtian part of the section at Bentiaba and is currently being prepared. A considerable proportion of the material preserved (field number MGUAN-PA274, nicknamed ‘Big Mo’) is complementary to the Maastricht specimen; particularly adding morphological information on the anterior snout, limb elements and caudal vertebrae.

Both *Prognathodon* specimens were scanned using Artec Leo and Artec Spider 3D scanners; additional scans were made of the cranial material of *Prognathodon kianda* from the same site (albeit from the lower Maastrichtian part of the section), particularly MGUAN-PA183. All 3D data were processed, mirrored, merged and retrodeformed using the lattice retrodeformation and sculpt tools in the 3D-graphics and animations software Blender. Constraints were imposed using the specimen’s own morphology as well as that of closely related taxa. 3D prints were prepared using Creality Print FDM Slicer software using the tree support option. Prints were made, depending on the size, on Ultimaker 7, Ender K1 max or Builder 1500 3D printers, using partially recycled PLA print material.

Seeing that no articulated tail or pygal series were preserved in either of the large *Prognathodon* specimens, skeletal proportions were modelled with additional guidance from an individual of *Prognathodon* from Canada, as described by Konishi *et al*. (2011) and the articulated portion of a pygal series in MGUAN-PA183. This has allowed to improve on the earlier skeletal reconstruction by Dortangs *et al*. (2002, fig. 7) by adding to the pygal vertebral count, adjustment of skull size/body proportions and inclusion of the tail fluke morphology as outlined by Lindgren *et al*. (2007, 2010, 2013).

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Benthic foraminiferal turnover and palaeoenvironmental changes across the Cretaceous–Paleocene transition in shallow-marine platform carbonates, Central Taurides (Türkiye)

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Complete records of the Cretaceous–Paleocene (K/Pg) transition in shallow-marine platform environments are rare in the Tethyan Realm due to breaks in sedimentation and/or erosion. Carbonate sedimentation in some parts of the Anamas-Akseki Platform in the Central Taurides was interrupted by short-term subaerial exposure between the Cretaceous and Paleocene due to regional tectonic activity. However, a few shallow-marine successions have managed to record sedimentologically continuous carbonate platform accretion across the K/Pg transition. The present study focuses on assessments of changes in benthic foraminiferal communities along with lithological and palaeoenvironmental analysis of the 40-m-thick Seyran Dağ and 30-m-thick Sülek sections which represent the Maastrichtian–Danian transition. Analyses of other K/Pg sections and additional sections logged from the localities of Elmasut and Akseki are ongoing.

The K/Pg boundary is constrained mainly between the highest occurrence of *Fleuryana adriatica* and the lowest occurrence of *Pachycolumella acuta* and *Stomatorbina* sp. in the two sections studied. The range of *Pachycolumella acuta* is upper Maastrichtian to Paleocene (e.g., Sirel, 1998, 2015; Solak *et al.*, 2017, 2019; Septfontaine *et al.*, 2019; Solak & Taslı, 2024). It is more common in Paleocene beds than in the upper Maastrichtian in Türkiye (Sirel, 1998, 2015; Solak *et al.*, 2017, 2019). However, *Pachycolumella acuta* becomes stratigraphically important for younger levels where it does not coexist with typical representatives of *Fleuryana adriatica*, an index species for the Maastrichtian (e.g., De Castro *et al.*, 1994; Solak *et al.*, 2017; Solak & Taslı, 2024). The boundary is not lithologically distinguishable (Fig. 1A, B). Dolomite interbeds are occasionally observed along transitional beds (Fig. 1B). Across the K/Pg transition carbonate successions show local changes in depositional settings from open circulation-influenced inner platform settings to restricted ones.

Seyran Dağ section. The uppermost Maastrichtian part of the Seyran Dağ section is composed predominantly of bioclastic packstone (Fig. 1C), an open-marine facies marked by the presence of hyaline larger benthic foraminifera such as *Orbitoides*, *Omphalocyclus* and *Siderolites*. It also includes intercalations of muddy-rich facies with imperforate benthic foraminifera (*Fleuryana adriatica*, miliolids, textulariids) reflecting restricted inner platform settings. In lower Paleocene beds immediately above the upper Maastrichtian, depositional conditions change from open circulation-influenced platform settings to entirely restricted platform settings together with foraminiferal and algal wackestone/packstone facies. The Paleocene is recognised by the presence of

Pachycolumella acuta, *Stomatorbina* sp. and abundant discorbids. Upsection, algae accompany this assemblage.

Sülek section. In the Sülek section, the upper Maastrichtian beds are composed of an alternation of white laminated dolomite and rudistid limestones (Fig. 1D). They are characterised by restricted muddy-rich inner platform facies containing imperforate benthic foraminifera *Rhapydionina liburnica* and *Fleuryana adriatica*. Restricted depositional conditions persisted in the early Paleocene with a tendency to become shallower. *Microcodium* is also added in the muddy-rich facies. The Paleocene begins with the lowest occurrence of *Pachycolumella acuta* and dasycladalean algae (e.g., *Clypeina*) and *Microcodium* fragments. Dolomite interbeds are occasionally associated with the limestones (Fig. 1B).

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Figure 1. Field photographs of the Cretaceous–Paleocene (K/Pg) transition successions, the Anamas-Akseki Carbonate Platform, Central Taurides. **A.** K/Pg transition, Seyran Dağ section. **B.** K/Pg transition with white dolomite interbeds, Elmasut section. **C.** Bioclastic limestone with rudists composed of bioclastic packstone, upper Maastrichtian, Akseki section. **D.** Rudistid limestone, upper Maastrichtian, Sülek section.

Late Cretaceous cockles (Bivalvia, Cardiida) from Liège-Limburg – there is more than meets the eye

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It is a well-known fact that Upper Cretaceous (lower Campanian-uppermost Maastrichtian) siliciclastic and carbonate strata in the extended type area of the Maastrichtian Stage (south-east Netherlands, north-east Belgium) are replete with bivalves, both in shell and internal/external mould preservation. To date, only calcitic pteriomorphs have received ample attention; other groups, with originally aragonitic shells, are much less well known. In recent years, cursory examinations of the latter have already shown that there is a lot of potential for taxonomic assessment, palaeoecological characterisation and considerations of biostratigraphical usefulness.

At several localities and a number of discrete levels, the siliciclastic Vaals Formation, of early Campanian age, has yielded numerous cardiids, mostly available in three-dimensionally preserved, silicified material (Holzapfel, 1889), while younger strata (Gulpen Formation, late Campanian to late Maastrichtian) are almost barren, except for a single, distorted composite mould of '*Cardium' fenestratum* from the Vijlen Member (interval 6, upper lower Maastrichtian) at the former CPL SA quarry, Haccourt (province of Liège). This species, erected by Kner in 1850 and assigned to *Nemocardium* by Abdel-Gawad (1986), has been variously interpreted by authors, who recorded it from the Campanian and Maastrichtian in England, Germany, Ukraine and Poland. Obviously, a revision is called for.

In the Maastricht Formation, indurated levels (e.g., above Lava and Laumont horizons, Emael and Nekum members, respectively), as well as in flint nodules in the latter unit (see e.g., Vogel, 1895a), medium- to large-sized cardiids are found. Mostly, these comprise *Granocardium productum* (J. de C. Sowerby, 1835) or a closely related species, in various growth stages (Fig. 1B), plus a currently indeterminate, but possibly closely related taxon (Fig. 1A).

In faunal lists, published by Bosquet (1860, 1868), there are only two cardiids from what we now consider to be the upper Gulpen and entire Maastricht Formation. Later, Vogel (1895a) recorded, in original nomenclature, *Cardium productum* Sow., *Cardium subalternatum* (as a new species), *Cardium lundgreni* (as a replacement name) and *Cardium* spec. In an appendix, he also referred to *Cardium propinquum* Goldfuss, but this is probably not from the Maastricht area.

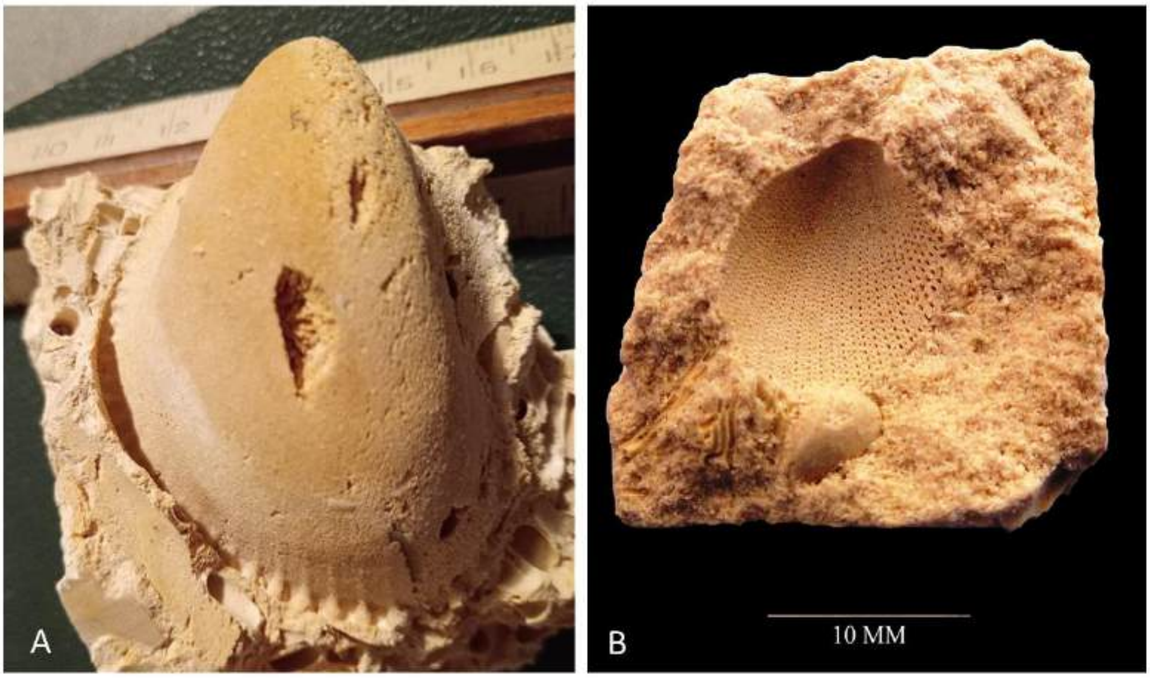

Figure 1. Late Maastrichtian cardiids from the Maastrichtian type area. **A**. Indeterminate cardiid, apparently close to *Granocardium productum*; basal Meerssen Member (Maastricht Formation), former Blom quarry, Berg en Terblijt (NHMM PK M1734). **B.** *Granocardium productum* (J. de C. Sowerby, 1835) juv. (G. Cremers Collection, Velden).

Of the above, *Cardium subalternatum* Vogel, 1895 (preoccupied by *C. subalternatum* d'Orbigny, 1850 and *C. subalternatum* Jenkins, 1864) is in need of a replacement name. Placement in *Granocardium* is appropriate; it differs from *G. productum* mainly by its much more distantly placed spines. Vogel's (1895a) '*Cardium* spec.', preserved in the body chamber of a baculitid ammonite, is of special note. This small species, at first sight resembling a neitheine bivalve, constitutes a new genus and species of endemic cardiid (Fig. 2C), to be described in detail soon.

