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The oldest definitive docodontan from central East Greenland sheds light on the origin of the clade

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ABSTRACT: The first mammaliaforms emerged in the Late Triassic, but their exact origins remain unclear due to the scarcity of fossils from this period. One of the earliest diverging mammaliaform groups, the order Docodonta, became unusually ecomorphologically diverse compared with other early mammals, and this may be connected to the possession of complex molar cusp morphology. The specimen described here, found in the Rhætelv Formation of the Kap Stewart Group (Rhaetian–Sinemurian) of central East Greenland, provides novel information on docodontan origins and evolution, as well as key biogeographic insights into early mammal dispersal. *Nujalikodon cassiopeiae* gen. et sp. nov. is the first mammaliaform found in the Rhætelv Formation, and is likely to be Early Jurassic (Hettangian) in age. Comprising an incomplete dentary with a single preserved molar, it was visualized using micro-computed tomography; the molar bears similarities to the putative early docodontan *Delsatia*, and docodontan *Dobunnodon*. Phylogenetic analysis places *Nujalikodon cassiopeiae* as a basal member of Docodonta or a close sister taxon, making it one of the oldest definitive docodontans and pushing the origin of the group back to at least the Early Jurassic. It provides insights into the development of docodontan dental complexity, a key factor in their ecological diversification during the Middle to Late Jurassic. Its presence in Greenland supports the hypothesis that docodontans originated in the region now comprising Europe and Greenland before dispersing across the rest of Laurasia.

Key words: mammal, molar complexity, Docodonta, Mesozoic, Rhætelv formation.

DOCODONTA is an early-diverging clade of Mesozoic mammaliaforms noted for their unusually complex dental morphology and exceptional ecomorphological diversity compared with contemporary early mammaliaforms. Until recently, they were known only from the Middle Jurassic to Lower Cretaceous, in the UK (Waldman & Savage 1972; Sigogneau-Russell 2003; Panciroli *et al.* 2019, 2021, 2024), Germany (Martin *et al.* 2024), Portugal (Lillegraven & Krusat 1991; Martin 2005), Russia (Martin & Averianov 2004; Lopatin & Averianov 2005), China (Ji *et al.* 2006; Meng *et al.* 2015) and USA (Simpson 1929; Rougier *et al.* 2014; Schultz *et al.* 2019). Their molar complexity is likely to have contributed to their exceptional ecological diversity (Kemp 2005; Luo & Martin 2007).

Understanding the emergence of Docodonta, particularly their earliest appearance and evolution during the Early Jurassic, provides insights not only into the evolutionary origins of their group, but also into the emergence of ecological diversity in mammaliaforms as a whole. However, given that they have been known definitively only from the Middle Jurassic onward until now, fossils spanning the gap will provide more information about their evolutionary trajectory.

Within the clade Mammaliaformes, Docodonta is one of the earliest-diverging groups (Rowe 1988; Luo 2007; Rougier *et al.* 2014). They emerged before the origin of mammals (Mammalia) *s.s.*, and are more closely related to crown mammals than to *Morganucodon* or *Sinoconodon* (Wible & Hopson 1993; Luo *et al.* 2002; Martin 2005, 2018). Although their overall position within Mammaliaformes has remained relatively stable in large-scale phylogenetic analyses (e.g. Luo & Martin 2007; Panciroli *et al.* 2021), there is still uncertainty regarding the affinities of putative early docodontans, and the phylogenetic

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relationships within Docodonta, particularly of proposed sub-groups, such as the Euramerican and Asian docodontans (Martin & Averianov 2001, 2004), which have been placed in the sub-divisions Tegotheriidae, Simpsonodontidae and Docodontidae by some authors (Martin & Averianov 2004; Averianov & Lopatin 2006; Averianov *et al.* 2010).

