

# A possible phytosaurian (Archosauria, Pseudosuchia) coprolite from the Late Triassic Fleming Fjord Group of Jameson Land, central East Greenland

JESPER MILÀN, OCTÁVIO MATEUS, MALTE MAU, ARKA RUDRA, HAMED SANEI  
& LARS B. CLEMMENSEN



Geological Society of Denmark  
<https://2dgf.dk>

Received 19 October 2020  
Accepted in revised form  
2 June 2021  
Published online  
21 June 2021

© 2021 the authors. Re-use of material is permitted, provided this work is cited.  
Creative Commons License CC BY:  
<https://creativecommons.org/licenses/by/4.0/>

Milàn, J., Mateus, O., Mau, M., Rudra, A., Sanei, H. & Clemmensen, L.B. 2021: A possible phytosaurian (Archosauria, Pseudosuchia) coprolite from the Late Triassic Fleming Fjord Group of Jameson Land, central East Greenland. *Bulletin of the Geological Society of Denmark*, vol. 69, pp. 71-80. ISSN 2245-7070.  
<https://doi.org/10.37570/bgds-2021-69-05>

A large, well-preserved vertebrate coprolite was found in a lacustrine sediment in the Malmros Klint Formation of the Late Triassic Fleming Fjord Group in the Jameson Land Basin, central East Greenland. The size and internal and external morphology of the coprolite is consistent with that of crocodylian coprolites and one end of the coprolite exhibits evidence of post-egestion trampling. As the associated vertebrate fauna of the Fleming Fjord Group contains abundant remains of pseudosuchian phytosaurs, the coprolite is interpreted as being from a large phytosaur.

**Keywords:** Late Triassic, coprolite, phytosaur, East Greenland.

Jesper Milàn [jesperm@oesm.dk], *Geomuseum Faxø, Østsjælland Museum, Rådhusvej 2, DK-4640 Faxø, Denmark.* Octávio Mateus [omateus@fct.unl.pt], *GEOBIOTEC, Departamento de Ciências da Terra, FCT-UNL Faculdade de Ciências e Tecnologia, Universidade Nova de Lisboa, Portugal & Museu da Lourinhã, Portugal.* Malte Mau [malm@ign.ku.dk], *Department of Geosciences and Natural Resource Management, University of Copenhagen, Øster Voldgade 10, DK-1350 Copenhagen K, Denmark.* Arka Rudra [arudra@geo.au.dk], *Lithospheric Organic Carbon (L.O.C) group, Department of Geosciences, Aarhus University, Aarhus, Denmark.* Hamed Sanei [sanei@geo.au.dk], *Lithospheric Organic Carbon (L.O.C) group, Department of Geosciences, Aarhus University, Aarhus, Denmark.* Lars B. Clemmensen [larsc@ign.ku.dk], *Department of Geosciences and Natural Resource Management, University of Copenhagen, Øster Voldgade 10, DK-1350 Copenhagen K, Denmark.*

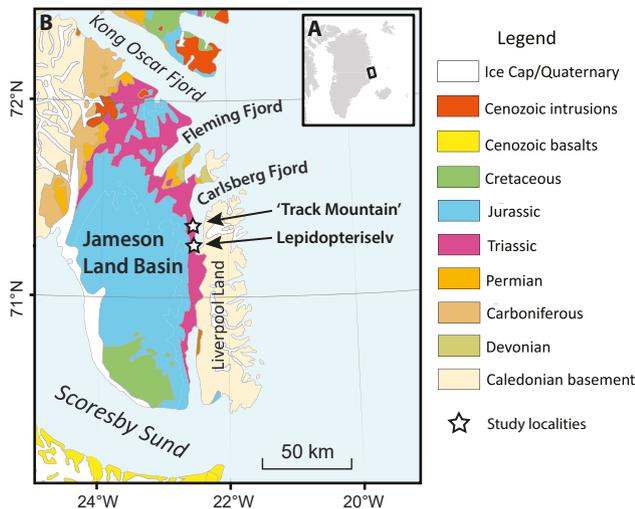
Coprolites are important palaeoecological indicators and are frequently included in fauna analyses, as they can provide important, additional information about extinct animals and their diet, in the form of preserved inclusions of undigested prey remains (e.g. Thulborn 1991; Hunt *et al.* 1994; Northwood 2005; Prasad *et al.* 2005; Chin 2007; Souto 2008; Eriksson *et al.* 2011; Milàn 2012; Milàn *et al.* 2012; Hansen *et al.* 2016). Coprolites are regarded as ichnofossils and were first recognized as fossil faeces by Rev. William Buckland (1835) who coined the term coprolite. Today vertebrate coprolites are known from the Silurian to the present (Hunt & Lucas 2012; Hunt *et al.* 2012).

During the 2018 expedition to the Lepidopterislev area at Carlsberg Fjord in Jameson Land (central East Greenland; Fig. 1), a very large coprolite was found

in a loose sediment slab belonging to the middle part of the Malmros Klint Formation of the Fleming Fjord Group (Clemmensen *et al.* 2020). The aim of this paper is to describe the newfound coprolite and to discuss its possible affiliation within the known Late Triassic vertebrate fauna of the Jameson Land Basin.

## Geological Setting

Late Triassic sediments occur in the Jameson Land Basin, which is located in central East Greenland at about 71 °N at the present-day land areas of Jameson Land and Scoresby Land (Fig. 1; Clemmensen *et al.* 2016, 2020). Particularly well-exposed mountain slopes

