



# The earliest-known mammaliaform fossil from Greenland sheds light on origin of mammals

Tomasz Sulej<sup>a</sup>, Grzegorz Krzesiński<sup>b,1</sup>, Mateusz Tałanda<sup>c</sup>, Andrzej S. Wolniewicz<sup>a,d</sup>, Błażej Błażejowski<sup>a</sup>, Niels Bonde<sup>e,f</sup>, Piotr Gutowski<sup>g</sup>, Maksymilian Sienkiewicz<sup>b</sup>, and Grzegorz Niedźwiedzki<sup>h,2</sup>

<sup>a</sup>Institute of Paleobiology, Polish Academy of Sciences, 00-818 Warsaw, Poland; <sup>b</sup>Faculty of Power and Aeronautical Engineering, Institute of Aeronautics and Applied Mechanics, Warsaw University of Technology, 00-665 Warsaw, Poland; <sup>c</sup>Department of Paleobiology and Evolution, Faculty of Biology, Biological and Chemical Research Centre, University of Warsaw, 02-089 Warsaw, Poland; <sup>d</sup>Department of Earth Sciences, University of Oxford, OX1 3AN Oxford, United Kingdom; <sup>e</sup>Geological Section, Natural History Museum of Denmark, University of Copenhagen, DK-2100 Copenhagen, Denmark; <sup>f</sup>Fur Museum, 7884 Fur, Denmark; <sup>g</sup>Department of Cranio-Maxillofacial Surgery, Oral Surgery and Implantology, Medical University of Warsaw, 02-091 Warsaw, Poland; and <sup>h</sup>Department of Organismal Biology, Evolutionary Biology Centre, Uppsala University, 752 36 Uppsala, Sweden

Edited by Zhe-Xi Luo, The University of Chicago, Chicago, IL, and accepted by Editorial Board Member David Jablonski August 29, 2020 (received for review June 16, 2020)

Synapsids are unique in having developed multirooted teeth and complex occlusions. These innovations evolved in at least two lineages of mammaliaforms (Tritylodontidae and Mammaliaformes). Triassic fossils demonstrate that close to the origins of mammals, mammaliaform precursors were “experimenting” with tooth structure and function, resulting in novel patterns of occlusion. One of the most surprising examples of such adaptations is present in the haramiyidan clade, which differed from contemporary mammaliaforms in having two rows of cusps on molariform crowns adapted to omnivorous/herbivorous feeding. However, the origin of the multicusp tooth pattern present in haramiyidans has remained enigmatic. Here we describe the earliest-known mandibular fossil of a mammaliaform with double molariform roots and a crown with two rows of cusps from the Late Triassic of Greenland. The crown morphology is intermediate between that of morganucodontans and haramiyidans and suggests the derivation of the multicusp molariforms of haramiyidans from the triconodont molar pattern seen in morganucodontids. Although it is remarkably well documented in the fossil record, the significance of tooth root division in mammaliaforms remains enigmatic. The results of our biomechanical analyses (finite element analysis [FEA]) indicate that teeth with two roots can better withstand stronger mechanical stresses like those resulting from tooth occlusion, than teeth with a single root.

Greenland | Late Triassic | mammaliaform | multirooted tooth | complex occlusion

Recent research suggests that early mammaliaforms underwent an adaptive radiation in the Jurassic, shortly after the acquisition of key mammaliaform characters during the Late Triassic (1–8). The majority of these morphological novelties were related to food processing and are visible in the structure and function of the teeth (1–3). The disparity of tooth crown morphology and transformation of molariform roots in Triassic mammaliaforms suggest that dietary diversification was a major factor in early mammalian evolution (3). Molariforms with multiple rows of cusps and divided roots are important traits, the appearance of which played a significant role in the early diversification of mammaliaforms, but the timing of their origin and their functional advantage over triconodont molariforms remain poorly understood (1, 9). Morganucodontans, kuehneotheriids, and haramiyidans, are early mammaliaform groups that differ from each other in dental morphology (1–8). Early haramiyidans with their complex teeth, were well adapted to an omnivorous/herbivorous diet, whereas contemporary morganucodontans and kuehneotheriids with triconodont tooth patterns and triangular cusp arrangements were clearly more insectivorous/carnivorous (6, 8).

Haramiyidans have a unique combination of anatomical features (1–5) and represent one of the most diverse mammaliaform clades of the Early Mesozoic. The oldest known haramiyidan

fossils are from the latest Norian and Rhaetian (Late Triassic), and are represented by isolated teeth (10), incomplete cranial or jaw remains, and postcranial elements (3). Significant differences between the earliest haramiyidans and other contemporary clades of mammaliaforms have complicated the problem of haramiyidan ancestry and their purported relationships to other stem or crown mammals. *Haramiyavia* from the early Rhaetian of East Greenland is the best-known Late Triassic haramiyidan, characterized by complex molars with longitudinal rows of multiple cusps (2, 3). Early haramiyidans (e.g., *Haramiyavia* and *Thomasia*) have been variably considered as related to the poorly known Late Triassic therapsids (10) and leutherodontids of the Middle–Late Jurassic/earliest Cretaceous (11), to the more derived multituberculates from the Middle Jurassic–Eocene (12), or as stem mammaliaforms (13). Some species of euharamiyidans with gliding adaptations (e.g., *Arboroharamiya*) from the Middle Jurassic of China, as well as other haramiyidans, have also been identified as basal “Allotheria” (14), a problematic taxonomic group that was diagnosed by dentition and mode of mastication (3, 15). These conflicting phylogenetic placements of

## Significance

Mammals underwent an adaptive radiation shortly after the acquisition of several morphological characters in their dentition and jaw. Most of these innovations evolved to facilitate more efficient food processing. The double-rooted molariforms with a specialized crown are one such innovation, but their role in the early diversification of mammals has remained poorly understood. This study shows a comprehensive analysis of an early mammaliaform dentary, which combines data from comparative anatomy, CT scanning, and FEA. The new fossil fills an important gap in our understanding of mammaliaform evolution showing a transitional stage between triconodont-like molariform pattern of morganucodontids and multicusp pattern of haramiyidans. Moreover, this study demonstrates that double-rooted teeth are more resistant to bite-related stresses than single-rooted teeth.

Author contributions: T.S., M.S., and G.N. designed research; T.S., G.K., M.T., A.S.W., B.B., N.B., P.G., M.S., and G.N. performed research; T.S., G.K., M.T., P.G., M.S., and G.N. analyzed data; and T.S., G.K., M.T., A.S.W., M.S., and G.N. wrote the paper.