Among Late Triassic and Early Jurassic mammaliaforms there are taxa with uncertain affinities that have been tentatively attributed to Docodonta, or suggested to be closely related. Among the 'Symmetrodonta' (a group that is now regarded as paraphyletic, comprising several unrelated branches of mammaliaforms; Luo *et al.* 2002; Kielan-Jaworowska *et al.* 2004; Martin *et al.* 2020) *Woutersia* and *Delsatia* are both Late Triassic in age, and were suggested to be closely related to docodontans, or even early representatives of the group (Sigogneau-Russell & Hahn 1995; Kielan-Jaworowska *et al.* 2004). *Tikitherium copei* (Datta 2005) is an extinct mammaliaform from the Upper Triassic (Carnian) of India that was also initially considered a close relative of Docodonta. However, Averianov & Voyta (2024) subsequently showed that the specimen is actually a tooth of a Neogene shrew.

The oldest undisputed docodontans include *Borealestes*, *Krusatodon* and *Dobunnodon* from Scotland and England (Waldman & Savage 1972; Panciroli *et al.* 2020, 2024), and *Hutegotherium* and *Itatodon* from Russia (Averianov *et al.* 2005, 2010; Lopatin & Averianov 2005), all from the Bathonian, Middle Jurassic. If the origin of Docodonta lies in the Late Triassic as previously suggested (Sigogneau-Russell & Godefroit 1997; Martin & Averianov 2004; Luo & Martin 2007), this leaves a gap of *c.* 40 myr between the proposed sister taxa to docodontans (*Woutersia* and *Delsatia*) (Sigogneau-Russell & Godefroit 1997) and the definite docodontans of the Middle Jurassic, during which the early evolution of the clade Docodonta presumably took place, including the development of their complex molar morphology.

Mammaliaform taxa discovered previously from the Jurassic–Triassic of Greenland have provided important information regarding the timing and phylogeny of radiations of the earliest mammaliaforms. The oldest known mammaliaform *Kalaallitkigum jenkinsi*, estimated to date to *c.* 215 Ma, appears to represent an intermediate form between early species such as the morganucodontans, and multicusped haramiyidans (Sulej *et al.* 2020). Another early taxon dated to *c.* 208 Ma, *Haramiyavia clemmenseni*, has plesiomorphic features that indicate that they are outside of Mammalia (Jenkins *et al.* 1997; Luo *et al.* 2015). This has proven pivotal in debates regarding the timing of the radiation of mammalians, and the placement of haramiyidans within the mammaliaform phylogeny.

The new taxon described herein, *Nujalikodon cassiopeiae* from the Lower Jurassic (Hettangian) of Greenland, provides new information on the origins and evolution of Docodonta. We assessed its phylogenetic position, and what it indicates about the evolution of dental complexity within the docodontan clade, and their biogeographical distribution.

GEOLOGICAL CONTEXT

The Kap Stewart Group is dated to the Rhaetian–Sinemurian and is well exposed in large areas of the Jameson Land Basin of central East Greenland, where it forms a thick succession of interbedded black mudstones and greyish sheet sandstones in large parts of the basin (Dam & Surlyk 1992; Surlyk 2003; Surlyk *et al.* 2021). The Kap Stewart Group is divided into the Innakajik and Primulaelv formations in the southernmost part of the basin (type area) and the Rhætelv Formation in the northern and largest part of the basin (Surlyk 2003; Surlyk *et al.* 2021). Dam & Surlyk (1992) interpreted the Kap Stewart Group sediments to have formed in and around a large wave- and storm-dominated anoxic lake. Coarse-grained sediment was transported to the lake from eastern, western and northern source areas and formed large delta systems. Clemmensen *et al.* (2021) found evidence of a short marine incursion into the lake basin and dated this marine episode to the middle or late Hettangian at *c.* 200 Ma.