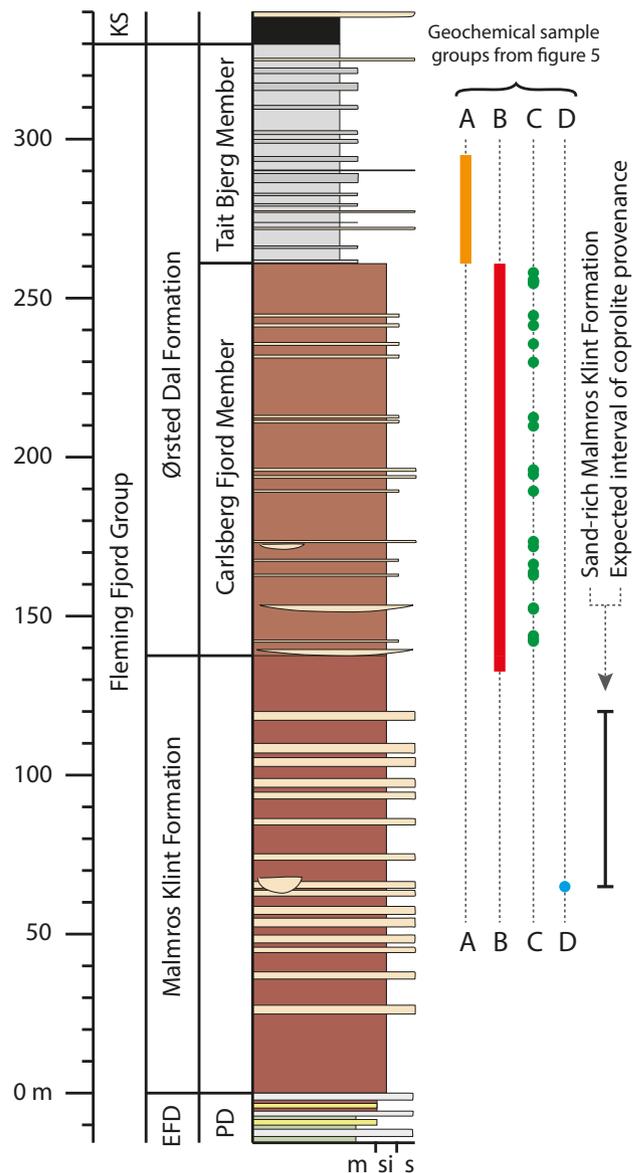


**Fig. 1. A:** Map of Greenland with Jameson Land indicated by a rectangle. **B:** Geological map of central East Greenland showing Triassic exposures in the Jameson Land Basin. The locations of Lepidopteriselv and 'Track Mountain' are indicated by stars. Modified from Guarnieri *et al.* (2017) and Clemmensen *et al.* (2020).

with Late Triassic sediments are present along the western shores of Carlsberg Fjord. These sediments belong to the uppermost Pingo Dal, Gipsdalen and Fleming Fjord Groups (Clemmensen *et al.* 2020) with the latter unit forming spectacular cliff sides at many localities. The Fleming Fjord Group consists of three units: Edderfugledal, Malmros Klint and Ørsted Dal Formations (Clemmensen *et al.* 2020). In the study area, the Edderfugledal Formation is about 50 m thick and characterized by cyclically bedded greenish grey mudstone and yellowish grey dolostone including stromatolitic limestone overlain by cyclically bedded grey quartz sandstone, red sandstone and siltstone, green mudstone and rare stromatolitic limestone. The Malmros Klint Formation is 135 m thick and composed of cyclically bedded brownish red to greyish red mudstone and fine-grained sandstone. The Ørsted Dal Formation is 125 m thick and composed of a cyclically bedded succession of red structureless mudstone associated with thin greenish grey siltstone and fine-grained sandstone of the Carlsberg Fjord Member overlain by poorly exposed light grey carbonate/marlstone and dark grey mudstone of the Tait Bjerg Member (Fig. 2).

The Fleming Fjord Group has until recently been considered to be of late Carnian, Norian and early Rhaetian age (Clemmensen 1980; Jenkins *et al.* 1994; Clemmensen *et al.* 2020). New magnetostratigraphic work, however, indicates that the group is of Norian age and spans a time interval between 220 and 209 Ma (Kent & Clemmensen 2021). The vertebrate fauna of the Fleming Fjord Group comprises a diverse as-

semblage, some of which was recently described, containing chondrichthyans and actinopterygian fishes, dipnoi such as *Ceratodus tenuensis* (Agnolin *et al.* 2018), theropod and sauropodomorph dinosaurs, temnospondyls such as *Cyclotosaurus naraserluiki*, turtles, aetosaurs, phytosaurs and pterosaurs (Jenkins



**Fig. 2.** Simplified lithological log of the Malmros Klint Formation and the Ørsted Dal Formation along Carlsberg Fjord. Geochemical sample groups are used to identify the original stratigraphic position of the coprolite-bearing rock slab. The stratigraphic levels of the geochemical samples are illustrated with the following letters: **A:** Samples from the lower part of the Tait Bjerg Member. **B:** Samples from the Carlsberg Fjord Member and upper part of the Malmros Klint Formation. **C:** Sandstone/siltstone samples from the Carlsberg Fjord Member. **D:** Samples from the phytosaur bone bed.

*et al.* 1994; Sulej *et al.* 2014; Clemmensen *et al.* 2016; Hansen *et al.* 2016; Marzola *et al.* 2017a, 2018; Agnolin *et al.* 2018). Furthermore, the fauna includes both teeth and skeletal elements of the mammaliforms *Haramiyavia clemmenseni*, *Brachyzostrodon*, and *Kuehneotherium* (Jenkins *et al.* 1994; Jenkins *et al.* 1997). Trace fossil evidence show the presence of abundant small theropod dinosaurs, sauropodomorphs, sauropods, and other achosaurus (Sulej *et al.* 2014; Clemmensen *et al.* 2016; Klein *et al.* 2016; Lallensack *et al.* 2017). The Malmros Klint Formation is less rich in vertebrate material compared to the overlying Carlsberg Fjord Member, but a quarry, nicknamed Mateus quarry, lying 65 m above the base of the Malmros Klint Formation at the Lepidopteriselv site contains a rich skeleton material of phytosaurs ascribed to *Mystriosuchus* as well as rarer bones tentatively ascribed to theropod dinosaurs (Clemmensen *et al.* 2016; Marzola *et al.* 2017b; 2018).

In the Late Triassic (late Norian-early Rhaetian), the Jameson Land Basin was located at 43°N on the northern part of the supercontinent Pangaea (Kent & Clemmensen 2021). This position placed the basin with lake and fluvial sediments in a transition zone between the relatively dry interior of the supercontinent Pangaea and the more humid peripheral part of this continent (Clemmensen *et al.* 1998; Sellwood & Valdes 2006), or well inside the humid temperate belt (Kent *et al.* 2014).

## Material and methods

A well-preserved coprolite preserved in a slab of greyish sandstone (Fig. 3) was found in 2018 on a mountain slope close to Lepidopteriselv at Carlsberg Fjord (Fig. 1). The loose slab was found in a small meltwater stream, situated in a stratigraphic level that equals the middle part of the Malmros Klint Formation and is found about 100 m south of the quarry with phytosaur remains. The slab had very likely been transported downwards by modern stream action or by solifluction.