Cardium crassum Lundgren, 1866 (Fig. 2D) was described from Upper Cretaceous-Paleocene greensand deposits in southern Sweden (vicinity of Malmø); this form possibly belongs to *Nemocardium*. Vogel's (1895a) replacement name *Cardium lundgreni* appears to be an earliest Paleocene (early Danian) species, with records from Caberg (north-westerly outskirts of Maastricht; see also Vogel, 1895b; Leloux, 2002), but for now unknown from the Geulhem area. A superficially similar, albeit smaller, species, with well-developed commarginal ornament on the anterior and median part of the disc (Fig. 2A, B), occurs in the basal Nekum Member, and likely is an undescribed species of *Protocardia.*

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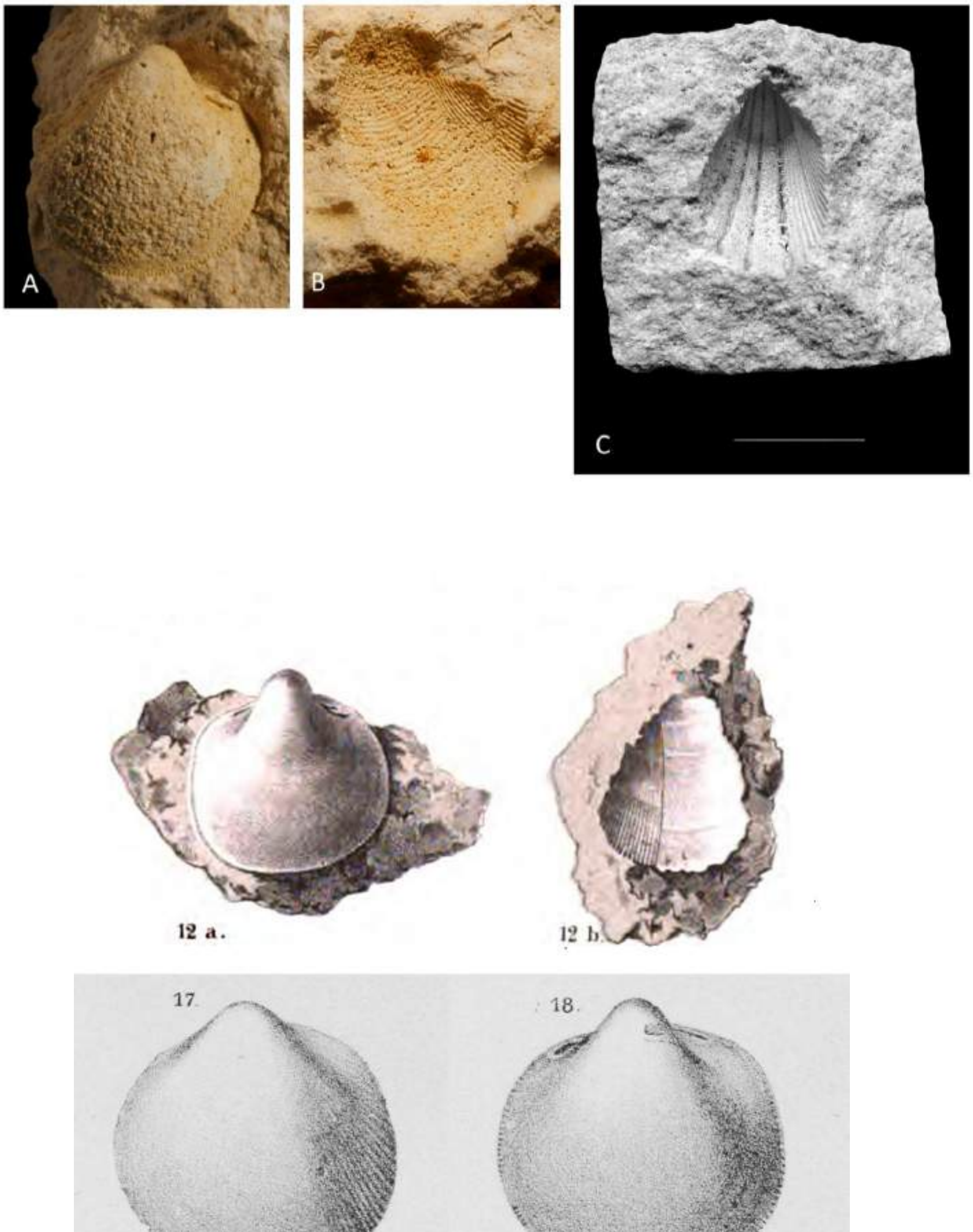

Figure 2. Late Maastrichtian and early Paleocene cardiids from southern Limburg, the Netherlands (A-C, E) and southern Sweden (D). **A, B**. *Protocardia* (?) nov. sp. [non *Cardium lundgreni* Vogel, 1895a], basal Nekum Member (Maastricht Formation), internal mould and partial external mould showing ornament (NHMM Jagt Collection). **C.** cardiid nov. gen., n. sp., external mould, uppermost Meerssen Member (IVf-6, Maastricht Formation), Geulhem area (NHMM JJ 3253). **D.** *Cardium crassum* Lundgren, 1866 (after Lundgren, 1866), perhaps best accommodated in *Nemocardium*. **E.** *Cardium lundgreni* Vogel, 1895a, Maastricht-Caberg, lower Paleocene, also best referred to *Nemocardium.*

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Long-bone histology of the Late Cretaceous island-dwelling ankylosaurian dinosaur *Struthiosaurus austriacus* Bunzel, 1871

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During the Late Cretaceous, Europe was covered by a shallow epicontinental sea with numerous islands that were home to a wide variety of terrestrial vertebrates (Csiki-Sava *et al.*, 2015). The ankylosaurian dinosaur *Struthiosaurus*, known from cranial and postcranial remains from Austria, Romania, France and Spain (Nopcsa, 1929; Pereda-Suberbiola *et al.*, 1995; Pereda-Suberbiola & Galton, 2001; Garcia & Pereda-Suberbiola, 2003) ranked amongst these Late Cretaceous island-dwellers. Traditionally included in the family Nodosauridae, *Struthiosaurus* is widely acknowledged to belong to the smallest known ankylosaurs, with an estimated body length of two to three metres (Pereda-Suberbiola, 1992; Pereda-Suberbiola & Galton, 2001; Riguetti *et al.*, 2022) and a mass of ~130 kg (Benson *et al.*, 2018). As currently accepted, the genus *Struthiosaurus* includes three species: *S. austriacus* Bunzel, 1871 from the lower Campanian of Austria, *S. languedocensis* Garcia & Pereda-Suberbiola, 2003 from the Campanian of France and *S. transylvanicus* Nopcsa, 1915 from the Maastrichtian of Romania. In addition, ankylosaurian remains tentatively referred to as cf. *Struthiosaurus* sp. from the Iharkút locality in Hungary suggest that the genus might have extended down into the Santonian (Ősi & Prondvai, 2013; Ősi & Pereda-Suberbiola, 2017). Skeletal remains reminiscent of *Struthiosaurus* have also been described by Ősi *et al*. (2014) from the Maastrichtian of Romania, but more complete material is needed to warrant an unambiguous identification.

The tentative assignment of Hungarian and Romanian ankylosaurian material to *Struthiosaurus* is not only based on adult body size estimates that suggest individuals of less than three metres in length, but also on histological evidence that supports their ontogenetic maturity (Ősi & Prondvai, 2013; Ősi *et al*., 2014; Ősi & Pereda-Suberbiola, 2017). The estimated diminutive adult body size of *Struthiosaurus* is based on a complete femur referred to the type species, *S. austriacus*, from the lower Campanian of Muthmannsdorf near Vienna in Austria (Pereda-Suberbiola & Galton, 2001; Riguetti *et al*., 2022). However, the adult status of this 265-mm-long specimen is challenged by much larger, but less well-preserved femoral material also attributed to *S. austriacus* (compare Seeley, 1881), suggesting that the species could have reached a much larger adult body size than previously assumed.

As part of an ongoing study, two femora, each representing a distinct size category, were subjected to a histological analysis in order to determine their ontogenetic status. The prepared thin-sections, which are housed at the Department of Palaeontology, University of Vienna (IPUW), were cut transversely at the mid-diaphysis or as close as possible to it.

The sectioned femora demonstrate continuous growth with highly vascularised parallel-fibred bone. The vascularisation occurs in the form of simple vascular canals, primary osteons and secondary osteons (Figs 1, 2). In the innermost cortex of both sections, multiple erosion cavities occur; however, they are more common in the larger specimen IPUW 2349/uncatalogued than in IPUW 2349/32. The IPUW 2349/uncatalogued section possesses scattered secondary osteons reaching up to the outermost cortex (Fig. 2), whereas in section IPUW 2349/32, the outermost cortex consists predominantly of primary osteons and only few secondary osteons are seen. In addition, the amount of primary bone filling the spaces between the osteons is much higher in specimen IPUW 2349/32. Osteocyte lacunae are very prominent in both sections. No growth marks in the form of Lines of Arrested Growth (LAGs) (Francillon-Vieillot *et al*., 1990) could be observed.

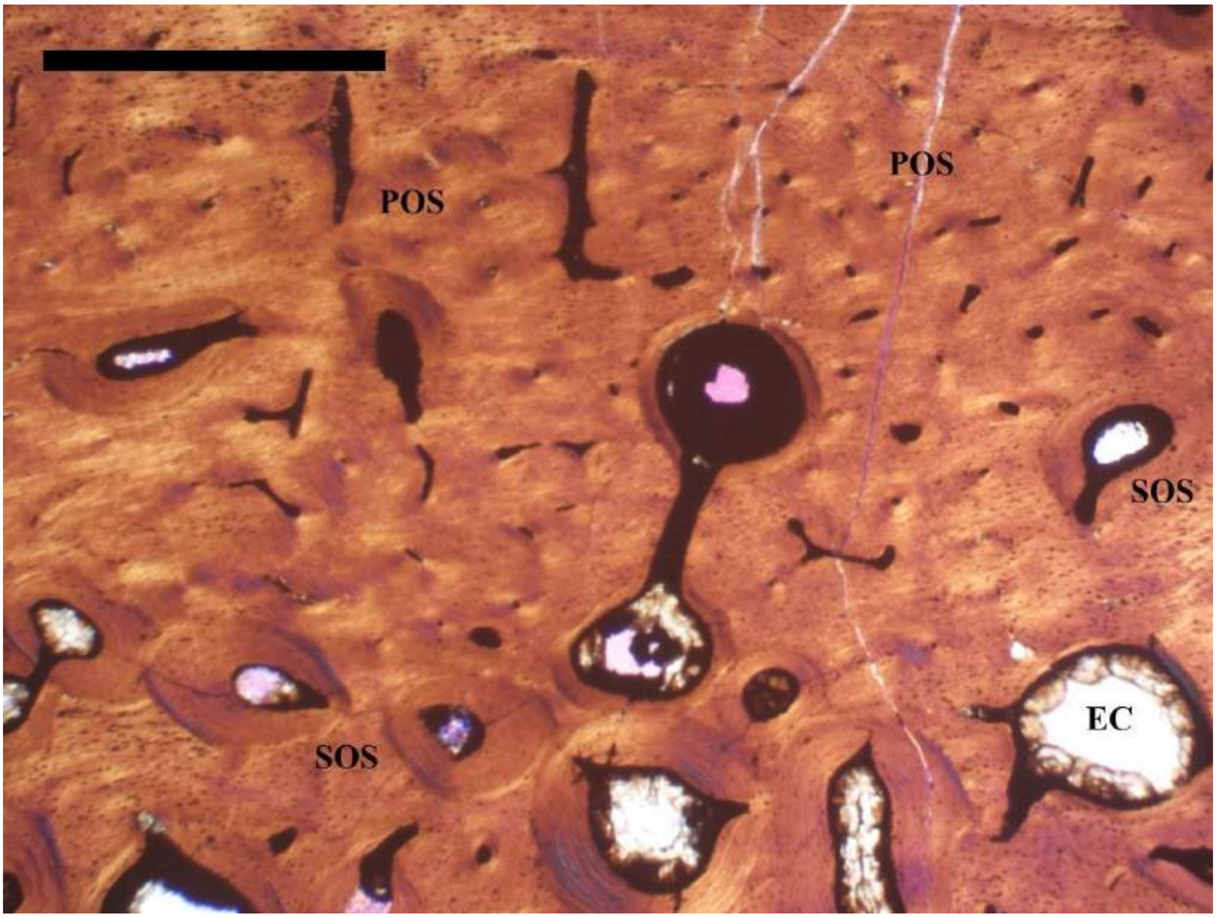

Figure 1. Histological growth of *Struthiosaurus austriacus* Bunzel, 1871; left femur IPUW 2349/32 corresponding to an early ontogenetic stage. The outermost cortex preserves a mix of scattered primary and secondary osteons. Note the commonly preserved patches of primary bone. Image taken under a polarisation microscope with retardation plate. Scale bar equals 1 mm. Abbreviations: EC = erosion cavity; POS = primary osteon; SOS = secondary osteon.