NHMD 1184958 was found in the study area at the eastern margin of the basin, at Lepidopteriselv. In Lepidopteriselv and nearby localities, the Kap Stewart Group sediments are restricted to the Rhætelv Formation, reaching a thickness of *c.* 300 m (Dam & Surlyk 1992; Surlyk 2003; Clemmensen *et al.* 2021). The Kap Stewart Group here overlies a 350-m-thick Upper Triassic (Norian) succession of continental (lacustrine and fluvial) deposits in the Fleming Fjord Group (Clemmensen *et al.* 2020; Kent & Clemmensen 2021). At Lepidopteriselv, an erosional boundary separates the Rhætelv Formation from the underlying Ørsted Dal Formation of the Fleming Fjord Group (Clemmensen *et al.* 2020), and new magnostratigraphical work (Kent & Clemmensen 2021) suggested that this unconformity could have a duration of 8 myr.

At Lepidopteriselv, Clemmensen *et al.* (2021) described a section in the middle part of the Rhætelv Formation as formed by interbedded black mudstones ('paper shales') and coarse-grained 1.5–3-m-thick sandstones. The black mudstones contain a number of thin sandstone beds: the thickest one contains plesiosaur bone remains, while *Nujalikodon cassiopeiae* NHMD 1184958 was found in one of the thinnest sandstones beds, in what appears to be a burrow fill (Clemmensen *et al.* 2021). The coarse-grained sandstones are interpreted as distributary channel deposits, while the black mudstones are open lacustrine or interdistributary bay deposits (Clemmensen *et al.* 2021). The sandstone beds contained in the black mudstones are tentatively interpreted to record inundation events that brought sand and bone material into the interdistributary bays.

MATERIAL & METHOD

Specimen

Specimen NHMD 1184958 consists of an incomplete right dentary with a single molar and roots of a second tooth (Figs 1, 2). There are several elements dispersed across the surface of the block, such as a possible semionotiform scale and a hybodontiform tooth. It was accessed for preparation and study while being held at the Lourinhã Museum (ML), and is now accessioned in the Natural History Museum of Denmark (NHMD).

The specimen was partially manually prepared using a needle and a Nexius Zoom Euromex Holland microscope. This uncovered a sufficient portion of the crown of the tooth and dentary to permit specimen identification. The specimen was not completely separated from the matrix because further preparation was likely to cause damage and/or instability.

Digitization & image treatment

NHMD 1184958 was tomographically imaged at Micronsense (Leiria, Portugal) using a MicroCT phoenix v|tome|x m device, with a voxel size of 83 µm, an acceleration voltage of 200 kV and a current of 500 µA. This generated 831 DICOM slices and the scan resolution was 15 µm. Segmentation was performed using the trial version of Avizo 2019.1 (Thermo Fisher Scientific) (see Appendix S2 for more information about the digitalization and image treatment). All computed tomography (CT) scan data and 3D models are available at MorphoSource (Patrocínio *et al.* 2025a).

Phylogenetic analysis

To explore the phylogenetic affinities of *Nujalikodon cassiopeiae* we scored this specimen using the dataset of