The internal morphology of the coprolite and surrounding sediment was investigated, and two samples

of the sediment were examined by X-ray fluorescence (XRF) to characterize its geochemical composition. The obtained result was compared with a large geochemical database from the uppermost Malmros Klint Formation and overlying Carlsberg Fjord Member and the main part of the Tait Bjerg Member at the Lepidopteriselv site and a nearby site to the north.

To study the organic matter preservation, the top dark part of the coprolite sample was crushed in clean agate-mortar and pestle. Approximately, 50 mg of the coprolite sample and a sample from the base sandstone was studied using Rock-Eval® analysis method, applied on Hawk Pyrolysis and TOC instrument, Wildcat Technologies. The pyrolysis cycle starts with an iso-temperature at 300 °C for 3 minutes followed by a temperature ramp up to 650 °C, at 25 °C per minute. Hydrocarbons released during pyrolysis; S1 and S2 (mg HC/g TOC) are detected by online Flame Ionization Detector. The CO<sub>2</sub> released during pyrolysis of oxygen-bearing organic compounds (S3; mg CO<sub>2</sub>/g of sample) is measured by online Infrared (IR) detectors. The oxidation phase starts with an isothermal stage at 300 °C (for 1 minute) to 850 °C at 25 °C/minute, with 5 minutes hold time. The CO and CO<sub>2</sub> released during combustion of residual organic carbon (S4; mg CO–CO<sub>2</sub>/g of sample) is measured by online (IR) detector (Lafargue *et al.* 1998; Strunk *et al.* 2020). The pyrolysis parameters were calibrated with standards having <0.1 % standard deviation from the actual value (Table 1).

A sample of the sediment was prepared for dinocyst analysis, but the sediment contained no recognizable microfossils. Rock samples used for statistical analyses, were rinsed with demineralized water, dried at 50 °C and crushed with a vibratory ball mill before any analysis. XRF analyses were performed with a fixed Olympus Delta Premium DP-6000 XRF analyzer. Each sample was analyzed for 2 × 120 seconds with a 10 kV beam and a 30 kV beam. The samples were covered with a thin Mylar film to improve the detection limit of the lightest elements. The accuracy was regularly tested by re-analyzing samples and by analyzing PACS-3 and SiO<sub>2</sub> standards. Three Pb measurements showed values below the detection limit (LOD). These missing values were replaced with the LOD value. Ele-

Table 1. Rock-eval analyses of the coprolite and sediment.

Sample	S1 mgHC/g	S2 mgHC/g	S3 mgCO <sub>2</sub> /g	Pyrolysable labile organic carbon wt%	Residual organic carbon wt%	TOC* wt%
Sediment	0.02	0.04	0.74	15 %	81 %	0.26
Coprolite	0.6	0.38	0.98	39 %	61 %	0.33

\* Total organic carbon

ments (variables) with a high number of LOD values were discarded from the multivariate analyses. The XRF data points were log-transformed with the natural logarithm before statistical analyses to normalize the data. This is done because Hotelling's T-squared test assumes normality. Furthermore, normality ensures more robust results when using compositional data such as geochemical data and likewise ensures more robust results from the principal component analysis (Gazley *et al.* 2015). Normality was validated with normal quantile plots and lagged residual plots. Principal component analyses (PCAs) were performed with the `pca` function in Matlab. Hotelling's two-sample T-squared tests were performed with the R

package Hotelling (Curran 2018). The test assumes that samples are independently drawn from two independent multivariate normal distributions with the same covariance and tests the hypothesis of equal means. Using this statistical test, samples from the coprolite-bearing rock slab were tested against four data groups defined by stratigraphical and lithological characteristics. The Hotelling R package includes a permutation test used to estimate the non-parametric P-value for the hypothesis test. The permutation test determines the statistical significance by computing a test statistic on the dataset for many random permutations. This provides a more robust test by building a permutation distribution. Therefore, the assumption of normal



**Fig. 3.** Photos of coprolite NHMD 875622. **A:** Complete specimen partly prepared out of matrix. Constricted zone indicated by arrows. **B:** Oblique view highlighting the trampled part of the coprolite, indicated by arrows. **C:** Cross section of the trampled part of the coprolite revealing the layered internal structure, as well as prominent deformation of the sediments below the trampled part of the coprolite, indicated by arrows.

distribution is not strictly needed. The permutation p-values were based on 10,000 permutations. The coprolite is now part of the collection of the Natural History Museum of Denmark (NHMD 875622).