The preliminary histological analysis presented here reveals the presence of continuous bone growth in both sectioned femora, indicating that *S. austriacus* had a rather fast growth rate. The character combination, e.g., cortex thickness, proportion between primary and secondary osteons and the amount of preserved primary bones, enables us to refer specimen IPUW 2349/32 to an early histological ontogenetic stage (Fig. 1) and the larger specimen IPUW 2349/uncatalogued to an older histological ontogenetic stage (Fig. 2). However, neither of the femora shows stratification by LAGs, nor could an External Fundamental System (Cormack, 1987) be observed. The latter indicates that the individual from which the larger, more stoutly built femur originated had not ceased growth at the moment of death. Therefore, it is very likely that *S. austriacus* was capable of attaining an even larger body size, easily exceeding three metres in length. This is in stark contrast to the material referred to as cf. *Struthiosaurus* sp. from the Santonian of Hungary and the Maastrichtian of Romania, providing a crucial basis for future research in the study of Late Cretaceous ankylosaur diversity and evolution.

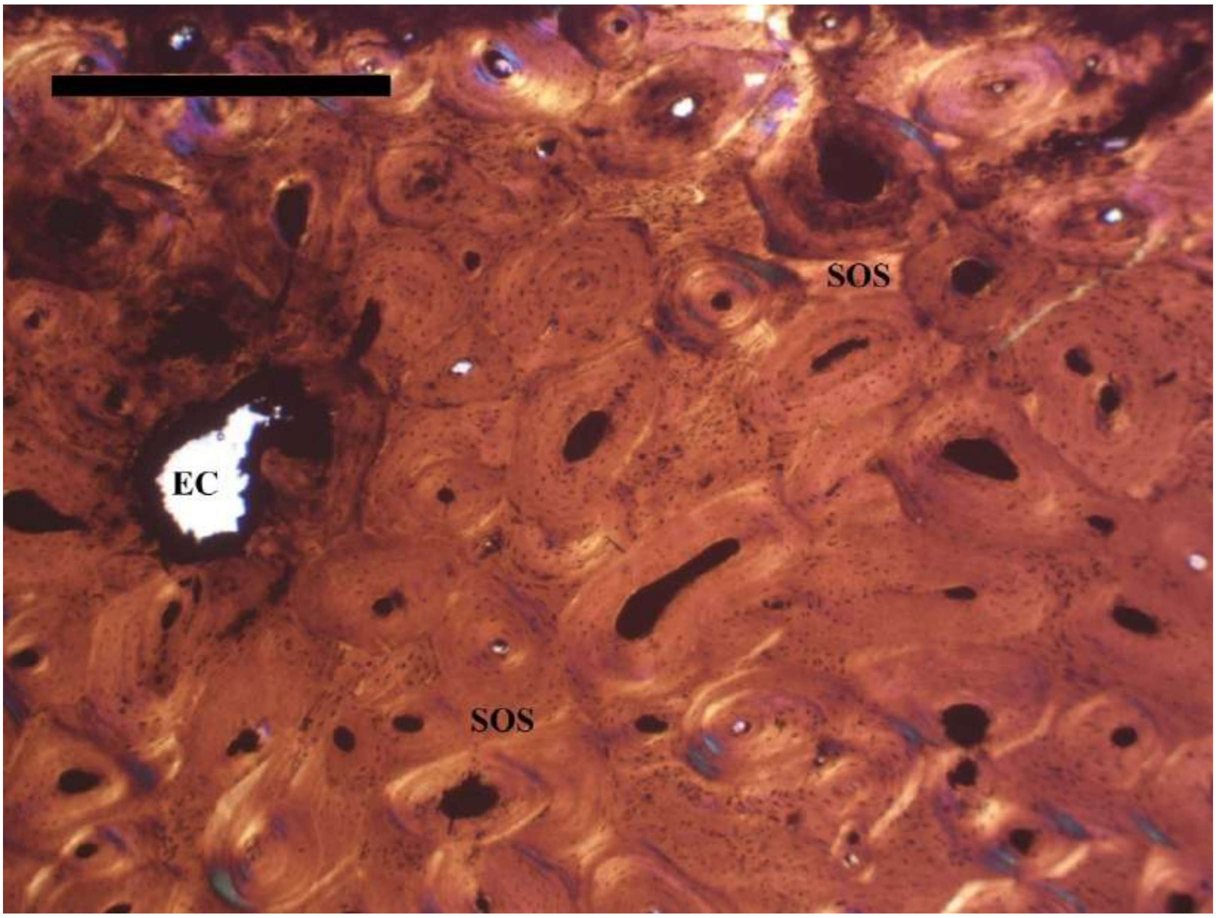

Figure 2. Histological growth of *Struthiosaurus austriacus* Bunzel, 1871, left femur (IPUW 2349/uncatalogued), corresponding to a later ontogenetic stage. The outermost cortex preserves mostly a mix of secondary osteons and erosion cavities, thus, implying advanced bone remodelling. Note the rarely preserved primary bone. Image taken under a polarisation microscope with retardation plate. Scale bar equals 1 mm. Abbreviations: EC = erosion cavity; SOS = secondary osteon.

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The Maastrichtian Geoheritage Project, a fertile cross-pollination of citizen science and academia

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The youngest time interval of the Cretaceous is known as the Maastrichtian Age, in reference to the strata exposed in the area surrounding the city of Maastricht, in the Netherlands-Belgium border region (Jagt, 2001; Fig. 1). The stratigraphical succession at the original type locality of the Maastrichtian (adjacent to the former ENCI-HeidelbergCement Group quarry, south of Maastricht) only covers the upper part of the Maastrichtian Stage as defined nowadays. However, recent integrated bio- and chemostratigraphical revision by Vellekoop *et al*. (2022) has shown that, in combination with similar lithological sequences at other quarries in the region (e.g., Hallembaye, Curfs; Fig. 1), a substantial part of the Maastrichtian Stage is represented (Fig. 2).

Over the past two and a half centuries, the type-Maastrichtian strata have provided a wealth of palaeontological data, comprising a wide array of vertebrate, invertebrate and botanical finds. Numerous skeletal remains of, for instance, mosasaurs, plesiosaurs, crocodiles, turtles, dinosaurs, often disarticulated yet excellently preserved, have made the Maastrichtian type area a classic site in the history of palaeontology.

Despite its importance to the global geological community, most of the quarries in the region have been closed over the last decades. Instrumental quarries such as that of Curfs have already been out of commission for more than a decade, while others, such as the ENCI quarry, were closed as recently as six years ago. Because most of the soft limestone rocks weather easily and become overgrown rapidly, access to, and study of, the Maastrichtian rock succession in its type area are becoming very limited.

To preserve the geological heritage of this original type locality of the Maastrichtian, and re-appraise the stratigraphy and palaeontology of this geologically important region, in 2018 we initiated the ‘Maastrichtian Geoheritage Project’, a collaborative project that brings together researchers from a variety of backgrounds and research institutes, both academics and citizen scientists. The goal of this project is to study temporary outcrops and both recent and historical quarries, using (1) digital imagery, including drone photogrammetry and Differential GPS Base & Rover to generate high-resolution and georeferenced 3D models of the most important quarries in the Maastrichtian type region; and (2) high-resolution sampling, thereby archiving the geological heritage of the Maastrichtian type area for future research. Relying on the knowledge and expertise of a regional network of citizen scientists, daily scouting the region for new building sites and other temporary exposures, this project represents a fertile cross-pollination of citizen science and academia.

Over the last few years, we have, for example, already collected high-resolution (5 cm spacing) reference sample sets from the Hallembaye (2018), ENCI (2019) and Sibbe-America (2022) quarries, as well as several temporary outcrops, and generated detailed geo-referenced 3D models for the first two quarries. For the near future, several other instrumental quarries will be targeted. Combining these records with those from a plethora of temporary outcrops, an ever-growing dataset of the geological successions in the Maastrichtian type area is generated. The acquired fully geo-referenced sample sets have already spurred a range of stratigraphical, geochemical and palaeontological studies (e.g., Vellekoop *et al*., 2022; Vancoppenolle *et al*., 2022), including detailed profiles of carbon isotope data, major elements, trace element profiles and many more to come. Together, these studies (1) allow a re-evaluation of the stratigraphy of the region – including the elusive stratigraphical position of the Kunrade chalk in the eastern part of the Maastrichtian type area, (2) provide insights into the complex sedimentary and diagenetic processes such as flint formation, and (3) enable placing the abundant palaeontological records from the type-Maastrichtian in a global context. Moreover, the Maastrichtian Geoheritage Project sample sets will be made available for collaboration with other researchers in the field.

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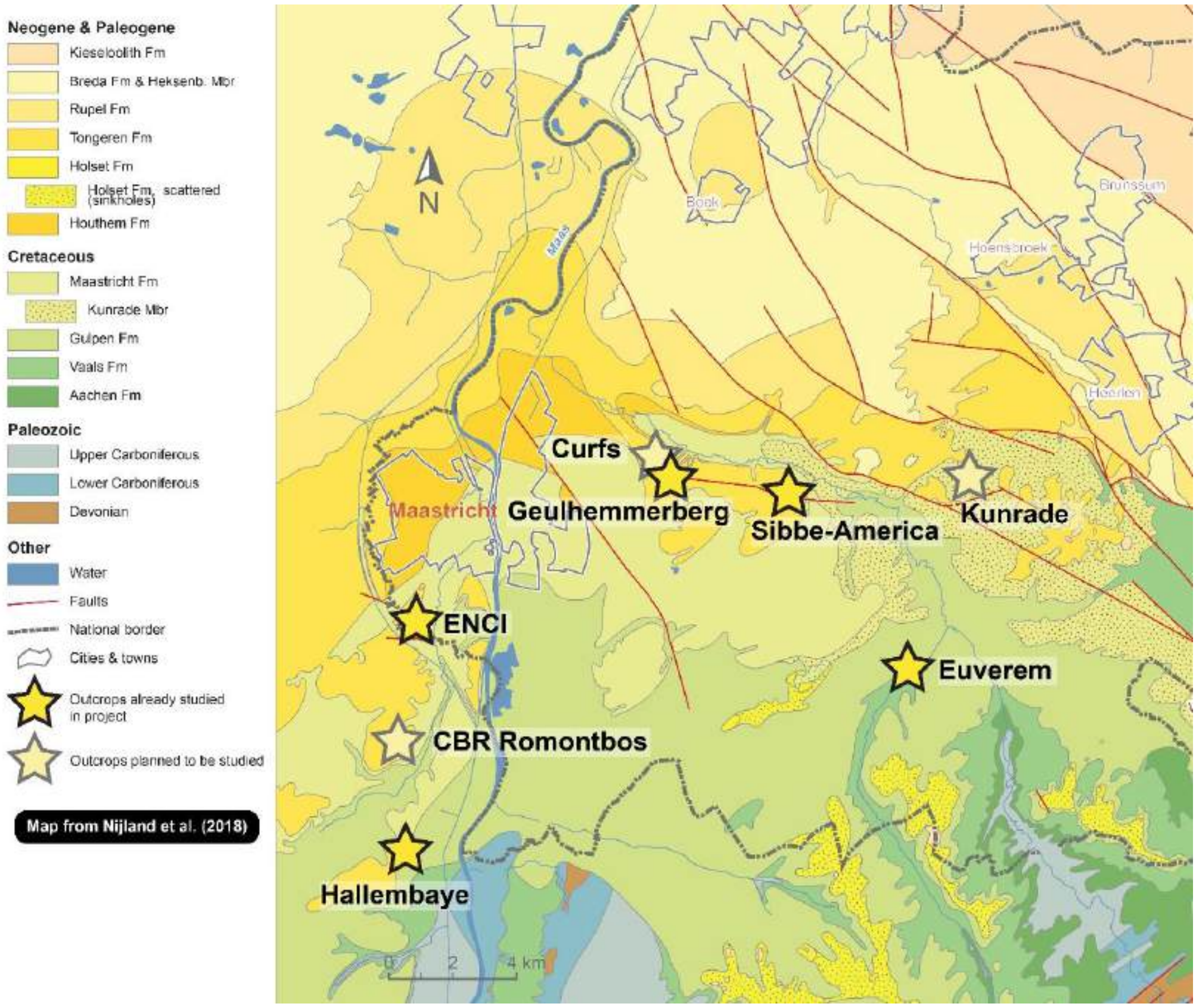

Figure 1. Geological map of the Maastrichtian type area, based on Nijland *et al*. (2018), with a selection of outcrops sampled within the context of the Maastrichtian Geoheritage Project.