The authors declare no competing interest.

This article is a PNAS Direct Submission. Z.-X.L. is a guest editor invited by the Editorial Board.

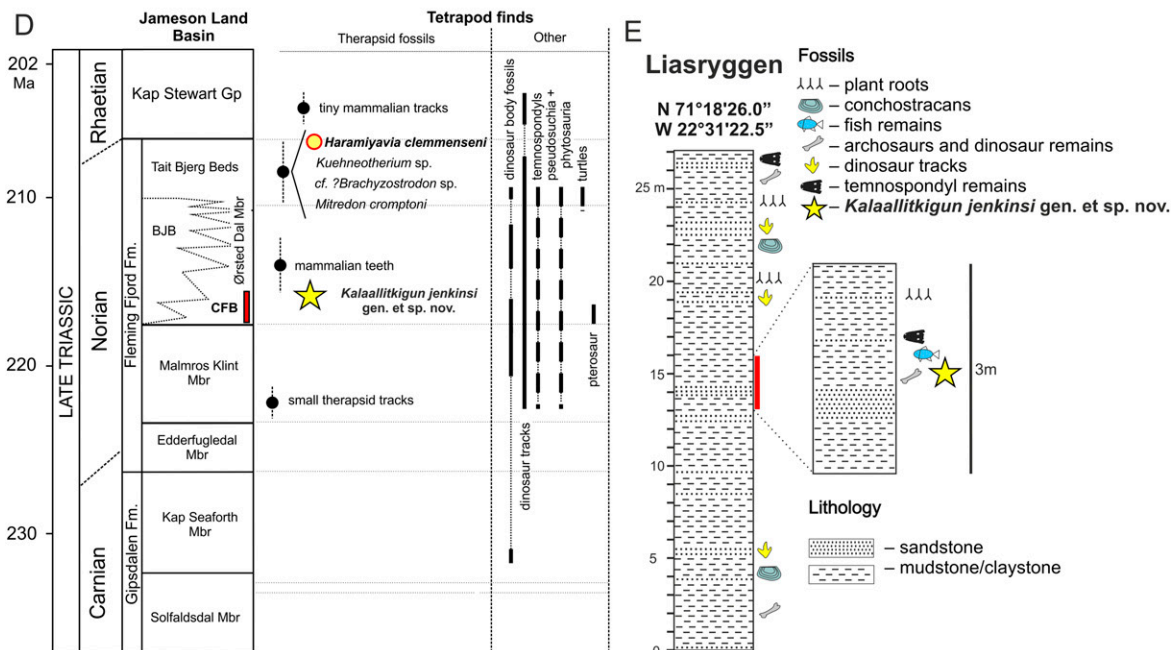
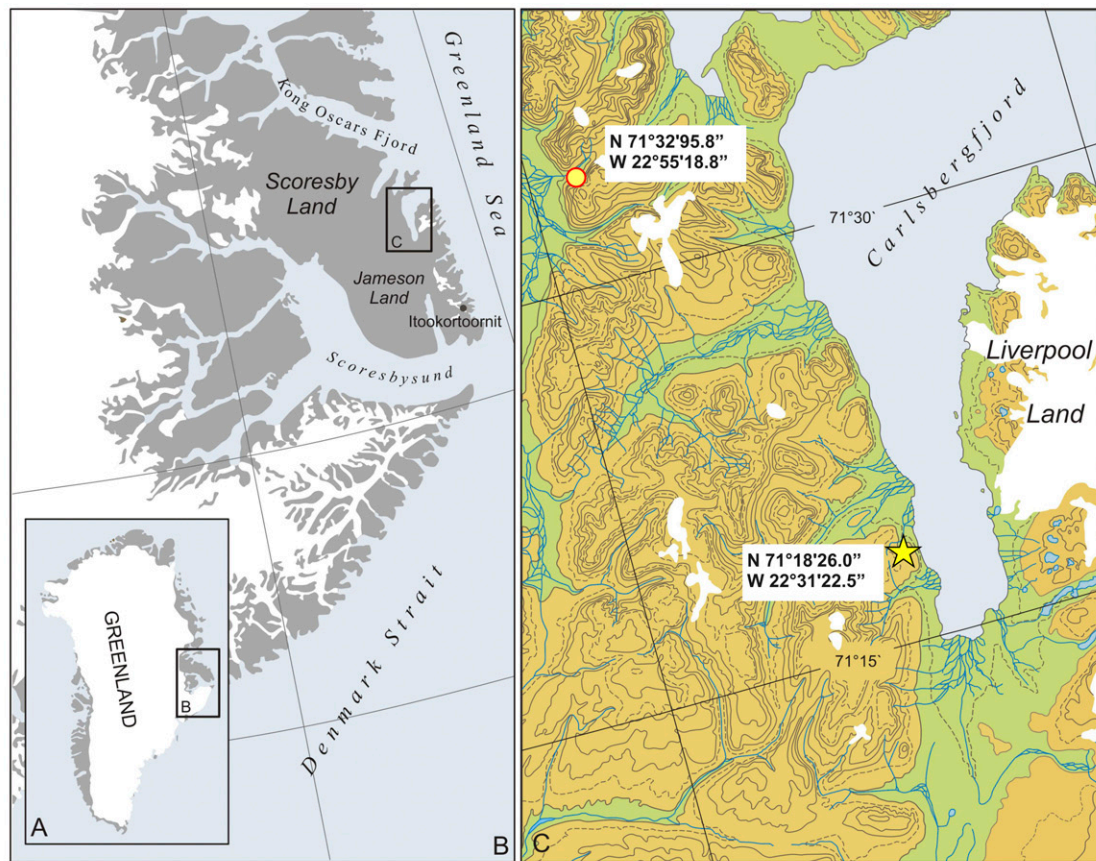
Published under the PNAS license.

<sup>1</sup>Deceased February 17, 2020.

<sup>2</sup>To whom correspondence may be addressed. Email: grzegorz.niedzwiedzki@ebc.uu.se.

This article contains supporting information online at <https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2012437117/-DCSupplemental>.

First published October 12, 2020.