## Description

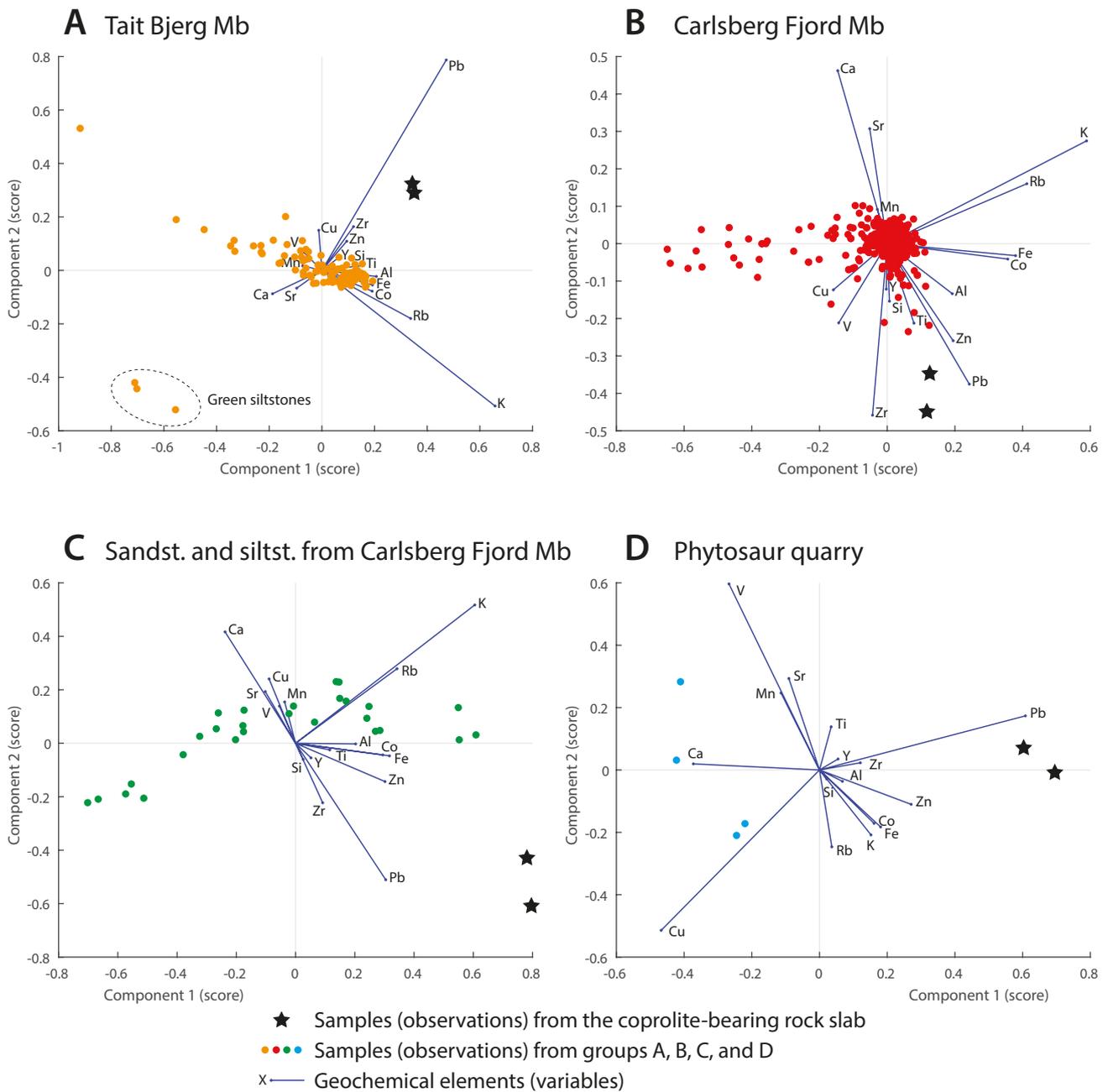
The specimen is 2/3 prepared out of the original matrix from the slab it was found in (Fig. 3). The specimen is 125 mm long and is flattened with a largest diameter of 49 mm and a flattened diameter of 24 mm. A prominent constricted zone is present in the widest part of the specimen locally reducing the widest diameter to 39 mm (Fig. 3A). One end is partly broken, suggesting a larger original total length. The specimen tapers towards the other end, before turning sharply to the side and revealing a rounded flattened zone in the bent part (Fig. 3B). Internally, the specimens consist of three concentric layers 1-2 mm thick, wrapped around a more structureless core. Each layer appears structureless in composition (Fig. 3C). The specimen contains no prey remains either in the form of bones, scales or plant fragments. The surface is smooth, with occasional small pits, grooves and irregularities.

The coprolite-bearing rock slab measures 5.5 cm in thickness and consists of a dark-grey fine sandstone with a light-grey colour in the topmost few centimetres. The internal structures are strongly deformed but show horizontal lamination and some horizons with poorly developed wave ripple lamination. The light-coloured top shows a very fine millimetre-scale horizontal lamination. There are no indications of trace fossils on the sole of the slab. The lack of trace fossils is typical for sandstones found in the Malmros Klint Formation. On the contrary, sandstones and siltstones from the Ørsted Dal Formation have sharp junctions with the mudstone below and therefore usually show interface preservation of trace fossils on the soles (Bromley *et al.* 1979). Sandstone beds are rare in the Ørsted Dal Formation but are more common in the Malmros Klint Formation. Coarse-grained beds in the Ørsted Dal Formation generally consist of siltstone and are less than 5 cm thick (Clemmensen *et al.* 1998).

To identify the source of the coprolite-bearing slab, the geochemical signature of the slab is compared to the geochemical distribution of a large quantity of samples from the stratigraphic units above the level where the coprolite was found. Unfortunately, no samples from the Kap Stewart Group or the main part of the Malmros Klint Formation were available for this analysis. The geochemical signature is based on XRF measurements of 16 chemical elements in the top and the bottom of the slab. These two samples are

compared to 116 samples from the Tait Bjerg Member (group A), 557 samples from the Carlsberg Fjord Member and the uppermost Malmros Klint Formation (group B), 27 samples from sandstone and siltstone from the Carlsberg Fjord Member (group C), and 4 samples from a phytosaur bone bed in the middle of the Malmros Klint Formation (group D; Fig. 2). For the initial assessment, we use principal component analysis (PCA) to reduce the 16 variables into a few principal components, which convey the most variation in the dataset. This provides a measure of how each sample is related to the chemical elements and which samples are alike. When performing PCAs for each data group, biplots of the two most important principal components show that samples from the coprolite-bearing slab plot well away from the rest of the samples (Fig. 4). This indicates that the geochemical composition of the slab is different from all four groups. Group A shows three outliers plotting in the lower left corner of the PCA biplot. These geochemical signatures represent green siltstone beds with low Pb concentrations (< LOD) which are most likely a result of diagenetic flushing of Pb and other elements like Fe giving them a greenish colour. To further test if the coprolite-bearing slab could originate from one of the sample groups, we use a multivariate statistic two-sample Hotelling's T-squared test combined with permutation testing. This tests the null-hypothesis that the slab mean and sample group mean are equal for all response variables (geochemical elements). The result of the statistic tests are significant permutation p-values ( $p = 0$ ) for sample group A, B and C meaning that the geochemical signature of the slab is significantly different from the units above the sand-rich Malmros Klint Formation. The few samples from the phytosaur bone bed (group D) does not allow for a test on the 16 geochemical variables. Instead, Hotelling's T-squared test with 10,000 permutations is performed on principal component one and two accounting for 96.7 % of the variance in the group. This gives a non-statistically significant p-value of 0.0666. However, this high p-value is likely a result of the small sample size. Using the asymptotic distribution of the T-squared test gives a p-value of 0.0007419. Thus, like group A, B, and C the geochemical signature of the slab is significantly different from rock samples from the phytosaur bone bed.