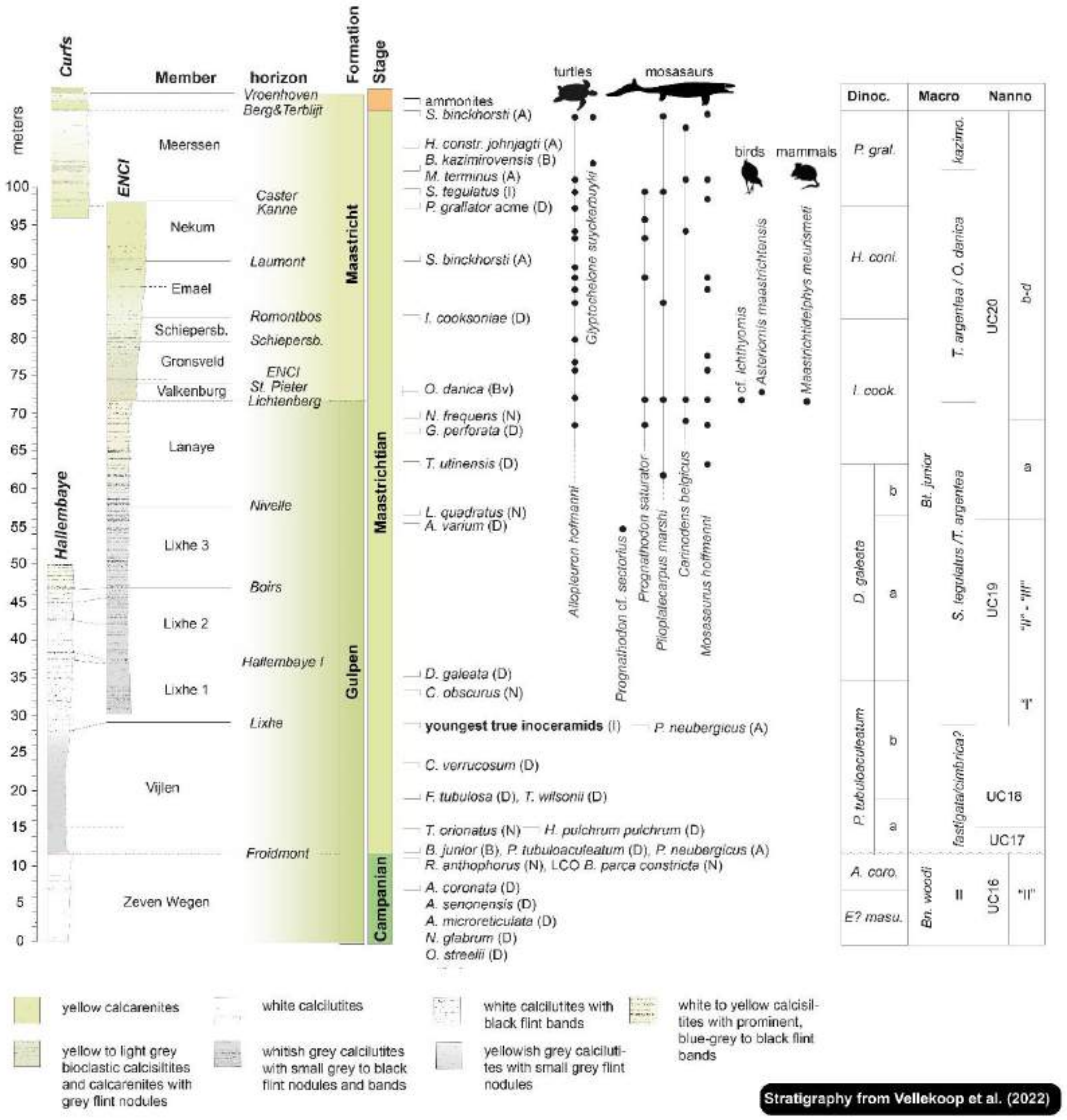

Figure 2. Overview of the litho- and biostratigraphy of the type-Maastrichtian, with the occurrences of key vertebrate fossils, based on Vellekoop *et al*. (2022).

The marine reptile fauna of the Bekrit syncline (El Koubbat Formation, lower Maastrichtian), Middle Atlas Mountains, Morocco

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In recent years, the Upper Cretaceous phosphatic successions of Morocco have produced numerous specimens of unique and varied marine reptiles (Bardet *et al.,* 2005a, b; Schulp *et al.,* 2009; Vincent *et al.,* 2011; Longrich *et al.,* 2021a, b, 2022, 2023, 2024; Rempert *et al.,* 2022). While the central phosphate basins at Oulad Abdoun and Ganntour have received most attention, phosphatic sediments in the northern Middle Atlas region also yield Cretaceous fossils. The locality of Bekrit (Bakrit), referred to as the Bekrit Syncline, is situated near the village of Bekrit, south of Timahdite and south-west of Boulemane, in the Middle Atlas Mountains of Morocco.

Geographical and stratigraphical setting. Phosphatic marine sedimentary rocks in the northern Middle Atlas Mountains result from the transgression of an epicontinental sea from the Atlantic into central and southern Morocco between the Late Cretaceous and Middle Eocene (Herbig, 1987, 1988). These successions are coeval with the economically important central Moroccan phosphate basins at Ganntour and Oulad Abdoun (Herbig & Trappe, 1994).

Post-Jurassic sedimentation in the northern Middle Atlas begins with limestones and marls of Cenomanian-Turonian and Santonian age. Rahhali (1970) described the litho- and biostratigraphy of the northwest flank of the Bekrit Syncline using foraminiferal faunas to establish the Oued Izem Formation (Campanian), the El Koubbat Formation (Maastrichtian) and the Irbzer Formation (Danian) (Fig. 1). These strata are overlain by the Bekrit-Timahdit Formation which is of Thanetian to mid-Lutetian age.

The El Koubbat Formation consists of 130 m of dark phosphatic and bituminous marls and clays. The selachian fauna comprises abundant remains of *Squalicorax*, *Serratolamna* and *Scapanorhynchus* (Noubhani & Cappetta, 1997). The presence of *Sq. benguerirensis* suggests biostratigraphical correlation with levels L6/L5 at Benguérir in the Ganntour Basin (Cappetta *et al.,* 2014a, b).

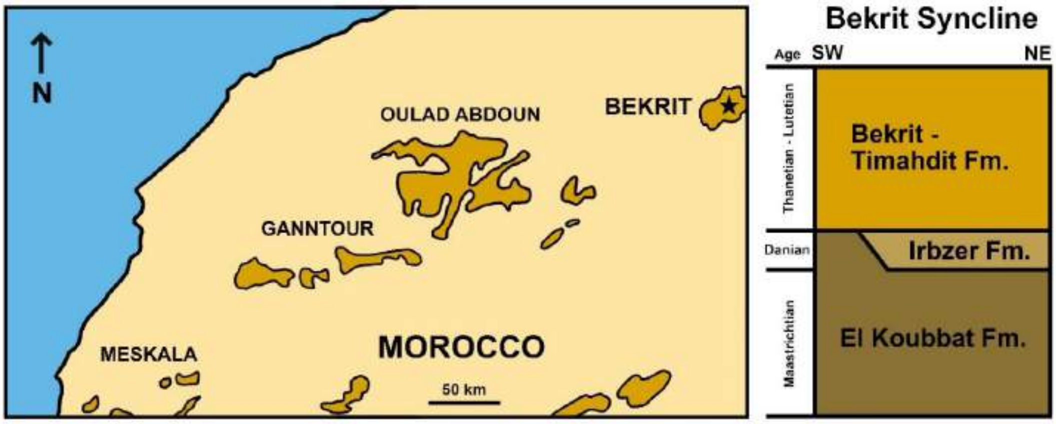

Figure 1. Left: Cretaceous phosphate deposits in Morocco. **Right:** Stratigraphical units at the Bekrit Syncline (modified from Herbig & Trappe, 1994).

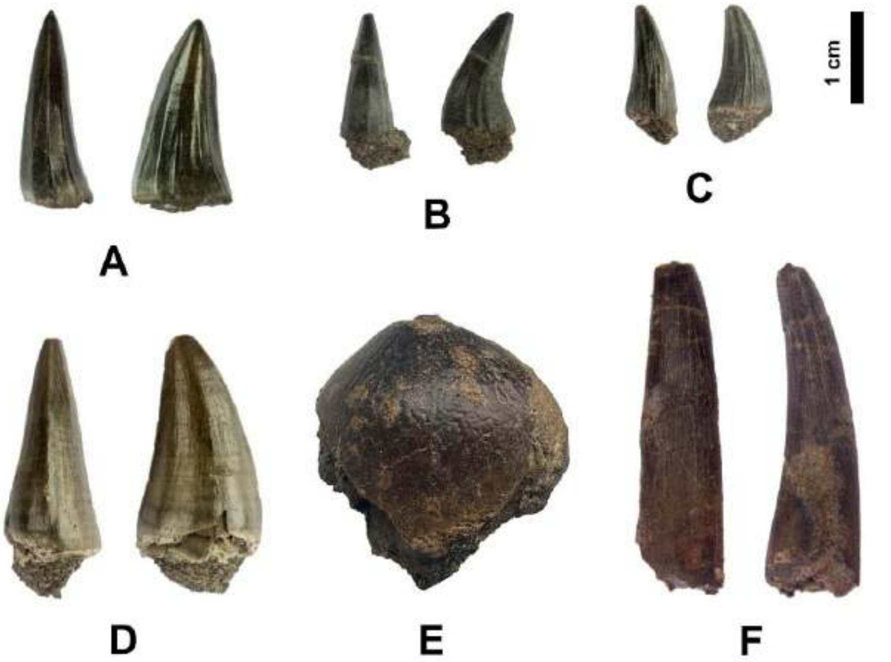

Figure 2. Mosasaurids and plesiosaurs from the Upper Cretaceous (lower Maastrichtian) of the Bekrit Syncline, near Bekrit-Timhdite, Morocco; **A**, *Mosasaurus* sp.; **B,** Halisaurinae indet.; **C,** *Gavialimimus* sp.; **D,** Prognathodontini indet.; **E,** *Globidens* sp.; **F,** Elasmosauridae indet. Teeth are shown in posterior and lateral views, except for E.

Fauna. Mosasaurids are represented by five taxa: an indeterminate halisaurine, the plioplatecarpine *Gavialimimus* sp. and three mosasaurines, *Globidens* sp., *Mosasaurus* sp. and an indeterminate prognathodontin. Tylosaurines are not currently known from the area. In addition to mosasaurids, an indeterminate elasmosaurid plesiosaur is also present.

Halisaurine teeth are hook-like in shape due to strong posterior curvature at half the crown height (Bardet *et al.,* 2005b). These teeth are characterised by small and pointed crowns with uncrenulated anterior and posterior carinae, smooth enamel and subcircular basal cross-sections. Shallow grooves near the crown base, such as those on *P. serpentis*, are present on some specimens (Longrich *et al.,* 2021a).