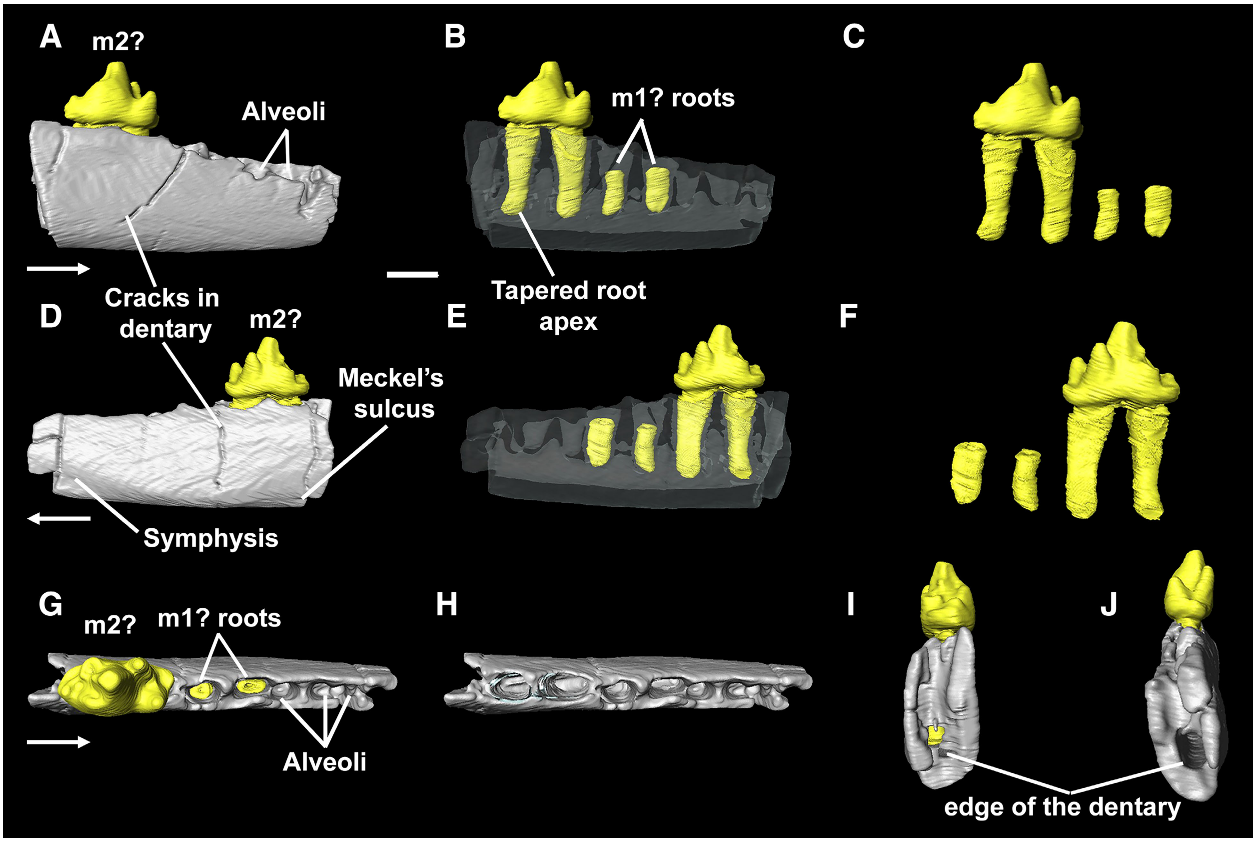

FIG. 1. Digital reconstructions of *Nujalikodon cassiopeiae*, NHMD 1184958, a right dentary with associated dentition. A–C, labial view; C, preserved molar and roots. D–F, lingual view; F, preserved molar and roots. G–H, occlusal view; H, with molars and roots removed digitally. I, posterior view. J, anterior view. Arrows indicate the anterior direction. Scale bar represents 1 mm.