In conclusion, assuming the coprolite-bearing rock slab has travelled down slope since deposition the lithological and chemical characteristics of the slab place the original level of deposition between the stratigraphic level of the phytosaur bone bed, and the uppermost muddy interval in the Malmros Klint Formation. This corresponds to the interval between 65 m and 120 m above the base of the Malmros Klint Formation (Fig. 2).



**Fig. 4.** PCA biplots for the four sample groups based on principal component one and two. The plots provide a measure of how each sample is related to the chemical elements and which samples are alike. Samples from the coprolite-bearing slab plot well away from the rest of the samples indicating that the slab is chemical different from all four sample groups. Thus, the slab is likely originating from this sandstone-rich part of the Malmros Klint Formation (i.e. between 65 m and 120 m above the base of the Malmros Klint Formation (Fig. 2)). The first two principal components explain 73.8 %, 88.3 %, 77.8 %, and 96.7 % of the variance in group A, B, C, and D respectively. **A:** Bulk sample group from the lower part of the Tait Bjerg Member (Ørsted Dal Formation). Outliers are encircled with dashed lines. **B:** Bulk sample group from the Carlsberg Fjord Member (Ørsted Dal Formation). **C:** Samples from sandstone and siltstone from Carlsberg Fjord Member. **D:** Samples from a phytosaur quarry in the middle of the Malmros Klint Formation.

## Discussion

### Identifying the faeces-maker

To precisely identify the producer of a coprolite, is at best a challenging task, with many uncertainties. This is because faeces from several unrelated groups of animals, can share the same morphology, due to similarities in diet of the producer and mode of egestion. This gets further complicated as faeces from the same individual can show a wide range of morphological variation as well (e.g. McAllister 1985; Lewin 1999; Chin 2002; Chame 2003; Milàn 2012).

The dimensions of the coprolite, with a maximum flattened diameter of 49 mm and a length of at least 125 mm suggest the producer to be among the larger archosaurs from the formation. While mammals have been reported from the formation (Jenkins *et al.* 1994, 1997; Sulej *et al.* 2020), they can quickly be excluded as possible producers as all Triassic mammals have a body-size significantly smaller than the length and width of the herein described specimen. Assuming that the coprolite stratigraphically belongs to the middle to upper part of the Malmros Klint Formation likely producers include the herbivorous dinosaur *Plateosaurus* and theropod dinosaurs (Clemmensen *et al.* 2016) and the phytosaurs (Jenkins *et al.* 1994; Clemmensen *et al.* 2016; Niedzwiedzki & Sulej 2020).

Coprolites from herbivores are generally scarcer in the fossil records than coprolites from carnivores, because the phosphate contents of the latter, originating from the soft tissue and bones from prey animals predispose them to mineralization (Thulborn 1991; Gill & Bull 2012). The herein studied specimen is well-preserved and well-mineralized and is interpreted as a carnivore coprolite. The theropods reported from the Fleming Fjord Formation, both inferred from tracks and skeletal material are all small sized animals (Jenkins *et al.* 1994; Clemmensen *et al.* 2016; Niedzwiedzki & Sulej 2020).

Despite the abundance of coprolites in Triassic sediments (e. g. Hunt *et al.* 2007), no coprolites have so far been convincingly been attributed to phytosaurs, despite phytosaurs being abundant elements in Late Triassic ecosystems. Umamaherawan *et al.* (2019), suggested that large coprolites from the Upper Triassic Maleri Formation, India, could be made by small to medium sized semi aquatic predators, and suggest phytosaurs as one of the possible makers. The Late Triassic coprolite ichnogenus *Alococoprus* (Hunt *et al.* 2007) comprises elongated, sub-rounded coprolites, with longitudinal striations, and has been assigned to basal arcosauromorphs.

Crocodylian coprolites are generally sausage shaped and circular in cross section with few structures visible on their outer surface except occasional

longitudinal striations, or traces from coprophageous organisms (Souto 2010; Milàn 2012). A study of the morphological variation within fresh faeces from 10 species of extant crocodylians demonstrated that a commonly occurring feature of crocodylian faeces is circumferal constriction marks and a bend between 120–150°, and their internal structure is composed of concentric layers of various thickness around a central core of more homogenous mass (Milàn & Hedegaard 2010; Milàn 2012). Crocodylian faeces are devoid of any bone or shell remains as the digestive system of crocodylians effectively dissolves any bone or shell remains of their prey (Fischer 1981), leaving only hair and feathers behind (Milàn 2012). The external and internal morphology of the herein described specimen, being elongated, with a subrounded cross-section, composed of several concentric layers around a homogenous core, and devoid of prey remains, and with a prominent constrained zone around its circumference, is in accordance with the morphology of crocodylian coprolites (Milàn & Hedegaard 2010; Milàn 2012). The phylogenetic hypotheses of the position of Phytosauria and its relationships with other archosaurs such as crocodylomorphs has changed over the years. In the most updated exhaustive analysis (Ezcurra 2016) phytosaurs are pseudosuchians, sister taxa of Suchia, which include crocodylomorphs (Fig. 5). Moreover, phytosaurs and crocodylomorphs share a number of anatomical convergences, general morphology, similar lifestyle, diet, and comparable sizes. Phylogenetically, similar faeces are also to be expected.

The total body length of a crocodile can be estimated from the diameter of the faeces (Milàn 2012). In this case, a diameter of 49 mm corresponds to a crocodylomorph with a body length of around 300 cm (Milàn 2012). Assuming that this ratio is true for Triassic crocodylomorphs, and pseudosuchians with their very similar body proportions, this estimated length falls within the sizes of phytosaurs skeletons found in the nearby quarry (Clemmensen *et al.* 2016).

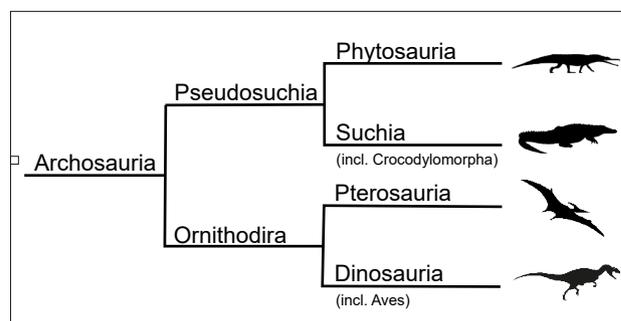


Fig. 5. Schematic representation of the main archosaurian groups. Phytosaurs appear as a sister group to Suchia, which include the modern crocodiles. Based on Ezcurra (2016).