**Fig. 1.** Location and stratigraphic section through Late Triassic of East Greenland and the section exposed at Liasryggen, the type locality of *K. jenkinsi*, gen et sp. nov. (A and B) Location of Jameson Land in East Greenland. (C) Detailed position of the fossil-bearing locality. (D) Late Triassic section from East Greenland showing the stratigraphic position of Liasryggen. Abbreviations: CFB, Carlsberg Fjord beds; and BJB, Bjerkronernes beds. Data from refs. 17–21. (E) Section and fossiliferous beds exposed at Liasryggen. The position of the type specimen of *K. jenkinsi* gen. et sp. nov. (KNK 4152 = NHMD 231331) is indicated with a yellow star. The stratigraphic position of *Haramiyavia clemmenseni* is indicated with a yellow circle.

early haramiyidans are in part attributable to uncertainties in interpreting isolated molariforms and differing interpretations of anatomical character states in *Haramiyavia* from the early

Rhaetian of East Greenland (2, 3) and other haramiyidans from the Middle–Late Jurassic (5, 14). Recently, more detailed studies of a dentary of *Haramiyavia* (3) and a cranium of the large possible



leutherodontid *Cifelliodon* from the lowermost Cretaceous of North America (15) suggested that haramiyidans are not a sister group of multituberculates, and Haramiyida has been excluded from the crown Mammalia.

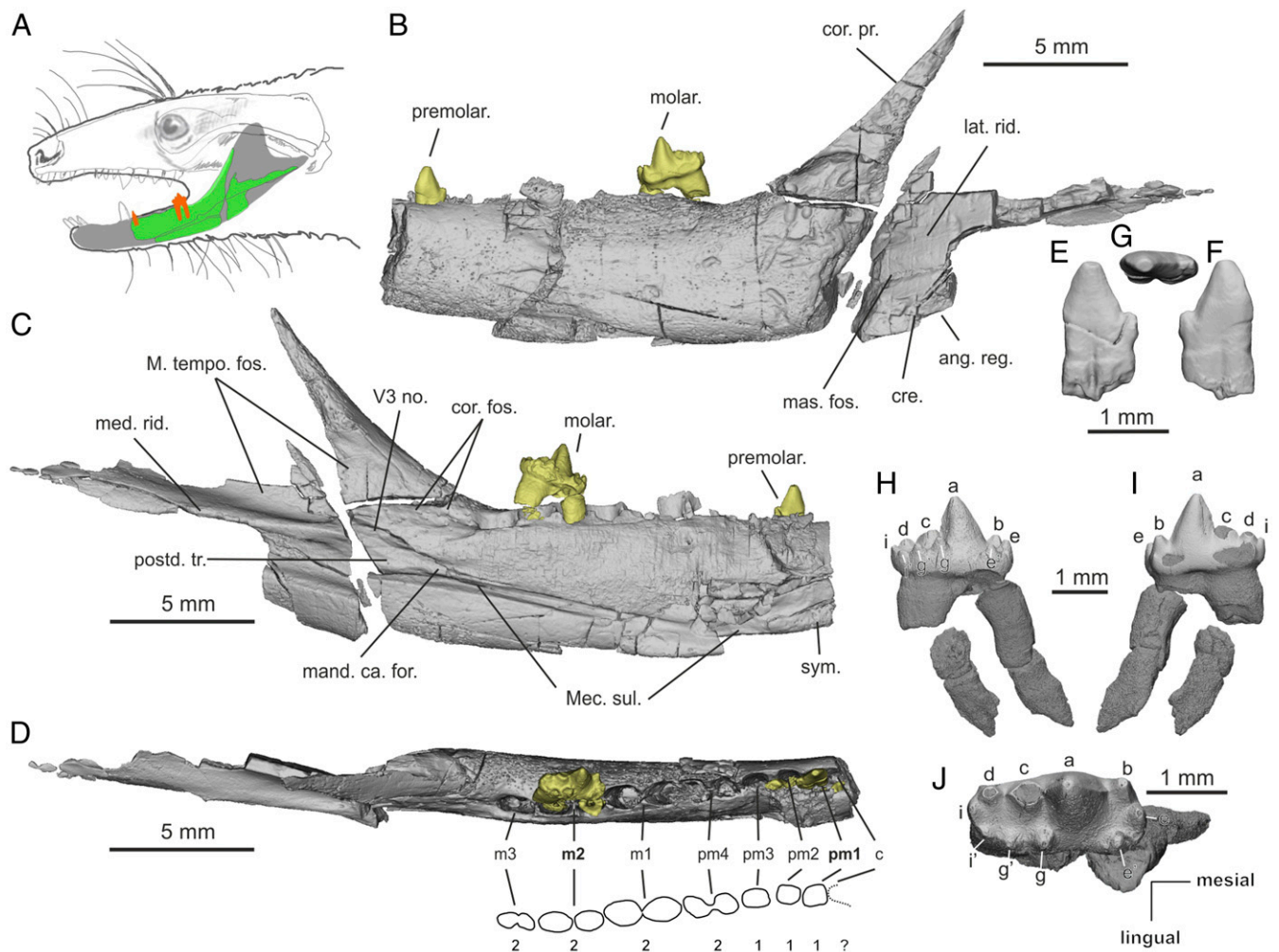
Here, we report a partially preserved dentary of a mammaliaform, *Kalaallitkigun jenkinsi* gen. et sp. nov., from the mid-late Norian (Late Triassic) of East Greenland (Fig. 1). This fossil (Fig. 2) fills substantial morphological and temporal gaps in our understanding of the early evolutionary history of mammaliaforms. Its age (ca. 215 Mya) and phylogenetic position (Fig. 3A) make it one of the oldest mammaliaform fossils in general. In addition, the new taxon represents a haramiyidan with molariform character states intermediate between the more derived *Haramiyavia* and *Thomasia* (Fig. 3B and C) and other contemporary mammaliaforms with plesiomorphic triconodont tooth patterns (1–3).