Teeth of *Gavialimimus* are uncommonly found at the Bekrit Syncline, matching the description of *"P." ptychodon* from the Oulad Abdoun (Arambourg, 1952, pl. 39, figs 1-7) and "Platecarpinae indet." from the Maastrichtian of Angola (Antunes, 1964, pl. 26, fig. 11). They consist of small crowns, with uncrenulated anterior and posterior carinae, acute apices, ovate basal cross-sections and enamel consisting of numerous apicobasal striations extending two-thirds of the crown height.

Globidens is the rarest mosasaur found at the Bekrit Syncline. Teeth are short and bulbous, with constricted crown bases, poorly defined apical nubbins, absent carinae and thick anastomosing enamel. Unlike *G. phosphaticus*, no vertical sulci are present on the medial or lateral faces (Bardet *et al.,* 2005a).

Teeth of *Mosasaurus* are the most abundant mosasaurid remains at the Bekrit Syncline and are readily recognised by the presence of well-defined enamel facets dividing the tooth surface into numerous flat planes. They are further characterised by the possession of D-shaped basal cross-sections, medially curving apices, lingual faces larger than the labial ones, and two well-developed and crenulated carinae.

Prognathodontin teeth consist of robust crowns with crenulated carinae, blunt apices, anastomosing enamel and subcircular basal cross-sections. These teeth can be either unicarinate anteriorly, bicarinate, or unicarinate posteriorly depending on whether the tooth originated from the anterior dental margin, mid-posterior margin or pterygoid jaw.

Elasmosaurid teeth are found at the Bekrit Syncline at considerably lower frequency compared to elasmobranchs and mosasaurids. They are long, slender, slightly recurved and exhibit mild labiolingual compression. Their enamel bears weakly defined anastomosing striae.

Palaeobiogeography. Initial sampling suggests the Bekrit Syncline contains a rich diversity of marine reptiles. The mosasaurid content is typical of the southern Mediterranean Tethys and the presence of archetypal southern taxa such as *Globidens* and *Gavialimimus* is consistent with other Upper Cretaceous phosphatic deposits from Africa (Angola, Morocco) and the Middle East (Israel, Jordan, Syria) (Bardet & Pereda-Suberbiola, 2002; Bardet, 2012).

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Rediscovering the Upper Cretaceous and Danian of the south-east Netherlands: recent research initiatives of the Geological Survey of the Netherlands

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Historically, the Geological Survey of the Netherlands (TNO-GDN) was very active in the south-eastern part of the country, better known as South Limburg. A long history of coal mining led to the presence of a permanent office in the city of Heerlen. Some 25 years ago that office was closed and activities of the survey were concentrated in Utrecht. However, the community of amateur geologists remained very active, but the Survey focused on other areas for mapping.

Now, 100 years after opening of the Geological Bureau in Heerlen, the interest of the Geological Survey of the Netherlands has once again shifted to South Limburg. An important reason for this is the abstraction of drinking water from the Upper Cretaceous and Danian succession, which is the main aquifer in the area. Many of the springs and brooks in the area show nitrate concentrations above 50 mg/L, due to leaching of agricultural fertilisers. This eutrophication has led to changes in vegetation. High nitrate concentrations are also found in groundwater, thus having an impact on the public and private water supply (Hendrix & Meinardi, 2004). Due to these high nitrate concentrations groundwater quality was considered to be insufficient in 2015 according to the EU Water Framework Directive (Planbureau voor de Leefomgeving, undated).

Current numerical groundwater flow models of South Limburg are based on the Digital Geological Model (DGM v2.2) and hydrogeological model REGIS II of TNO-GDN. Simulation of groundwater quantity and quality with these numerical groundwater flow models remains unsatisfactory, especially at local scales (Pors, 2011). This hampers predictions of the effects of groundwater management measures aimed at reducing nitrate concentrations.

The Upper Cretaceous and Danian succession forms a so-called dual porosity aquifer. The complexity of the flow system in this aquifer is determined primarily by the degree of karstification (Teutsch, 1993). Karstification has taken place but a mature karst system is not present in South Limburg (Van Rooijen, 1993). Only the upper 40 m of the Cretaceous aquifer are thought to have been karstified to a certain degree (Vernes *et al.*, 2009). However, estimates of hydraulic conductivity of REGIS II that are based on this assumption do not match measured values well (Vernes *et al.*, 2018).

The current geological model (DGM v2.2, TNO-GDN, 2024a) and derived hydrogeological model (REGIS II v2.21, TNO-GDN, 2024b) do not provide sufficient detail and accurate information of the Upper Cretaceous and Danian succession to simulate groundwater quantity and quality correctly. One of the reasons for this is that the models only represent formation-level detail of the stratigraphy, even though a more detailed stratigraphical, but not formalised, framework is available (Felder & Bosch, 2000). Additionally, as explained above, the primary and secondary porosity and permeability of the chalk need to be incorporated better into the hydrogeological property model of the region.

For these reasons, TNO-GDN has started the GeoZuid mapping project in collaboration with the Province of Limburg. The target area of the project is the southern part of the province. As part of this project, one us (M. Kroth, PhD student) investigates the sedimentology and hydrological properties of the Upper Cretaceous and Danian succession in detail. Added to this is an effort to enlarge the amount of subsurface data from the area for the studied succession. This is done by obtaining geophysical borehole logs from existing boreholes and historic water wells. The project also aims at incorporating data from the neighbouring countries.

The presentation of this paper will guide you through some of the history of the geological mapping in the region of the original Maastrichtian type section, and illustrate the modern mapping approaches adopted.

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A gigantic, hook-bearing coleoid from the end-Cretaceous of Denmark

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Gigantism is pervasive in the Coleoidea during the Late Cretaceous; it has been interpreted as resulting from an evolutionary "arms race" with marine reptiles and large actinopterygian fish (Fuchs & Stinnesbeck, 2021). Large-bodied coleoids are markedly absent from Maastrichtian strata and the entire Cenozoic. Causes for this apparent termination of gigantism have so far not been established. Here we present a partial arm hook (Natural History Museum of Denmark collections, NHMD 625044) of a new coleoid from the Upper Cretaceous (~69.5 Ma) pelagic chalk of the Møns Klint Formation (eastern Denmark), documenting the first piece of evidence of a Maastrichtian-aged giant coleoid. This novel taxon is assigned to the Belemnotheutidae and extends the stratigraphical range of this family by ~45 myr (see Doyle & Shakides, 2004; Rogov & Bizikov, 2006). While other belemnotheutid taxa are of small to-medium size (~30-70 cm), the Maastrichtian arm hook is approximately ten times larger than hooks from other belemnotheutids, and an approximately 4-metre-body length is estimated for the new taxon. The occurrence of a giant coleoid in the Maastrichtian suggests that gigantism trends persisted until the end of the Mesozoic, and subsequently terminated at the K/Pg boundary.

Taxonomic affinities. Based on the scoring of seven discrete characters observed in representative genera of hook-bearing coleoid clades, the closest affinities with the family Belemnotheutidae were recovered for the new coleoid from Møns Klint. Taxa included in our appraisal were the phragmoteuthid *Phragmoteuthis montefiorei* (Donovan, 2006), the diplobelid *Clarkeiteuthis conocauda* (Fuchs *et al*., 2013) and the belemnotheutid *Belemnotheutis antiquus* (Donovan & Crane, 1992). NHMD 625044 is morpho-functionally distinct from large "mega-hooks" of passaloteuthid belemnopseins, most notably based on the apparent absence of an inner cavity in the latter (Fuchs & Hoffmann, 2017); these were therefore excluded from the taxonomic appraisal. Our assessment has revealed very little similarity between NHMD 625044 and *P. montefiorei* (one shared character) and a slightly closer similarity to *C. conocauda* (two shared characters). In contrast, NHMD-625044 is morphologically congruent with hooks preserved in specimens of *B. antiquus*, with both showing a slender construction and gentle hook curvature and bearing striae. A smooth shaft lacking spurs, as documented in *B. antiquus* (Fuchs *et al*., 2013), is inferred for the novel belemnotheutid despite the fact that NHMD 625044 represents an incomplete hook. The inner section of this specimen is preserved to a greater extent than the outer, and shaft spurs in belemnoid hooks generally occur along the inner margin. This suggests a fourth shared character with *B. antiquus*.

The Maastrichtian coleoid arm hook record. Hooks are a key component of the arm armature of several coleoid clades (Fuchs *et al.*, 2021). However, despite the fact that coleoids were diverse and geographically widespread during the Late Cretaceous, arm hooks are globally rare in Upper Cretaceous deposits, in stark contrast with fairly abundant records from the Jurassic and Lower Cretaceous (Klug *et al.*, 2020). This likely is a taphonomic artefact, as other body fossils from potentially hook-bearing coleoids (e.g., phragmocones, rostra) occur relatively frequently in Upper Cretaceous deposits. Coleoid hooks are notably scarce in the Maastrichtian, with exceedingly scant records in Europe and absence from other deposits globally. Four morphotypes are now known, each represented by a single or very few specimens: *Striatuncus cretacicus* and *Paraglycerites* parasp. from the north-east German island of Rügen (Reich & Frenzel, 1997), cf. *Paraglycerites* from Evrytania in Greece (Klug *et al.*, 2020) and NHMD 625044. Apart from the Møns Klint Formation material, these arm hook morphotypes are classified according to a parataxonomic framework, as it is challenging to assign them to coleoid orthotaxa (Fuchs & Hoffmann, 2017).

Size estimates for the "Møns Klint belemnotheutid". Estimations of mantle, arm and total body lengths of the novel belemnotheutid are based on comparison with the well-studied belemnotheutid *Belemnotheutis antiquus*, in function of arm hook-length. *Belemnotheutis antiquus* has 3- to 5-mm-long arm hooks, and complete, well-preserved specimens of this species (e.g., Natural History Museum of London, NHMUK PI 25966) indicate a ~150 mm mantle length. Scaling up based on arm hook measurements would suggest a 2,500 ± 150 mm mantle length (ML) for the "Møns Klint belemnotheutid". Fuchs (2020) established a framework for determining coleoid size classes based on mantle length. Within this, the new belemnotheutid is considered as a "very large" coleoid (ML ≥ 1,500 mm), placing it in the same size class as the largest Late Cretaceous coleoid taxa such as *Yezoteuthis* and *Haboroteuthis* (Fuchs & Stinnesbeck, 2021). The total body length for this coleoid is extrapolated to be approximately 4 m, including arms measuring ~1.25 m; more complete material would be required to verify these estimated dimensions.

Implications for the evolutionary history of belemnotheutids. The family Belemnotheutidae has previously been considered to range from the upper Middle Jurassic to the Lower Cretaceous. Four definitive genera are known: *Belemnotheutis* (lower Callovian-upper Kimmeridgian), *Acanthoteuthis* (Callovian-lower Aptian?), *Antarctiteuthis* (Tithonian-Berriasian) and *Volgobelus* (Callovian-Hauterivian) (Doyle & Shakides, 2004). Phragmocones of ?*Acanthoteuthis* sp. from the lower Aptian of the Chegem River area (Russia), represent the stratigraphically youngest belemnotheutid occurrences (Rogov & Bizikov, 2006). The "Møns Klint belemnotheutid" extends the stratigraphical range of belemnotheutid coleoids by ~45 Ma to the upperlower Maastrichtian, therefore representing a late surviving member of this family and revealing persistence throughout the Cretaceous. The very large size estimated for this new taxon indicates the first occurrence of gigantism in the Belemnotheutidae. Belemnotheutids are generally diminutive and do not exceed a total body length of ~30 cm ("small" coleoid size class *sensu* Fuchs, 2020). It is interesting to note that later occurrences of *Volgobelus* (*V. colossus*) from the Hauterivian of Ulyanovsk Oblast (Russia) are represented by partial, massive phragmocones roughly three times larger than those of small-bodied belemnotheutids such as *Belemnotheutis* (Rogov & Bizikov, 2006). These comparatively large fossils indicate a ~70-

cm-total body length (ML ≈ 40 cm; "medium" size class), suggesting a transitional form between diminutive, earlier taxa and the gigantic Maastrichtian taxon. The presence of a very large-bodied taxon in the Maastrichtian is therefore consistent with apparent trends of size increase in the Belemnotheutidae.