### Organic content

The coprolite sample has S1 0.6 mgHC/g rock, S2 0.38 mgHC/g rock and 0.33% total organic carbon (TOC), with 39 % reactive and 61 % residual organic carbon. This suggests that the sample has lighter degradable hydrocarbons (S1) as well as preserved macromolecular organic carbon (S2). In contrast, the host sandstone has negligible S1 and S2 fractions of hydrocarbons, 0.26% TOC with 81% residual OC (Table 1). The S1 fraction represents the labile proto-hydrocarbon fractions, probably derived from the original egested by-product, combined by the microbial decay of the macromolecules in the coprolites in the depositional site. Higher S2 in the coprolite than the sandstone indicates the preservation of the stable organic carbon in the coprolite. These hydrocarbon compounds might represent the remnants of the egested food material by the phytosaur combined by post-egestion changes in the coprolite depositional sites. The chemical composition further excludes the possibility that the specimen should be an inorganic concretion.

### Trampling

The distorted area in one end of the coprolite, is rounded in the bottom, and in the exposed broken edge of the flattened area, it is evident that the coprolite has been deformed to a bowl-shaped cross section (Fig. 3B, C), contrary to the oval cross section in the undeformed rest of the coprolite. Further, the flattened area is depressed down into the surrounding sediment, relative to the rest of the coprolite, suggesting the deformation is the result of a significant force exercised on this part of the coprolite. Similar deformations are observed in Miocene mammalian coprolites from Portugal, where even identifiable footprints are found preserved depressed into coprolites. These footprints are interpreted as being formed by post egestion trampling of the coprolite before it dried up (Antunes *et al.* 2005). Based on the similarity to the depressions in the Portuguese coprolites, and the observation that the deformed parts of the coprolite is pushed down into the sediment in a very similar way to what is observed when examining subsurface deformation below theropod tracks in cross section, from the same formation (Milàn *et al.* 2004, 2006), we interpret the deformed part of NHMD 875622 to be the result of trampling by either the maker of the coprolite or another vertebrate animal inhabiting the area.

### Conclusion

A large well-preserved coprolite from the middle to upper part of the Malmros Klint Formation (65-120

m above the base of the formation at the study site), Fleming Fjord Group of Jameson Land, central East Greenland is interpreted as being from a phytosaur, based on its size, internal and external morphology and stratigraphical context. This is the first record of a convincing phytosaur coprolite from the Late Triassic globally. Geochemical examinations of the coprolite reveal preservation of organic carbon, which might represent degraded food residues egested by the organism/phytosaur. Furthermore, the coprolite shows evidence of trampling by either the producer of the coprolite or another individual from the associated Late Triassic fauna of East Greenland.

### Acknowledgements

This project is part of a combined sedimentological, palaeontological and magnetostratigraphical investigation of the Late Triassic vertebrate-bearing continental deposits in central East Greenland supported by the Independent Research Fund Denmark. We thank Dennis V. Kent for productive discussions on Late Triassic stratigraphy. We are grateful to Karen Dybkjær, GEUS, for help with palynological examination of the coprolite. We thank Bo Markussen, Department of Mathematical Sciences at the University of Copenhagen, for guidance about statistical analyses. We gratefully acknowledge support from Dronning Margrethes og Prins Henriks Fond, Arbejdsmarkedets Feriefond, Oticon Fonden, Knud Højgaard's Fond, Louis Petersens Legat, Det Obelske Familiefond, Ernst og Vibeke Husmans Fond, the Carlsberg Foundation and Geocenter Møns Klint. GEUS provided valuable logistical support. We thank Adrian Hunt and an anonymous referee for constructive reviews.

### References

- Agnolin, F.L., Mateus, O., Milàn, J., Marzola, M., Wings, O., Adolfsson, J.S. & Clemmensen, L.B. 2018: *Ceratodus tunuensis*, sp. nov., a new lungfish (Sarcopterygii, Dipnoi) from the Upper Triassic of central East Greenland. *Journal of Vertebrate Paleontology* 38, e1439834. <https://doi.org/10.1080/02724634.2018.1439834>
- Antunes, M.G., Ausenda C. Balbino, A.C. & Ginsburg, L. 2005: Miocene mammalian footprints in coprolites from Lisbon, Portugal. *Annales de Paléontologie* 92, 13–30. <https://doi.org/10.1016/j.annpal.2005.09.002>
- Bromley, R. & Asgaard, U. 1979: Triassic freshwater ichnocoenoses from Carlsberg Fjord, east Greenland. *Palaeogeography, Palaeoclimatology, Palaeoecology* 28, 39–80. [https://doi.org/10.1016/0167-0613\(79\)90031-9](https://doi.org/10.1016/0167-0613(79)90031-9)