### Stratigraphic Background

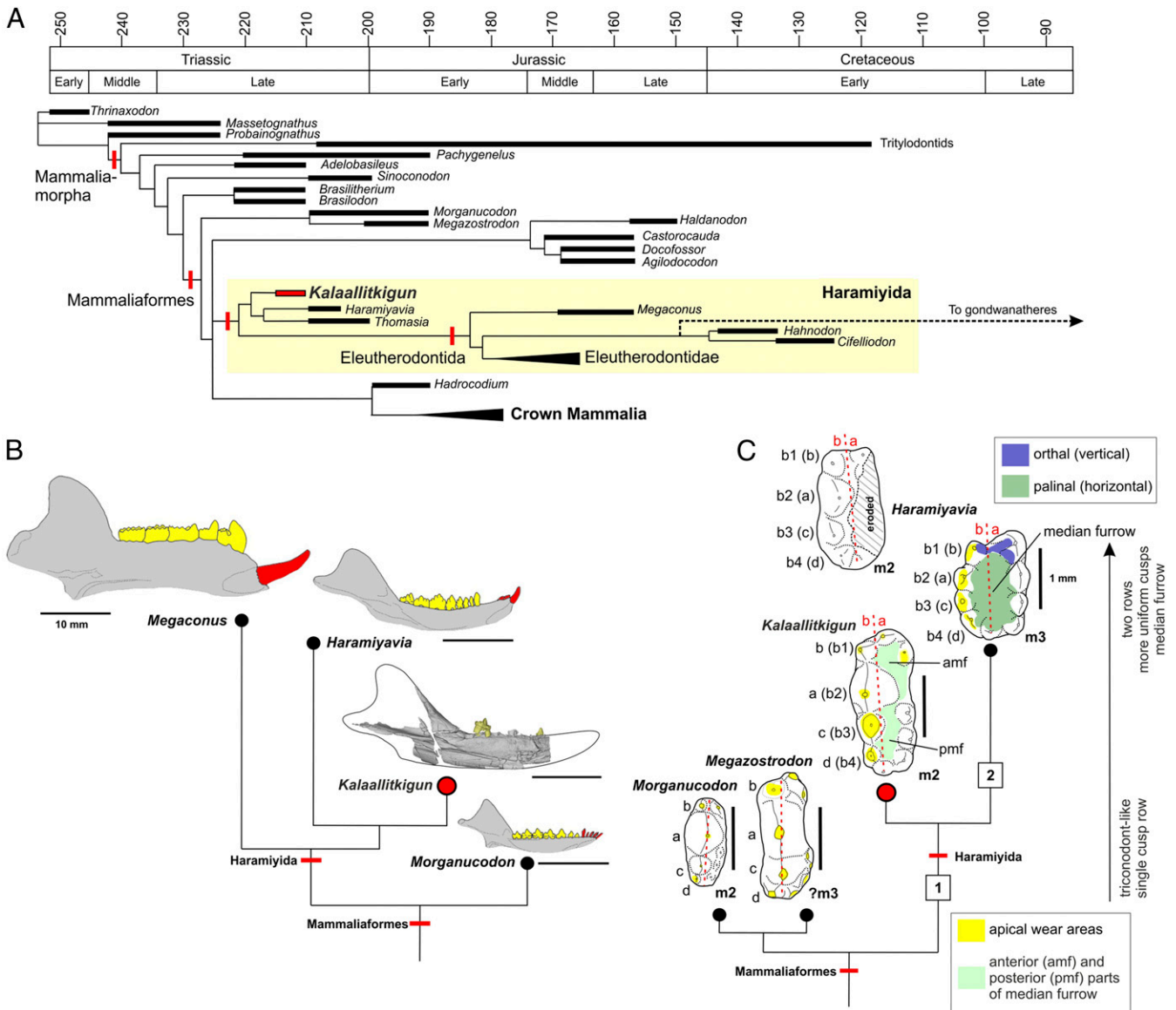
The Late Triassic fossiliferous strata of the Fleming Fjord Formation are exposed in an area of the Jameson Land Basin, which is located in central East Greenland between 70°05' and 73°N

(Fig. 1). The terrestrial succession of this formation is largely confined to the Jameson Land and Scoresby Land regions. During the Late Triassic, Jameson Land was positioned in the northern arid to semiarid belt, 20° to 35° north of the equator (16, 17). The dating of both formations is rather imprecise, as is often the case for early Mesozoic continental deposits.

The Fleming Fjord Formation, dated as early Norian-late Rhaetian in age, contains cyclically bedded lacustrine and sub-ordinary fluvial deposits and is subdivided into three members—the lowermost Edderfugledal Member, the intermediate Malmros Klint Member, and the upper Ørsted Dal Member (18). The Ørsted Dal Member is composed of red mudstones of the Carlsberg Fjord beds, which are overlain by greenish to brown claystone, mudstone, and gray dolomitic limestone of the Tait Bjerg beds. In the Ørsted Dal Member, the Carlsberg beds were probably deposited in constant, dry climatic conditions, whereas the Tait Bjerg beds sedimentology suggests a shift from dry to more humid conditions during deposition (18). The Fleming Fjord Formation is covered by deltaic and lacustrine deposits of the mid-late Rhaetian–Sinemurian Kap Stewart Formation (18).



**Fig. 2.** Digital rendering of the holotype left dentary (KNK 4152 = NHMD 231331) of *K. jenkinsi*, gen. et sp. nov., from the mid-to-late Norian of the Fleming Fjord Formation, East Greenland. (A) The life position of the preserved part of the dentary. (B–D) The dentary in labial (B), lingual (C), and occlusal (D) views. (E–G) The only preserved premolariform in labial (E), lingual (F), and occlusal (G) views. (H–J). The only preserved molariform (m2) in lingual (H), labial (I), and occlusal (J) views. m1–3 mark the position of molariforms (2 is double rooted); pm1–4 mark the position of the premolariforms (1 is single, 2 is double rooted); c marks the position of the canine; (A, G, and B) 1–b4 indicate cusp assignments in the molariform. Abbreviations: ang. reg., angular region; cre., crest; premolar., premolariform; molar., molariform; cor. pr., coronoid process; cor. fos., coronoid fossa; M. tempo. fos., M. temporalis fossa; V3 no., V3 notch for the mandibular nerve entering the mandibular canal; Mec. sul., Meckel's sulcus; mand. ca. for., mandibular canal foramen; mas. fos., masseteric fossa; lat. rid., lateral ridge; postd. tr., postdentary trough; med. rid., medial ridge; and sym., symphysis. Sources for anatomical nomenclature are refs. 1–3, 26, 27.



**Fig. 3.** Time-calibrated phylogeny and transformations of mandibular and molariform structures among mammaliaforms and mammaliaforms. (A) Bayesian consensus cladogram for the analysis of 125 mammalian and nonmammalian synapsid taxa (+*Kalaallitkigun jenkinsi* gen. et sp. nov.) and 538 morphological characters based on ref. 15. For details of the phylogenetic analyses, see *SI Appendix*. (B) Comparison of mammaliaform jaws showing the differences in size and anatomy, mapped onto a simplified phylogeny. (C) Disparate molariform tooth (m2 and m3) occlusal patterns (cusps a-d or b1-b4) in *Morganucodon*, *Megazostrodon*, *Kalaallitkigun*, and *Haramiyavia* (the earliest representatives of Haramiyida) mapped onto a simplified phylogeny. 1 = shift of the b-a-c-d cusp row toward the labial margin, narrowing of cusp a, adding a lingual (cingular) row of more uniform cusps, development of a median furrow; 2 = enlargement of all cusps in the lingual row, widening of the median furrow. Morphology and extent of wear on molariforms of *Haramiyavia*, *Morganucodon*, and *Megazostrodon* based on refs. 2, 3, 8.