Late Cretaceous coleoid gigantism. Gigantism in the "Møns Klint belemnotheutid" is highly significant, as it underscores a broad trend of very large proportions in the Coleoidea during the Late Cretaceous (Fig. 1). Giant coleoids are well represented in Turonian-Campanian deposits of the Pacific Realm (e.g., putative Oegopsida: Tanabe *et al*., 2006), as well as the Western Interior Seaway (e.g., Muensterelloidea; Fuchs *et al*., 2020). A large-bodied potential octobrachiate has recently been recorded from Turonian shallow-water deposits in central Russia (Mironenko, 2023). NHMD 625044 documents the first occurrence of a giant coleoid in the epeiric "Chalk Sea", which covered north-west Europe during the Late Cretaceous. As a result, it is becoming increasingly clear that very large-bodied coleoids were important components of Late Cretaceous pelagic ecosystems, particularly in epicontinental seas of the Northern Hemisphere. Moreover, considering the stratigraphical position of NHMD 625044 (mid-Maastrichtian), it is revealed that trends in coleoid gigantism persisted throughout the Late Cretaceous, up to the end of the Mesozoic. Subsequent dramatic size reduction, and giant coleoid absence in the Cenozoic, suggests that the termination of coleoid gigantism was linked with the K/Pg boundary event. Particularly, only small-bodied coleoids (<20 cm mantle length) are known throughout the Paleogene (see Fuchs, 2023). This is attributed to global ecological restructuring in marine biotas resulting from the K/Pg mass extinction event. Therefore, as well as representing the first Maastrichtian large-bodied coleoid, the "Møns Klint belemnotheutid" is purported to be the last giant coleoid prior to the K/Pg mass extinction.

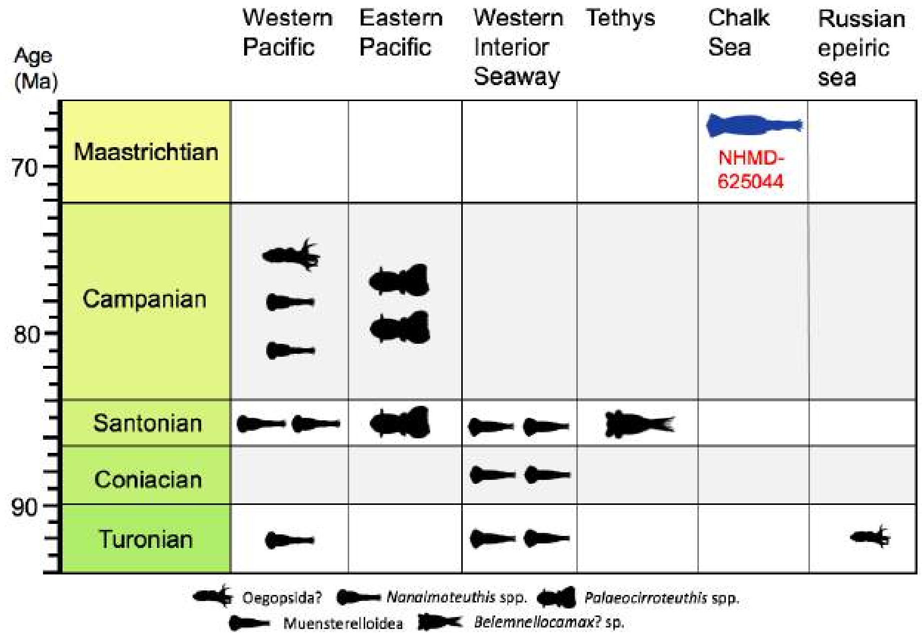

Figure 1. Stratigraphical and geographical distribution of gigantic coleoids during the Late Cretaceous. The better-established presence in the Western Interior and Pacific realms can potentially be attributed to more intense, and longer-lasting sampling in those regions. All

occurrences are concentrated within the Northern Hemisphere. NHMD 625044 represents the sole belemnotheutid in this assemblage. Data collated after Fuchs & Stinnesbeck (2021), Mironenko (2023), Tanabe & Misaki (2023) and Voiculescu-Holvad & Sheldon (work underway).

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The Dercetidae from the type Maastrichtian – an enigmatic group of bony fish

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Dercetids, an extinct family of highly specialised marine fish, are characterised by a slender, elongated body and snout; the body is covered with one or more rows of typically heart-shaped or triradiate scutes (Silva & Gallo, 2011; Taverne & Goolaerts, 2015). They first occur in the Cenomanian and range up into the lower Paleocene (Danian) (Davis, 1890; Taverne, 1987, 2005; Chalifa, 1989; Silva & Gallo, 2011). Dercetids are found in marine deposits across Europe, North Africa, North and South America and Asia (Agassiz, 1834; von der Marck, 1858, 1863; Hay & Day, 1903; Taverne, 2005, 2006a, b; Silva & Gallo, 2011; Taverne & Goolaerts, 2015; Vernygora et al., 2017; Díaz-Cruz *et al*., 2022; Chida *et al*., 2023).
Fish remains are quite common in the type Maastrichtian, although their record is confined mainly to isolated teeth, scales and vertebrae (Friedman, 2012). They are mostly found inside the ichnofossil (burrow) *Lepidenteron lewesiensis* (Mantell, 1822; Jagt, 2019), but associated remains or more or less complete specimens are quite rare (Friedman, 2012; Taverne & Goolaerts, 2015). To date, five species of Dercetidae have been recorded from the type area of the Maastrichtian Stage, namelu *Dercetis triqueter*, *Ophidercetis italiensis*, *Cyranichthys jagti*, *Apuliadercetis indeherbergei* and *Pelargorhynchus grandis*, based on a total of seven specimens (Taverne & Goolaerts, 2015; Wallaard *et al.*, 2019), which makes it a group with a high diversity.

Recently, several new specimens have been discovered during fieldwork and in public and private collections alike. These specimens will add to the diversity and augment our knowledge of members of the family Dercetidae in the type Maastrichtian (Figs 1, 2).
Institutional abbreviation. MAB, Oertijdmuseum, Boxtel, the Netherlands.

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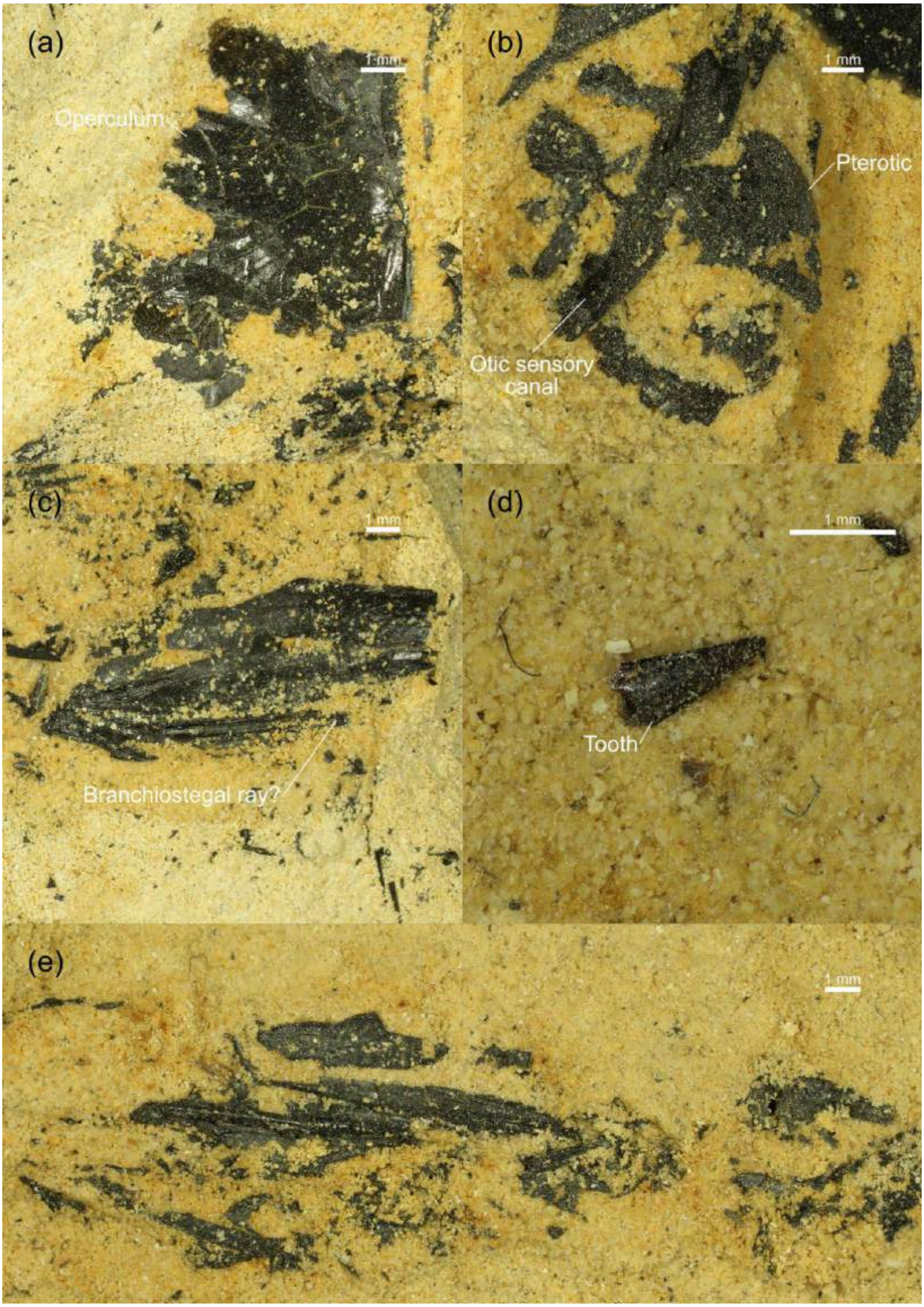

Figure 1. *Cyranichthys* sp. (MAB 16118); (a) operculum; (b) lateral side of cranium; (c) potential branchiostegal ray; (d) single isolated tooth; (e) rostrum.