- org/10.1016/0031-0182(79)90112-3
- Buckland, W. 1835: On the discovery of coprolites, or fossil faeces, in the Lias at Lyme Regis, and in other formations. *Transactions of the Geological Society of London* 3, 223–238. <https://doi.org/10.1144/transgslb.3.1.223>
- Chame, M. 2003: Terrestrial mammal feces: a morphometric summary and description. *Memoirs Instituto Oswaldo Cruz, Rio de Janeiro* 98 (Supplement I), 71–94. <https://doi.org/10.1590/s0074-02762003000900014>
- Chin, K. 2002: Analyses of coprolites produced by carnivorous vertebrates. *Paleontological Society Papers* 8, 43–50. <https://doi.org/10.1017/s1089332600001042>
- Chin, K. 2007: The paleobiological implications of herbivorous dinosaur coprolites from the Upper Cretaceous Two Medicine Formation of Montana: Why eat wood? *Palaios* 22, 554–566. <https://doi.org/10.2110/palo.2006.p06-087r>
- Clemmensen, L.B. 1980: Triassic lithostratigraphy of East Greenland between Scoresby Sund and Kejser Franz Josephs Fjord. *Grønlands Geologiske Undersøgelse Bulletin* 139, 56 pp. <https://doi.org/10.34194/bullggu.v139.6681>
- Clemmensen, L.B., Kent, D.V. & Jenkins, F.A., Jr. 1998: A Late Triassic lake system in East Greenland: facies, depositional cycles and palaeoclimate. *Palaeogeography, Palaeoclimatology, Palaeoecology* 140, 135–159. [https://doi.org/10.1016/s0031-0182\(98\)00043-1](https://doi.org/10.1016/s0031-0182(98)00043-1)
- Clemmensen, L.B., Milàn, J., Adolfssen, J.S., Estrup, E.J., Frobøse, N., Klein, N., Mateus, O. & Wings, O. 2016: The vertebrate-bearing Late Triassic Fleming Fjord Formation of central East Greenland revisited: stratigraphy, palaeoclimate and new palaeontological data. *Geological Society of London Special Publications* 434, 31–47. <https://doi.org/10.1144/sp434.3>
- Clemmensen, L.B., Kent, D.V., Mau, M., Mateus, O. & Milàn, J. 2020: Triassic lithostratigraphy of the Jameson Land basin (central East Greenland), with emphasis on the new Fleming Fjord Group. *Bulletin of the Geological Society of Denmark* 68, 95–132. <https://doi.org/10.37570/bgsd-2020-68-05>
- Curran, J. 2018: Hotelling's  $T^2$  test and variants. R package Hotelling version 1.0-5.
- Eriksson, M.E., Lindgren, J., Chin, K. & Månsby, U. 2011: Coprolite morphotypes from the Upper Cretaceous of Sweden: novel views on an ancient ecosystem and its implications for coprolite taphonomy. *Lethaia* 44, 455–468. <https://doi.org/10.1111/j.1502-3931.2010.00257.x>
- Ezcurra, M. D. 2016: The phylogenetic relationships of basal archosauromorphs, with an emphasis on the systematics of proterosuchian archosauriforms. *PeerJ* 4, e1778. <https://doi.org/10.7717/peerj.1778>
- Fischer, D.F. 1981: Crocodylian scatology, microvertebrate concentrations, and enamel-less teeth. *Paleobiology* 7, 262–275. <https://doi.org/10.1017/s0094837300004048>
- Gazley, M.F., Collins, K.S., Roberston, J., Hines, B.R., Fisher, L.A. & McFarlane, A. 2015: Application of principal component analysis and cluster analysis to mineral exploration and mine geology. *AusIMM New Zealand Branch Annual Conference*, 131–139. Dunedin, New Zealand.
- Gill, F.L. & Bull, I.D. 2012: Lipid analysis of vertebrate coprolites. *New Mexico Museum of Natural History and Science Bulletin* 57, 93–98.
- Guarnieri, P., Brethens, A. & Rasmussen, T.M. 2017: Geometry and kinematics of the Triassic rift basin in Jameson Land (East Greenland). *Tectonics* 36, 602–614. <https://doi.org/10.1002/2016tc004419>
- Hansen, B.B., Milàn, J., Clemmensen, L.B., Adolfssen, J.S., Estrup, E.J., Klein, N., Mateus, O. & Wings, O. 2016: Coprolites from the Late Triassic Kap Steward Formation, Jameson Land, East Greenland: Morphology, classification and prey inclusions. *Geological Society of London Special Publications* 434, 49–69. <https://doi.org/10.1144/sp434.12>
- Hunt, A.P. & Lucas, S.G. 2012: Classification of vertebrate coprolites and related trace fossils. *New Mexico Museum of Natural History and Science, Bulletin* 57, 137–146.
- Hunt, A.P., Chin, K. & Lockley, M.G. 1994: The paleobiology of vertebrate coprolites. In: Donovan, S., (ed.): *The palaeobiology of trace fossils*, 221–240. London: John Wiley and Sons.
- Hunt, A.P., Lucas, S.G., Milàn, J. & Spielmann, J.A. 2012: Vertebrate coprolites: status and prospectus: *New Mexico Museum of Natural History and Science, Bulletin* 57, 5–24.
- Hunt, A.P., Lucas, S.G., Spielmann, J.A. & Lerner, A.J. 2007: A review of vertebrate coprolites of the Triassic with descriptions of new Mesozoic ichnotaxa. *New Mexico museum of Natural History and Science Bulletin* 41, 88–107.
- Jenkins, F.J., Shubin, N.H., Amarel, W.W., Gatesy, S.M., Schaff, C.R., Clemmensen, L.B., Downs, W.R., Davidson, A.R., Bonde, N.C. & Osbaeck, F. 1994: Late Triassic continental vertebrates and depositional environments of the Fleming Fjord Formation, Jameson Land, East Greenland. *Meddelelser Om Grønland, Geoscience* 32, 25 pp.
- Jenkins, F.A., Jr., Gatesy, S.M., Shubin, N.H. & Amaral, W.W. 1997: Haramiyids and Triassic mammalian evolution. *Nature* 385, 715–718. <https://doi.org/10.1038/385715a0>
- Kent, D.V. & Clemmensen, L.B. 2021. Northward dispersal of dinosaurs from Gondwana to Greenland at the mid-Norian (215–212 Ma, Late Triassic) dip in atmospheric pCO<sub>2</sub>. *PNAS* 118. <https://doi.org/10.1073/pnas.2020778118>.
- Kent, D.V., Malnis, P.S., Colombi, C.E., Alcober, O.A. & Martínez, R.N. 2014: Age constraints on the dispersal of dinosaurs in the Late Triassic from magnetostratigraphy of the Los Colorados Formation (Argentina). *PNAS* 111, 7958–7963. <https://doi.org/10.1073/pnas.1402369111>
- Klein, H., Milàn, J., Clemmensen, L.B., Frobøse, N., Mateus, O., Klein, N., Adolfssen, J.S., Estrup, E. & Wings, O. 2016: Archosaur footprints (cf. *Brachychirotherium*) with unusual morphology from the Upper Triassic Fleming Fjord Formation (Norian–Rhaetian) of East Greenland. *Geological Society of London Special Publications* 434, 71–85. <https://doi.org/10.1144/sp434.1>
- Lafargue, E., Marquis, F. & Pillot, D. 1998: Rock–Eval 6 applications in hydrocarbon exploration, production, and soil contamination studies. *Oil Gas Science Technology Review*