The mammaliaform specimen described here, KNK (Greenland National Museum and Archives) 4152 = NHMD (Natural History Museum of Denmark, University of Copenhagen) 2313312, was found on the northwest slope of Liasryggen in fluvial brown to red sandstone-mudstone sequence of the lower part of the Carlsberg Fjord beds (lower part of the Ørsted Dal Member) (Fig. 1 C and D). Rare and poorly preserved invertebrate fossils, tetrapod body, and trace fossils, and pollen spores suggest a late Carnian–early Norian age for the Malmros Klint, and a mid–late Norian–early Rhaetian age for the Ørsted Dal Member (17, 18, 20, 21). Numerous fish scales and bone fragments, including fragmentary temnospondyl (plagiosaurid and capitosaurid) remains, a large archosaur tooth (of pseudosuchian or theropod affinity), and the proximal part of a small dinosaur femur were found in close

proximity of KNK 4152 = NHMD 231331 (20). Above and below these bone-bearing deposits, isolated tetrapod bone fragments, numerous slabs with dinosaur tracks (*Grallator* isp.), and mass accumulations of poorly preserved conchostracan carapaces were collected (Fig. 1E). This conchostracan assemblage includes a relatively large form, which is morphologically similar to representatives of the genus *Shipingia*. This genus is a characteristic Norian component of freshwater strata and its fossils are commonly found in late Norian successions in North America and Europe (22).

In summary, the lithostratigraphic position of the site (location in the lower part of the Carlsberg Fjord beds of the Ørsted Dal Member) and faunistic data (co-occurrence with *Shipingia* clam shrimp, dinosauriform, early dinosaur, and temnospondyl fossils) clearly suggest a mid–late Norian age of KNK 4152 = NHMD 231331 (Fig. 1E).

## Results

KNK 4152 = NHMD 231331 (holotype of *Kalaallitkigun jenkinsi* gen. et sp. nov.) is a partial left dentary, with two teeth still preserved in their respective alveoli (Fig. 2). The dentary lacks its anterior and most of its posterior portions, but the anterior edge of the coronoid process and the medial ridge above the postdentary trough are preserved (Fig. 2C).

The preserved part of the dentary is broken into three fragments, but these fragments are only slightly displaced from each other. The medial surface of the dentary is well preserved, but the lateral surface is damaged posteriorly, so that the masseteric fossa is poorly preserved and the proximal area is eroded (Fig. 2B). However, enough of the mandibular body is preserved to show that the masseteric fossa did not extend onto the horizontal ramus below the tooth row. The visible part of the masseteric fossa is bound by a low, but prominent, crest on its ventral margin (Fig. 2B). The dentary condyle is not preserved in KNK 4152 = NHMD 231331, but was probably connected with the lateral ridge, which is still recognizable in the area of the eroded fragment of the masseteric fossa (Fig. 2B). The medial side of the dentary shows a prominent postdentary trough, which is connected to Meckel's sulcus. The premolariform (pm1) has one constricted root, whereas the molariform (m2) bears two roots. In the molariform, tooth cusp c is broken and cusp e' is slightly displaced due to a crack located at its base. Both roots are broken, and the crown is slightly displaced anteriorly. The finite element analysis (FEA) and phylogenetic results are described in detail in *SI Appendix*.

## Systematic Paleontology

Clade Mammaliaformes Rowe, 1988

Clade Haramiyida Hahn, 1989

*Kalaallitkigun jenkinsi* gen. et sp. nov. Sulej and Niedźwiedzki (Fig. 2)

**Etymology.** The generic name meaning "Greenlandic tooth" derived from *Kalaallit* (Inuit, "Greenland") and *kigun* (Inuit word meaning "tooth"). The specific epithet *jenkinsi* is in honor of Farish A. Jenkins, Jr., former professor at Harvard University who devoted his illustrious career to studies of Mesozoic mammals, functional anatomy of tetrapods, and who discovered the first fossils of mammaliaforms in the Late Triassic of Greenland.

**Holotype.** KNK 4152 = NHMD 231331 (Fig. 2) is an incomplete left dentary with two teeth (pre-molariform pm1 and molariform m2) exposed in labial view.

**Locality and Horizon.** KNK 4152 = NHMD 231331 was collected in brown/red mudstone in the Liasryggen site (N71°18'26.0"; W22°31'22.5") located on the left bank of the Carlsberg Fjord, Jameson Land, East Greenland (Fig. 1). There are rocks representing the Carlsberg Fjord beds (lower part of the Ørsted Dal Member, Fleming Fjord Formation). Biostratigraphic dating and lithostratigraphic correlation place the age between the middle and late Norian (see *Stratigraphic Background*).

**Differential Diagnosis.** A Triassic haramiyidan is characterized by the following combination of characters (\* denotes autapomorphies): 1) medial ridge forming the upper boundary of the postdentary trough beneath the coronoid process pronounced [less well developed in *Erythrotherium* (23) and *Morganucodon* (24)]; 2) Meckel's sulcus dorsoventrally narrow approximately halfway along its anteroposterior length and dorsoventrally wide at the posterior end [in morganucodontans and docodontans Meckel's sulcus is dorsoventrally narrow along its entire anteroposterior length (23, 25–27)]; 3)

Meckel's sulcus anterior to the inferior mandibular foramen proportionately wider than that in *Morganucodon* and similar in size to that in *Haramiyavia*; 4) dental lamina groove (=Crompton's groove) absent, which differs from morganucodontids (25, 28); 5) dental formula is ?c1.pm4.m3 and corresponds to that of *Haramiyavia* (i3.c1.pm4.m3); 6) molariform m2 with an arrangement of dental cusps in two rows; 7) enlarged cusps e', g, and the next distal lingual (cingular) cusps\*; 8) presence of widespread basins (anterior and posterior parts of median furrow) in m2—basins are located between cusps a, b, and cusps e + e', mesially, and between cusp c and cusp d, and the g, g', i', i cusps, distally\*, which differentiates it from *Morganucodon* and *Megazostrodon* (6, 8, 23, 24); 9) differs from nonmammaliaform mammaliaforms, with the exception of Tritylodontidae, *Mitredon*, and *Meurthodon*, in the development of a full division of molariform roots; 10) roots are very massive and circular in cross-section at their bases (Fig. 2); 11) coronoid fossa well separated from postdentary trough (inferred from the presence of the coronoid bone); 12) a discernible and massive angular region located beneath the postdentary trough; 13) poorly developed lateral ridge located in the masseteric fossa; 14) masseteric fossa bound by a crest on its ventral margin; and 15) masseteric fossa not extending onto the ascending ramus of the dentary.