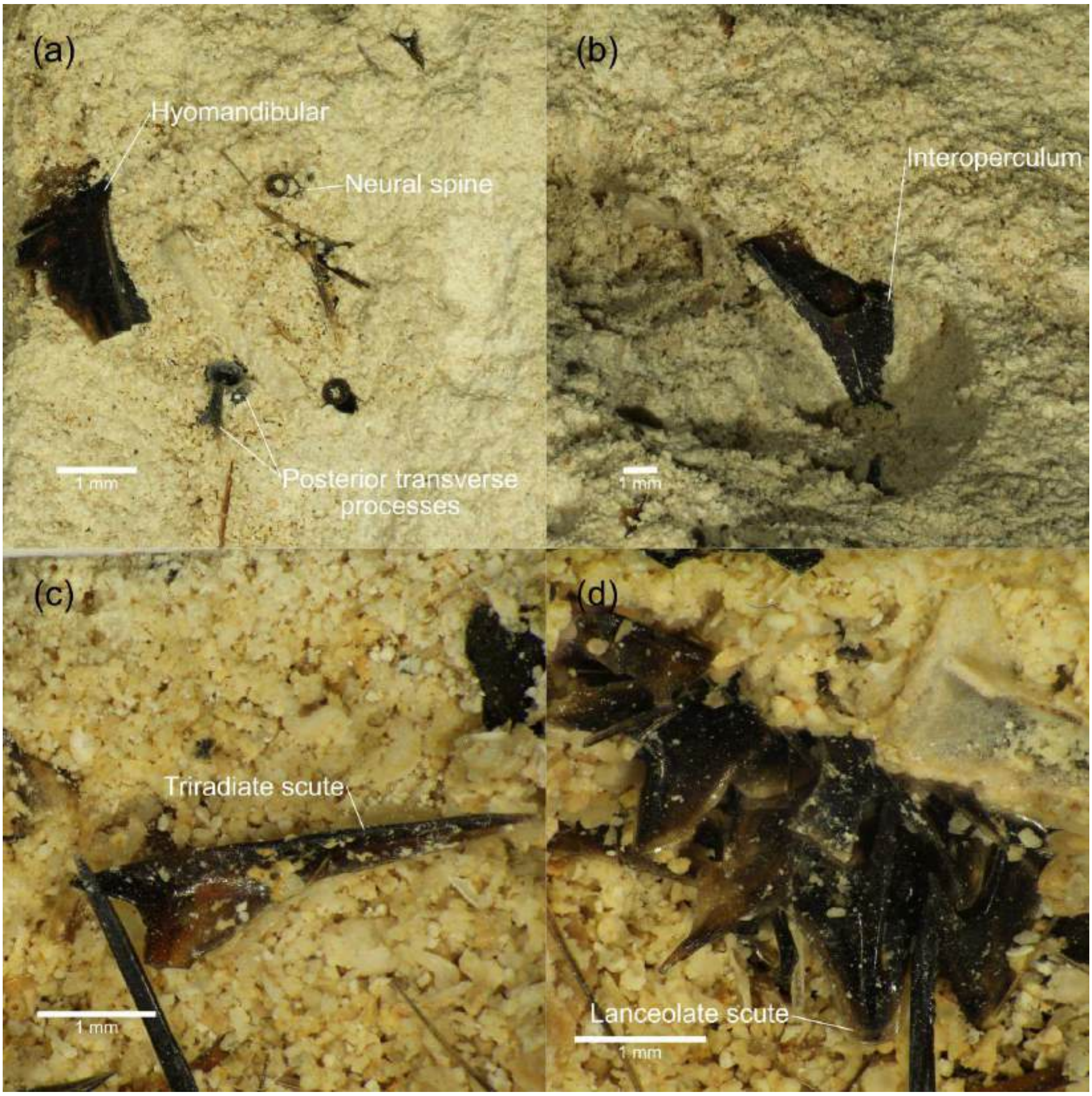

Figure 2. *Dercetoides* sp. (MAB 16117); (a) hyomandibular and isolated vertebrae; (b) interoperculum; (c, d) two morphotypes of scutes in the present specimen.

Old wine in new bottles? Emerging intellectual networks in Maastricht during the French Period of 1794-1815

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In October 1778, the fossilised skull of a large prehistoric creature, at first thought to be a crocodile or a sperm whale relative, was discovered in the Sint-Pietersberg near Maastricht (Faujas Saint Fond, 1798-1803). This significant find garnered attention both locally and internationally. The skull was acquired, preserved and presented by Canon Godding (Hovens, 2020). Here we examine the intellectual networks in Maastricht during the period immediately preceding and encompassing the French era, roughly from 1775 to 1815 – a particularly tumultuous time for the city (Spiertz, 1964). Revolutionary fervour was being ignited throughout the region, driven by both ruling authorities and those challenging their power.

The French Revolution erupted in 1789, triggering a wave of upheavals that also reached Brussels and Liège in the same year. As a consequence, hundreds of clergy and nobility fled France, seeking refuge in Maastricht before continuing their escape, often towards Germany. Maastricht, being a condominium of Liégeois and Dutch powers, offered a unique haven during these chaotic times.

The city endured French sieges in 1793 and 1794, which inflicted considerable damage. Subsequently, Maastricht, along with the Southern Netherlands, was annexed by France in 1795. Consequently, Maastricht was never part of the Kingdom of Holland nor of the Batavian Republic. In 1815 it became part of the Netherlands/Dutch Kingdom.

The French annexation brought about profound changes. For the first time, Maastricht became the capital of a larger region, namely the French Département de la Meuse-Inférieure, a new administrative division formed from a complex amalgamation of various state forms and political entities that now roughly correspond to the provinces of Belgian Limburg and Dutch Limburg (Jacobs, 2019). Maastricht lacked a tradition of administering such a vast area, as the city was never home to a central government larger than the city itself.

During this period of upheaval, the fossil skull, later to be named *Mosasaurus hoffmanni*, was nationalised by the French government and transported to Paris (Lingham-Soliar, 1995; Mulder, 1999; Street & Caldwell, 2017; Schulp *et al.*, 2024). Rumour had it that the skull was bought for 600 bottles of wine, but no evidence for this has been found. Alongside the mosasaur skull, numerous art treasures and book collections from across the department were also seized transported to Paris. Jan Pieter Minckelers, a scientist, former professor at Louvain university and inventor known best for his development of gas lighting and from

1797 a professor at the École Centrale in Maastricht, sent a second mosasaur specimen to Paris (Spekkens, 1951). Who were the collectionneurs in those days and in what intellectual context in Maastricht did this collection export take place?

A significant portion of the intellectual elite in Maastricht consisted of commanders from the city's garrison, as well as of school professors, medical doctors, pharmacists and self-educated merchants. However, during the French era, Maastricht's importance as a garrison town diminished, resulting in the absence of a part of this intellectual elite during that period. This article tries to shed light on these dynamic intellectual networks and the significant historical shifts that shaped Maastricht during the late 18th and early 19th centuries.

Research questions

During the turbulent period of the first half of the French era in Maastricht, a pivotal question arises: was a new intellectual network established and, if so, how was it established? This question serves as the cornerstone of our inquiry, prompting us to delve into the complexities of this historical period.

One of the fundamental aspects we explore is the genesis of this network – who were its architects, and what impelled its creation? Central to this investigation is the role played by the establishment of the educational system of Maastricht, of which the École Centrale takes a central place (Evers, 1992; Schaapveld, 2017). We examine the key figures involved in the school's inception, including its educators, as well as the collectionneurs of scientific and historical objects (Wetzels, 2022). Where did they originate from, and what calibre of instruction did they impart?

Moreover, we scrutinise the composition of the student body. Who were these pupils, and what were their backgrounds? Understanding their familial ties and societal roles provides invaluable insight into the fabric of this nascent intellectual community. Additionally, we conduct a comparative analysis between the École Centrale in Maastricht and its counterparts in Ghent, Mons and Liège, posing analogous inquiries to elucidate overarching patterns and disparities (Isaac & Sorgeloos, 2004; Maours, 1961).

Furthermore, we explore the networks from which this intellectual enclave emerged. Was it an organic outgrowth of existing affiliations, or was it made from scratch? In this context, we examine the role of the Maastricht City Library—a repository of knowledge that intersected with the burgeoning intellectual scene. Curiously, unlike its counterpart in Ghent, the City Library in Maastricht did not remain closely affiliated with the school, prompting questions regarding its autonomy and influence.

Lastly, we investigate the fate of the erstwhile intellectual elite of the garrison. Did segments of this elite remain in Maastricht, and if so, how did they integrate into or diverge from the emergent intellectual landscape? By addressing these multifaceted inquiries, we endeavour to construct a comprehensive narrative elucidating the formation and dynamics of the intellectual network that took root amidst the tumultuous backdrop of Maastricht's French era.

Aims

The aims of our research are multifaceted. Primarily, we seek to portray the tumultuous nature of this historical period. By contextualising the intellectual milieu within the broader tapestry of revolutionary change, we aim to underscore the volatility and uncertainty that characterised Maastricht during this era.

Moreover, our investigation aims to shed light on the novelty and fragility of these emergent networks. Through thorough inquiry and analysis, we seek to delineate the evolving nature of these networks amidst a backdrop of instability and change. However, it is imperative to acknowledge the inherent limitations of this study. While we endeavour to unravel the complexities of these networks, we do recognise this research may only scratch the surface. As such, this study serves as an introductory exploration, offering a roadmap for future inquiries into these networks. We aim to provide insights into the methodologies and source materials available for such investigations.

Methods

Our research primarily involves a comparative analysis of secondary literature and already explored research done by the authors. We examine recent publications on the French era in Maastricht and the Limburg regions to understand how scholarly perspectives on intellectual networks during this time have evolved.

Additionally, we conduct archival research to identify primary sources relevant to our inquiry. While we do not aim for exhaustive archival investigation, we search for materials that can support and enrich our understanding of these networks.

By combining historical analysis, literature review, and archival investigation, we offer a nuanced understanding of Maastricht's intellectual landscape during this tumultuous period, enabling to sketch a deeper comprehension of its past.

Note: The title “old wine” refers to the supposed 600 bottles of wine that were paid for the mosasaur skull, as well as to the underlying question whether the intellectual networks postdating the French period were really new networks, or rather old existing networks reintroduced.

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Quantifying extinction and ecological change across the Cretaceous-Paleogene (K/Pg) boundary on Seymour Island, Antarctica

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The highest southern latitude onshore record of the Cretaceous-Paleogene (K/Pg) mass extinction is found on Seymour Island, Antarctica. The boundary occurs within the upper levels of the ~1,100 m-thick López de Bertodano Formation, a highly expanded (sedimentation rates of 0.2 cm/yr) and abundantly fossiliferous sequence of silty sandstones with occasional glauconite-rich horizons. The boundary is marked by a small iridium anomaly, linked to the Chicxulub bolide impact, and the last occurrence of Cretaceous ammonites and microfossil taxa. These occur ~30 cm below a 1- to 5-m-thick glauconitic sandstone interval which outcrops across southern Seymour Island.

Previous work has recognised the profound change in the marine micro- and macrofauna at this horizon (Elliot *et al.*, 1994; Witts *et al.*, 2016; Whittle *et al.*, 2019; Da Silva *et al.*, 2023). However, there has been little work examining ecological change across the boundary at high latitudes, and persistent debate as to the timing of the K/Pg mass extinction in Antarctica. Tobin *et al*. (2012) and Tobin (2017) used faunal range data from Seymour Island to suggest a two-phase extinction, with losses at the boundary itself and a precursor extinction during the late Maastrichtian which they linked to a phase of climate warming driven by the Deccan Traps Large Igenous Province. Witts *et al*. (2016) and Whittle *et al*. (2019) refuted this claim based on range data from large taxonomically revised macrofossil collections made by the British Antarctic Survey (BAS). These studies suggested that the precursor extinction was an artifact of poor sampling and poorly resolved taxonomic identifications.

During the 2023-24 field season we conducted a detailed study of the K/Pg boundary interval on Seymour Island, measuring multiple sections and making quantitative fossil collections in the uppermost Maastrichtian and lowermost Danian of the López de Bertodano Formation along strike for ~2.5 km. Our new collections extend the stratigraphical ranges of several marine invertebrate taxa closer to, and in one case across, the K/Pg boundary. They also indicate that several undescribed species of benthic molluscs are present in the upper López de Bertodano Formation below the K/Pg boundary.

Data from our quantitative sampling (timed fossil collections made over a standardised area) indicate that while existing macrofossil collections from Seymour Island may provide an accurate picture of species richness, they do not adequately capture the ecological composition of the marine ecosystem in either the pre- or post-boundary intervals. Shifts in the dominance and abundance of particular taxa do occur within the final ~1 million years of the Maastrichtian, before a profound ecological change at the K/Pg to an early Danian community numerically dominated by the large infaunal bivalve *Lahillia larseni*. These ecological changes, as well as their environmental context and drivers, are the focus of this presentation.

Preliminary field investigations also support a single extinction event at the K/Pg boundary in Antarctica (Witts *et al*., 2016; Whittle *et al.*, 2019). Apparent early disappearances of macrofossil taxa on Seymour Island are likely a result of changing outcrop conditions in the uppermost Maastrichtian, an interval marked by an increase in steep scarp slopes *vs*. easy-to-sample dip-slopes, and a rarity oflarge early diagenetic carbonate concretions in which most macrofossils are found.