- 53, 421–437. <https://doi.org/10.2516/ogst:1998036>
- Lallensack, J.N., Klein, H., Milan, J., Wings, O., Mateus, O. & Clemmensen, L.B. 2017: Sauropodomorph dinosaur trackways from the Fleming Fjord Formation of East Greenland: Evidence for Late Triassic Sauropods. *Acta Palaeontologica Polonica* 64, 833–843. <https://doi.org/10.4202/app.00374.2017>
- Lewin, R.A. 1999: *Merde*, excursions into scientific, cultural and socio-historical coprology, 164 pp. London: Aurum Press.
- Marzola, M., Mateus, O., Shubin, N.H. & Clemmensen, L.B. 2017a: *Cyclotaurus naraserluiki*, sp. nov., a new Late Triassic cyclotaurid (Amphibia, Temnospondyli) from the Fleming Fjord Formation of the Jameson Land Basin (East Greenland). *Journal of Vertebrate Paleontology* 37, e1303501. <https://doi.org/10.1080/02724634.2017.1303501>
- Marzola, M., Mateus, O., Milàn, J. & Clemmensen, L.B. 2017b: The 2016 Dinosaur Expedition to the Late Triassic of the Jameson Land Basin, East Greenland, 249–253. Abstract book of the XV Encuentro de Jóvenes Investigadores en Paleontología, Pombal.
- Marzola, M., Mateus, O., Milàn, J., Clemmensen, L.B. 2018: A review of Palaeozoic and Mesozoic tetrapods from Greenland. *Bulletin of the Geological Society of Denmark* 66, 21–46. <https://doi.org/10.37570/bgisd-2018-66-02>
- McAllister, J.A. 1985: Re-evaluation of the formation of spiral coprolites. *University of Kansas, Paleontological Contributions* 144, 1–12.
- Milàn, J., Clemmensen, L.B., Adolfsson, J.S., Estrup, E.J., Frøbøse, N., Klein, N., Mateus, O. & Wings, O. 2012a: A preliminary report on coprolites from the Late Jurassic part of the Kap Steward Formation, Jameson Land, East Greenland. *New Mexico Museum of Natural History and Science Bulletin* 57, 203–205.
- Milàn, J. 2012: Crocodylian scatology – a look into morphology, internal architecture inter- and intraspecific variation and prey remains in extant crocodylian feces. *New Mexico Museum of Natural History and Science, Bulletin* 57, 65–71.
- Milàn, J. & Hedegaard, R. 2010: Interspecific variation in tracks and trackways from extant crocodylians. *New Mexico Museum of Natural History and Science, Bulletin* 51, 15–29
- Milàn, J., Clemmensen, L.B. & Bonde, N. 2004: Vertical sections through dinosaur tracks (Late Triassic lake deposits, East Greenland) – undertracks and other subsurface deformation structures revealed. *Lethaia* 37, 285–296. <https://doi.org/10.1080/00241160410002036>
- Milàn, J., Avanzini, M., Clemmensen, L.B., García-Ramos, J.C. & Piñuela, L. 2006: Theropod foot movement recorded from Late Triassic, Early Jurassic and Late Jurassic fossil footprints. *New Mexico Museum of Natural History and Science Bulletin* 37, 352–364.
- Milàn, J., Rasmussen, B.W. & Lynnerup, N. 2012: A coprolite in the MDCT-scanner – internal architecture and bone contents revealed. *New Mexico Museum of Natural History and Science Bulletin* 57, 99–103.
- Niedzwiedzka, G. & Sulej, T. 2020: Theropod dinosaur fossils from the Gipsdalen and Flemming fjord formations (Carnian-Norian, Upper Triassic), East Greenland. Abstracts and Proceedings of the Geological Society of Norway, p. 151, 34th Nordic Geological Winter Meeting, 8–10 January 2020, Oslo, Norway. Available at [https://geologi.no/images/NGWM20/Abstractvolume\\_NGWM20.pdf](https://geologi.no/images/NGWM20/Abstractvolume_NGWM20.pdf)
- Northwood, C. 2005: Early Triassic coprolites from Australia and their palaeobiological significance. *Palaeontology* 48, 49–68. <https://doi.org/10.1111/j.1475-4983.2004.00432.x>
- Prasad, V., Caroline, A.E., Stromberg, C.A.E., Alimohammadian, H. & Sahni, A. 2005: Dinosaur coprolites and the early evolution of grasses and grazers. *Science* 310, 1177–1180. <https://doi.org/10.1126/science.1118806>
- Sellwood, B.W. & Valdes, P.J. 2006: Mesozoic climates: General circulation models and the rock record. *Sedimentary Geology* 190, 269–287. <https://doi.org/10.1016/j.sedgeo.2006.05.013>
- Souto, P.R.F. 2008: *Coprolitos do Brasil – Principais ocorrências e studio*, 93 pp. Rio de Janeiro: Publit.
- Souto, P.R.F. 2010: Crocodylomorph coprolites from the Bauru basin, Upper Cretaceous, Brazil. *New Mexico Museum of Natural History and Science, Bulletin* 51, 201–208.
- Strunk, A., Olsen, J., Sanei, H., Rudra, A. & Larsen, N.K. 2020: Improving the reliability of bulk sediment radiocarbon dating. *Quaternary Science Reviews* 242, 1–13. <https://doi.org/10.1016/j.quascirev.2020.106442>
- Sulej, T., Wolniewicz, A., Bonde, N., Błazejowski, B., Niedzwiedzki, G. & Tałanda, M. 2014: New perspectives on the Late Triassic vertebrates of East Greenland: preliminary results of a Polish–Danish palaeontological expedition. *Polish Polar Research* 35, 541–552. <https://doi.org/10.2478/popore-2014-0030>
- Sulej, T., Krzesinski, G., Tałanda, M., Wolniewicz, A.S., Błazejowski, B., Bonde, N., Gutowski, P., Sienkiewicz, M. & Niedzwiedzki, G. 2020: The earliest-known mammaliaform fossil from Greenland sheds light on origin of mammals. *PNAS* 117, 26861–26867. <https://doi.org/10.1073/pnas.2012437117>
- Thulborn, R.A. 1991: Morphology, preservation, and palaeobiological significance of dinosaur coprolites. *Palaeogeography, Palaeoclimatology, Palaeoecology* 83, 341–366. [https://doi.org/10.1016/0031-0182\(91\)90060-5](https://doi.org/10.1016/0031-0182(91)90060-5)
- Umamaheswaran, R., Prasad, G.V.R., Rudra, A. & Dutta, S. 2019: Biomarker signatures in Triassic coprolites. *Palaios* 34, 458–467. <https://doi.org/10.2110/palo.2019.023>