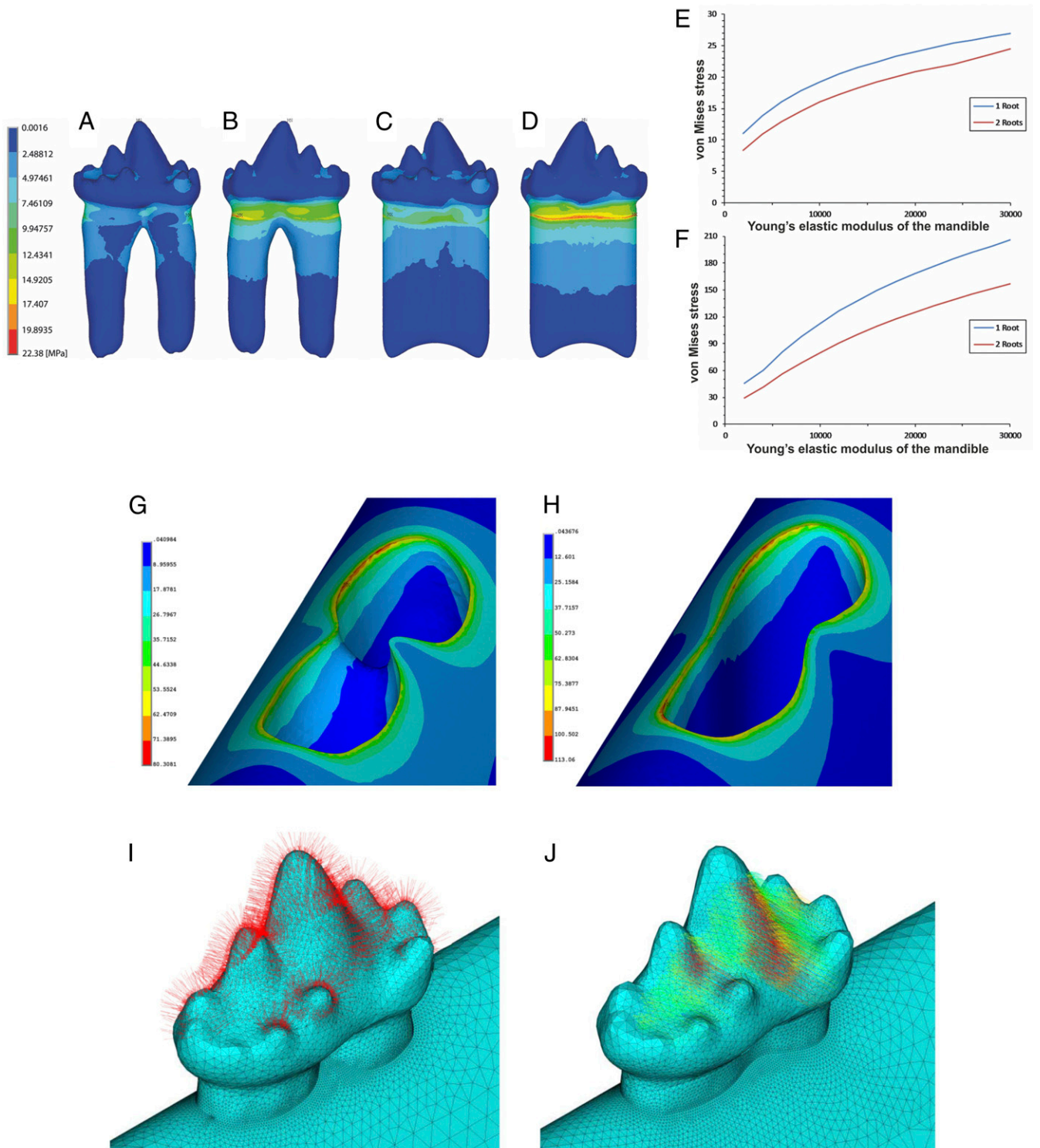
## Discussion

Some anatomical aspects make *Kalaallitkigun* unique. Firstly, the described dentary is unexpectedly large, being nearly twice as large as all known dentaries of morganucodontids, but similar in size to the dentary of *Haramiyavia* (Fig. 3B). This bone is also relatively more massive in relation to the length of the molariform alveoli. The dentary of *Kalaallitkigun* is twice as deep as those of *Morganucodon* and *Megazostrodon*. Secondly, the derived morphologies of the dentary and molariform of *Kalaallitkigun* are surprising, despite its older stratigraphical age. Most interesting is the lack of a dental lamina groove, which is a derived character state shared with *Haramiyavia* (3). The dental formula of *Kalaallitkigun*, as well as the postdentary trough with a flat floor, also correspond to those of *Haramiyavia*. Similarly to *Haramiyavia*, *Kalaallitkigun* possesses a large coronoid process, a mammaliaform plesiomorphy, with a relatively large area for the insertion of the temporalis muscle. *Kalaallitkigun* has a well-developed postdentary trough, indicating the presence of a plesiomorphic mandibular middle ear. The preserved molariform (m2) shows complex and derived morphologies of the crown and two fully distinct roots.

These derived features in the molariform of *Kalaallitkigun* suggest changes in dental function, and an adaptation to an omnivorous/herbivorous diet. Dietary diversification and specialization occurred early in mammaliaform evolution—by the mid-late Norian (2, 3). This was previously indicated by various findings of isolated complex molariforms (e.g., *Thomasia*, *Theroteinus*) from the latest Norian and Rhaetian of Europe (4, 8) and the more complete material of *Haramiyavia* from the early Rhaetian of Greenland (2, 3). However, it was not clear from which predecessor lineages the first mammaliaforms with parallel cusp rows evolved (2, 3). The morphology of the molariform and jaw of *Kalaallitkigun* show intermediate conditions between morganucodontans on one hand and the more specialized structures present in *Haramiyavia* on the other (2, 3). This suggests that haramiyidans may have evolved from a hypothetical ancestor with a triconodont molariform pattern.