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The ChaSE project: ChaIk Sea Ecosystem and Cretaceous environmental change in the Chalk Group of the United Kingdom

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During the Late Cretaceous, pelagic chalk deposition occurred throughout marine basins in north-west Europe. In the United Kingdom, the onshore British Chalk Group provides a continuous and well-exposed rock and fossil record spanning the Cenomanian to early Maastrichtian stages (100.5 – ~69 Ma). This interval contains numerous key climactic events, including peak Cretaceous warming and a biodiversity crisis across the Cenomanian–Turonian boundary and Oceanic Anoxic Event 2 (Jenkyns *et al*., 2004; Jenkyns, 2010), the highest global sea levels of the last 250 million years (Hancock, 1989; Van der Meer *et al*., 2022), and a long-term cooling trend from the Coniacian through to the Maastrichtian which included the lowest temperatures of the Late Cretaceous (O'Brien *et al*., 2017; Huber *et al*., 2018).

As an economically important resource, the UK Chalk Group has been studied and quarried for >200 years and a detailed stratigraphical framework is available (Hopson, 2005). High-resolution correlation is possible by litho-, bio-, chemo- and cyclostratigraphy (e.g., Gale *et al*., 2005; Jarvis *et al*., 2006; Pearce *et al*., 2020). The sequence is also abundantly fossiliferous, recording every trophic level expected in marine ecosystems from phytoplankton to apex predators. The Chalk has long been a target for fossil collectors (e.g., Gale & Cleevely, 1989), and huge collections are available in museums across the UK, although only a fraction of these have been published or are available in publicly accessible datasets.

This poster will showcase initial results from the ChaSE (Chalk Sea Ecosystems) project. We are conducting the first 'whole-ecosystem' study of the Chalk Sea using material from new field work conducted across the UK and combining this with the extensive samples available in historic museum collections. The Natural History Museum, London (NHMUK) contains a huge collection of more than 50,000 macrofossil specimens from the UK Chalk, including examples of rare taxa and material from historic localities that are no longer accessible.

Many of these specimens contain very limited metadata, and ages or stratigraphical position are often poorly constrained. To unlock this archive of ‘dark data‘ we are currently re-dating matrix samples from >1,500 vertebrate and invertebrate macrofossil specimens using a modified version of the calcareous nannofossil biostratigraphy of Burnett *et al*. (1998).

Using quantitative palaeoecological and morphometric analyses we are examining how taxonomic and functional diversity change throughout deposition of the UK Chalk Group, as well as ecological abundance and size changes in selected microfossil and invertebrate and vertebrate macrofossil taxa throughout the Cenomanian – Maastrichtian interval.Together these datasets will provide an unprecedented record of the effects of global Cretaceous climatic change on marine ecosystems at a variety of temporal and spatial scales, within the same depositional system.

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Tylosaurine diversity informed by morphological variation in extant *Varanus*

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Background and approach

Tylosaurines are mosasaurids (Squamata, Mosasauridae) characterised in part by long, rounded edentulous anterior extensions of the premaxilla and dentaries and giant body size. The earliest documented tylosaurines are from Turonian and Coniacian (~94-87 Ma) in Africa and south-western North America, and they are the first mosasaur clade to achieve gigantic (>7 m) body size during the Coniacian (~85 Ma) (Bell *et al.,* 2013; Jiménez-Huidobro & Caldwell, 2019). While they are arguably the least morphologically diverse mosasaur clade, they were extremely successful, spreading to Europe and Antarctica and persisting until the Maastrichtian (~71-66 Ma). In this work, I shall test recent hypotheses of tylosaurine mosasaur taxonomy and diversity informed by developmental biology of extant reptiles and an extensive new dataset of photographs, measurements and scans of over 500 mosasaur and extant *Varanus* specimens.

The most recent analysis of the Tylosaurinae posits that it comprises two genera (*Tylosaurus*,\ *Taniwhasaurus*) and seven valid species. Tylosaurine fossils are relatively common in Europe and the Western Interior Seaway, particularly in the Niobrara Formation of North America, from which two species are currently recognised: *Tylosaurus proriger* and *T. nepaeolicus*. Recent work (Jiménez-Huidobro *et al.,* 2016; Zietlow, 2020) has synonymised a third Niobrara species, *T. kansasensis*, with *T. nepaeolicus* because the former purportedly possesses immature character states observed in the better-sampled *T. proriger*. However, the underlying assumption of those studies was that all specimens considered *T. proriger* are valid referrals. Some of the assumptions underpinning prior studies are here explored, the validity of *T. kansasensis* reassessed and broader issues surrounding tylosaurine systematics addressed.

It is nearly impossible to identify with absolute certainty whether minor anatomical differences between fossil specimens are inter- or intraspecific. The preservation of relevant soft tissue features (e.g., integument) is too inconsistent to inform taxonomic identification, and genetic data are inaccessible for much of the fossil record. Therefore, palaeobiologists are limited to making taxonomic delimitations based primarily on skeletal morphology. Ideally, these decisions are informed by comparison to an extant relative for which general patterns of intra- *vs* interspecific variation are well understood to reduce the likelihood that they are misidentified.

Amniote embryogenesis follows a conserved sequence of major morphogenic events: (1) pattern formation (i.e., development of body plan); (2) development of major neurovascular structures and skeleton chondrification and (3) skeleton ossification (de Beer, 1937; Hanken & Thorogood, 1993).

Although many differences in adult morphology between species are necessarily derived from differences in embryogenesis, these differences occur *during* these aforementioned stages, and do not affect the sequence itself – i.e., no terminal structure can form prior to pattern formation, and a bone cannot ossify before it chondrifies. Therefore, although we cannot observe the embryogenesis of fossil taxa in real time as we can for extant taxa, we may assume that extinct amniotes also followed this order of developmental events and infer possible intraspecific variation in fossil taxa accordingly.

Extant squamate ontogeny assessment. Hypotheses of the phylogenetic placement of Mosasauroidea within Squamata are far from unanimous (e.g., Lee, 2005; Augusta *et al.,* 2022). However, regardless of their relationship to them, the skulls of both basal and derived mosasauroids are undeniably similar in gross morphology to varanids (e.g., elongate snouts, retracted nares, etc.), making extant representatives reasonable models for understanding the biological underpinnings of skeletal variation in mosasaurs (especially considering that there is no reason to suspect that neither group diverges from the standard patterns of amniote embryogenesis). Therefore, I here review previous studies of ontogenetic skeletal changes in extant squamates, and augment these with my own observation of intraspecific morphological variation across 16 extant species of *Varanus*. I identify the general *types* and *causes* of intraspecific variation, rather than discrete character differences, so that my observations are more likely to be representative of patterns in lizards generally.

Species hypodigms. I describe and compare the holotypes of *T. kansasensis* (FHSM VP-2295), *T. nepaeolicus* (AMNH FARB 1565) and *T. proriger* (MCZ VPRA 4374) using first-hand observations, CT data and photogrammetric models. I then identify *Tylosaurus* specimens that preserve material overlapping and unambiguously matching the morphology of each holotype of interest, and then use these specimens to supplement my concept of each species. I then reassess specimens referred to *T. proriger* informed by review and observation of intraspecific trends in extant lizards. Finally, I use these new species hypodigms to reassess the hypothesis that morphological differences between *T. kansasensis* and *T. nepaeolicus* are ontogenetic.

Results and discussion

Intraspecific variation in Varanus *and other extant squamates*. In varanids and other extant squamates, postnatal ontogenetic changes to skeletal morphology include a general increase in bone size and robustness, continuation of ossification and fusion of skull sutures. Diagnostic features, however, are present throughout all growth stages – i.e., a species is identifiable at all stages of post-hatching ontogeny, and changes in bone shape are attributable to bone growth, increased stresses from surrounding musculature and/or continued ossification of cartilage. Ontogenetic changes in the morphology of the quadrate and the position of the pineal foramen are central to resolving issues of taxonomic validity and the relationships of *T. kansasensis* and *T. nepaeolicus.* I therefore present the results for these below.

In my review of relevant literature as well as observation of *Varanus* specimens, I find that, although the quadrate increases in robustness, it does not change in overall shape as proposed for *Tylosaurus* by previous work (Jiménez-Huidobro *et al.,* 2016; Zietlow, 2020). Another ontogenetic change proposed to occur in *Tylosaurus* by previous work (Jiménez-Huidobro *et al.,* 2016; Zietlow 2020) is the posterior migration of the parietal foramen. However, in extant lizards, there is no evidence of “migration” during growth, nor evidence that the relationship with the frontal-parietal suture changes dramatically. Individual variation in the position of the parietal foramen does exist, but it is not associated with ontogeny. This is consistent with the conserved sequence of amniote developmental events: major neurovascular structures, such as the parietal foramen, are present prior to bone ossification and are therefore fixed in their relative position post-hatching.

***Comparison of* T. kansasensis *with* T. nepaeolicus.** The only informative bone that is preserved in both holotypes is the quadrate, which, notably, is only four mm larger in *T. nepaeolicus* than in *T. kansasensis*. Despite being effectively the same size, the quadrate differs in each specimen with respect to several features, including the shape and mediolateral curvature of the suprastapedial process, mediolateral thickness of the alar conch and anteroposterior expansion of the anterodorsal portion of the alar rim. I identify other specimens that match the holotype quadrates (e.g., *T. kansasensis* FGM V-43, *T. nepaeolicus* AMNH FARB 2167) and find that other morphological features (e.g., skull roof anatomy) previously attributed to ontogeny are in fact consistent across a range of specimen sizes: I find large specimens that possess the purportedly “immature” characters of *T. kansasensis*, and small specimens that possess the purportedly “mature” characters of *T. nepaeolicus*. I also identify several specimens of varying size that cannot be reliably referred to either existing species, and conclude that they may represent another new species. Within my new species paradigms, I do not observe major morphological changes that appear to arise during ontogeny that cannot be attributed to normal bone growth, which is consistent with what is seen in extant squamates as well as in *T. proriger* and specimens of a new species that were previously referred to *T. proriger*.

***Reassessment of* T. proriger.** *Tylosaurus proriger* is the most well-sampled tylosaurine species, known from over 100 specimens; thus, previous studies of tylosaurine ontogeny have used it as a point of reference. However, I identify several specimens that differ morphologically from the holotype and other specimens that match it. These morphological differences are seen in specimens that represent a wide range of body sizes and are the same geological age. I am confident that this assemblage represents a new species distinct from *T. proriger*, and note that several characters diagnostic of it, which are unambiguously present in both small and large individuals, were mistaken as the “mature” morphology of *T. proriger* in previous work (e.g., Zietlow, 2020). In both this new species and *T. proriger*, I find that tylosaurines, and likely mosasaurs in general, follow the same ontogenetic trends known in extant squamates.

Conclusions: the validity of *T. kansasensis* and implications for tylosaurine diversity

The null hypothesis is that mosasaurs (and all other extinct reptiles) were subject to the same developmental patterns as extant reptiles. Extant squamates do not undergo phylogenetically relevant ontogenetic changes to skeletal morphology (e.g., migration of neurovascular foramina, reduction of existing bony processes) that have been proposed in *Tylosaurus* (and other fossil reptiles more generally). Therefore, I find the purported “ontogenetic” changes previously proposed to distinguish “mature” *T. nepaeolicus* from “immature” *T. kansasensis* are falsified and, in some cases (e.g., migration of parietal foramen), biologically impossible. Reassessment of specimens referred to *T. proriger* support this trend: diagnostic features are consistent across a wide range of specimen sizes, and thus morphological differences between them are more likely to represent interspecific, rather than intraspecific, variation. I conclude that *T. kansasensis* is a valid species and identify at least two new unnamed *Tylosaurus* species, a result that is indicative of underestimation of mosasaur diversity more generally.

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List of contributors, arranged alphabetically

(black = Maastrichtian-175 years meeting; blue = Mosasaur Meeting)

Natuurhistorisch Museum Maastricht

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Maastrichtian 175 years
The 175th Anniversary of the Maastrichtian
A Celebratory Meeting
Maastricht, September 8-11 - 2024

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