The Late Triassic mammaliaforms also displayed a gradual tendency toward root division of the molariforms. This process occurred probably independently in at least two lineages (tritylodontids and mammaliaforms; 9, 29, 30). Until now, the oldest two-rooted molariforms are those of morganucodontans and haramiyidans of the latest Norian–Rhaetian (ca. 210 to 201 Mya) of Europe (1, 8, 31–33) and Greenland (2, 3, 34). The jaw of *Kalaallitkigun*, like other finds of isolated double-rooted pre-molariforms from Greenland (34), was found in part of the





**Fig. 4.** Stress distribution on the lingual and labial surfaces of 3D models of single- and double-rooted molariforms (for details of analyses, see *SI Appendix*). (A and B) The reconstructed molariform of KNK 4152 = NHMD 231331, the holotype of *K. jenkinsi* gen. et sp. nov., with a double root in lingual and labial views. (C and D) Hypothetical molariform with a single root, based on the second molariform (m2) of KNK 4152 = NHMD 231331. Colors represent distribution of von Mises forces, with warmer colors indicating higher stresses. (E and F) Scatterplots showing maximum von Mises stress within the dentary bone structure against Young's modulus of the dentary (E, vertical force, y axis; F, lingual force, x axis). (G and H) Stress distribution in the mandible for both models. Warmer colors indicate higher stresses. (I and J) Pressure applied at the crown surfaces (I, vertical force, y axis; J, lingual force, x axis).

section securely dated as mid-late Norian. Therefore, this indicates that the emergence of double-rooted dentition in mammaliaforms is a relatively ancient evolutionary event. Some

recent studies have shown a well-constrained relationship between developmental pathways responsible for crown differentiation and root formation (35). However, the exact evolutionary sequence of

these developmental steps has not been examined due to the lack of relevant fossils. This transition is extremely important, as multiple-rooted teeth have been retained in nearly all mammaliaform lineages. It has been speculated that root division is linked to changes in the masticatory system and the evolution of occlusion (36). We hypothesize that the root division in molariforms was one of the key innovations that enhanced the biomechanical properties of the dentition and perhaps allowed subsequent feeding diversification of early mammaliaforms (Fig. 4). We tested this hypothesis using three-dimensional (3D) models and FEA of double- and single-rooted molariforms (Fig. 4 A–D) bearing the same crown (modeled from the holotype of *K. jenkinsi*), implanted in the same dentary (Fig. 4 G and H). The teeth were placed in the model of a virtual dentary and exposed to typical loads generated during food processing (Fig. 4 I and J). This was done in order to isolate the relevant factor responsible for the mechanical properties (SI Appendix).

In both cases, the highest stresses appeared in the root immediately below the base of the crown and near the crown–root junction. The double-root model shows lower levels of stress in that area (Fig. 4 A and B and see SI Appendix). This means that during food processing, the crown base of the double-rooted tooth would have been more resistant to failure.

Our simulation demonstrates that the division of the molariform root improves the biomechanical properties of the entire tooth. This apomorphic structure conveys mechanical advantage. This suggests that the disparate morphologies of molariform crowns of mammaliaforms evolved together with biomechanically optimized roots. The root division is made feasible by some

similar development as in the cervical tongue patterning of extant mammals that regulate the process of root division (37).

## Materials and Methods

The specimen KNK 4152 = NHMD 231331 was micro-CT scanned at the Laboratories of Cathodoluminescence Microscopy and Microtomography, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland using a Zeiss XRadia MicroXCT-200 scanner equipped with a low-energy X-ray source (from 20 to 90 kV). The reconstructed computed tomography (CT) data were converted into TIFF image stacks that were subsequently imported and segmented in VGStudio MAX version 3.0 (Volume Graphics Inc.).

**Data Availability.** The data supporting the findings of this study (specimen, scan data, virtual sections, additional photos) are available at the Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland (the data will be shared by jkobylynska@twarda.pan.pl). All FEA analysis datasets and scripts are presented in SI Appendix. The specimen KNK 4152 = NHMD 231331 belongs to the collection of the Natural History Museum of Denmark, University of Copenhagen and is temporarily deposited at the Institute of Paleobiology, Polish Academy of Sciences.

All study data are included in the article and supporting information.

**ACKNOWLEDGMENTS.** We thank K. Janiszewska (project supported by NanoFun POIG.02.02.00-00-025/09) and M. Bińkowski for CT scans of the specimen and D. Snitting for the 3D models of the dentary and teeth. We thank D. Snitting for help with phylogenetic studies and the interpretation of the CT data. The study was supported by the National Science Centre, Poland (grant 2012/07/B/NZ8/02707). Partial funding for this research was also provided by the Swedish Vetenskapsrådet (grant 2017-05248). We also thank the staff of the Constable Point (East Greenland) airport, and especially S. Schirmer, for logistic help.

- Z. Kielan-Jaworowska, R. L. Cifelli, Z.-X. Luo, *Mammals from the Age of Dinosaurs: Origins, Evolution, and Structure*, (Columbia University Press, New York, 2004).
- F. A. Jenkins Jr., S. M. Gatesy, N. H. Shubin, W. W. Amaral, Haramiyids and Triassic mammalian evolution. *Nature* **385**, 715–718 (1997).
- Z.-X. Luo, S. M. Gatesy, F. A. Jenkins Jr., W. W. Amaral, N. H. Shubin, Mandibular and dental characteristics of Late Triassic mammaliaform *Haramiyavia* and their ramifications for basal mammal evolution. *Proc. Natl. Acad. Sci. U.S.A.* **112**, E7101–E7109 (2015).
- P. M. Butler, Review of the early allotherian mammals. *Acta Palaeontol. Pol.* **45**, 317–342 (2000).
- Q.-J. Meng *et al.*, New gliding mammaliaforms from the Jurassic. *Nature* **548**, 291–296 (2017).
- P. G. Gill *et al.*, Dietary specializations and diversity in feeding ecology of the earliest stem mammals. *Nature* **512**, 303–305 (2014).
- Z.-X. Luo *et al.*, New evidence for mammaliaform ear evolution and feeding adaptation in a Jurassic ecosystem. *Nature* **548**, 326–329 (2017).
- M. Debuyschere, E. Gheerbrant, R. Allain, Earliest known European mammals: A review of the morganucodonts from saint-nicolas-de-port (upper triassic, France). *J. Syst. Palaeontology* **13**, 825–855 (2015).
- M. D. Shapiro, F. A. Jenkins Jr., A cynodont from the upper triassic of East Greenland: Tooth replacement and double-rootedness. *Bull. Mus. Comp. Zoo. Harv. Univ.* **156**, 49–58 (2001).
- M. Debuyschere, A reappraisal of *Theroteinus* (Haramiyida, Mammaliaformes) from the upper triassic of saint-nicolas-de-port (France). *PeerJ* **4**, e2592 (2016).
- T. Martin, A. O. Averianov, H.-U. Pfretzschner, Mammals from the late jurassic Qigu formation in the southern junggar basin, Xinjiang, northwest China. *Palaeodiver. Palaeoenvir.* **90**, 295–319 (2010).
- G. Hahn, D. Sigogneau-Russell, G. Wouters, New data on Theroteinidae—Their relations with paulchoffatiidae and Haramiyidae. *Geologica et Palaeontologica* **23**, 205–215 (1989).
- T. Rowe, Definition, diagnosis, and origin of Mammalia. *J. Vertebr. Paleontol.* **8**, 241–264 (1988).
- G. Han, F. Mao, S. Bi, Y. Wang, J. Meng, A Jurassic gliding euharamiyidan mammal with an ear of five auditory bones. *Nature* **551**, 451–456 (2017).
- A. K. Huttenlocker, D. M. Grossnickle, J. I. Kirkland, J. A. Schultz, Z.-X. Luo, Late-surviving stem mammal links the lowermost Cretaceous of North America and Gondwana. *Nature* **558**, 108–112 (2018).
- D. V. Kent, L. B. Clemmensen, Paleomagnetism and cycle stratigraphy of the triassic Fleming Fjord and Gipsdalen formations of East Greenland. *Bull. Geol. Soc. Den.* **42**, 121–136 (1996).
- L. B. Clemmensen, Triassic rift sedimentation and palaeogeography of central East Greenland. *Bull. Grøn. Geol. Unders.* **136**, 1–72 (1980).
- L. B. Clemmensen, D. V. Kent, F. A. Jenkins Jr., A late triassic lake system in East Greenland: Facies, depositional cycles and palaeoclimate. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **140**, 135–159 (1998).
- G. Dam, F. Surlyk, “Cyclic sedimentation in a large wave and storm-dominated anoxic lake; Kap Stewart Formation (Rhaetian-Sinemurian), Jameson Land East Greenland” in *Sequence Stratigraphy and Facies Associations*, W. Posamentier, C. P. Summerhayes, B. U. Haq, G. P. Allen, Eds. (The International Association of Sedimentologists, 1993), vol. H, pp. 417–448.
- T. Sulej *et al.*, New perspectives on the late Triassic vertebrates of East Greenland: Preliminary results of a Polish–Danish palaeontological expedition. *Pol. Polar Res.* **35**, 541–552 (2014).
- L. B. Clemmensen *et al.*, The vertebrate-bearing late triassic Fleming fjord formation of central East Greenland revisited: Stratigraphy, palaeoclimate and new palaeontological data. *Geol. Soc. Lond. Spec. Publ.* **434**, 31–47 (2016).
- H. W. Kozur, R. E. Weems, “The biostratigraphic importance of conchostracans in the continental Triassic of the northern hemisphere” in *The Triassic Timescale*, S. G. Lucas, Ed. (Geological Society, London, Special Publications, 2010), vol. 334, pp. 315–417.
- A. W. Crompton, A preliminary description of a new mammal from the Upper Triassic of South Africa. *Zool. Soc. Lond. Proc.* **142**, 441–452 (1964).
- K. A. Kermack, F. Mussett, H. W. Rigney, The lower jaw of *Morganucodon*. *Zool. J. Linn. Soc.* **53**, 87–175 (1973).
- K. A. Kermack, F. Mussett, The jaw articulation of the Docodonta and the classification of Mesozoic mammals. *Proc. R. Soc. Lond. B Biol. Sci.* **149**, 204–215 (1958).
- J. A. Schultz, B. A. S. Bhullar, Z.-X. Luo, Re-examination of the Jurassic mammaliaform *Docodon victor* by computed tomography and occlusal functional analysis. *J. Mamm. Evol.* **26**, 9–38 (2017).
- E. L. Panciroli, R. B. Benson, Z.-X. Luo, The mandible and dentition of *Borealestes serendipitus* (Docodonta) from the middle jurassic of skye, scotland. *J. Vertebr. Paleontol.* **39**, e1621884 (2019).
- Z.-X. Luo, “Sister-group relationships of mammals and transformations of diagnostic mammalian characters” in *In the Shadow of the Dinosaurs—Early Mesozoic Tetrapods*, N. C. Fraser, H.-D. Sues, Eds. (Cambridge University Press, Cambridge, 1994), pp. 98–128.
- E. A. Hoffman, T. B. Rowe, Jurassic stem-mammal perinates and the origin of mammalian reproduction and growth. *Nature* **561**, 104–108 (2018).
- A. G. Martinelli, M. B. Soares, C. Schwanke, Two new cynodonts (therapsida) from the middle-early late triassic of Brazil and comments on south American probainognathians. *PLoS One* **11**, e0162945 (2016).
- D. Sigogneau-Russell, G. Hahn, “Late triassic microvertebrates from central Europe” in *In the Shadow of the Dinosaurs—Early Mesozoic Tetrapods*, N. C. Fraser, H.-D. Sues, Eds. (Cambridge University Press, Cambridge, 1994), pp. 197–213.
- D. Sigogneau-Russell, Haramiyidae (Mammalia, Allotheria) en provenance du Trias supérieur de Lorraine (France). *Palaeontographica Abt. A Paläozool. Stratigr.* **206**, 137–198 (1989).
- M. Świło, G. Niedźwiedzki, T. Sulej, Mammal-like tooth from the upper triassic of Poland. *Acta Palaeontol. Pol.* **59**, 815–820 (2014).
- F. A. Jenkins Jr. *et al.*, Late triassic continental vertebrates and depositional environments of the Fleming Fjord Formation, Jameson Land, East Greenland. *Medd. Grøn. Geosci.* **32**, 1–25 (1994).
- J. Li, C. Parada, Y. Chai, Cellular and molecular mechanisms of tooth root development. *Development* **144**, 374–384 (2017).
- N. H. Shubin, A. W. Crompton, H.-D. Sues, P. E. Olsen, New fossil evidence on the sister-group of mammals and early mesozoic faunal distributions. *Science* **251**, 1063–1065 (1991).
- H. Seo *et al.*, Regulation of root patterns in mammalian teeth. *Sci. Rep.* **7**, 12714 (2017).