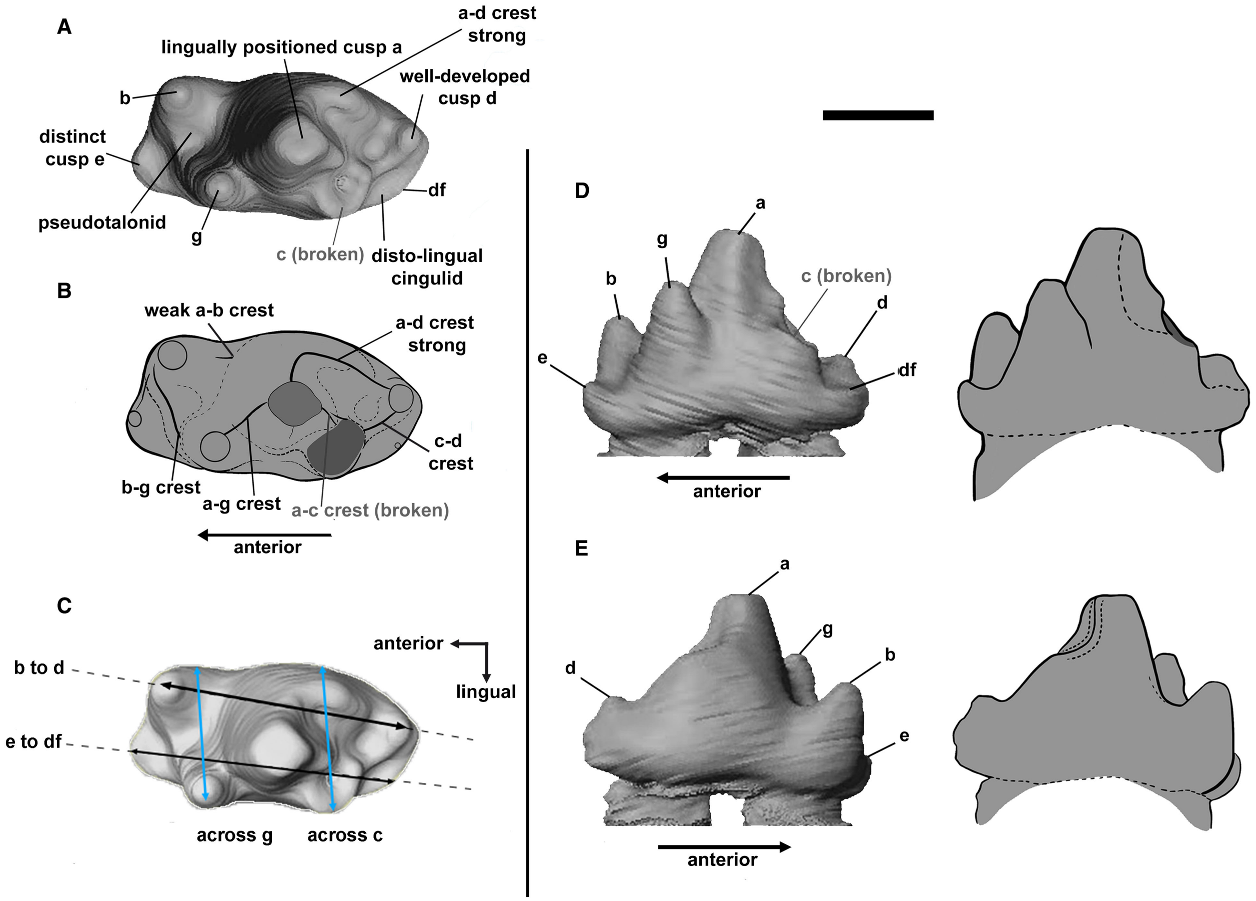

FIG. 2. Diagnostic dental features of *Nujalikodon cassiopeiae* and respective measurements, shown on a digital reconstruction of specimen NHMD 1184958, m2. A–B, occlusal view showing cusps; B, schematic diagram showing crests. C, methodology for measurements. D, lingual view showing cusps, alongside schematic diagram. E, labial view showing cusps, alongside schematic diagram. Measurements taken digitally in Avizo with the Measurement tool, using the methodology of Panciroli *et al.* (2019). Terminology from Butler (1997) and Luo & Martin (2007) (Appendix S1). Scale bar represents 1 mm.

Zhou *et al.* (2019), which was expanded from those used by Luo & Martin (2007), Averianov *et al.* (2010) and Meng *et al.* (2015). This dataset includes mostly dental characters and is optimized for early mammaliaforms, making it possible to include a wider range of taxa that are known only from dentition. This datasets broadly samples early-diverging mammaliaforms and docodontans, including a total of 26 taxa scored for 57 discrete unordered characters. We updated and amended characters as appropriate, scored *Nujalikodon cassiopeiae*, and performed phylogenetic analyses using both maximum parsimony and Bayesian characters. Hereafter, we describe in detail the analytical protocol for each analysis. The matrix, details of changed scores, nexus files, R scripts and full results are all available in Appendices S3–S7 and Patrocínio *et al.* (2025b).

Maximum parsimony. To analyse the dataset we used TNT v1.6 (Goloboff & Morales 2023), using the script of Vila *et al.* (2022), emended as in Rotatori *et al.* (2023). We adopted a New Technology Search to obtain the most parsimonious trees (MPTs), using a driven search with 10 initial addition sequences, finding the minimum length 10 times. The analysis used 100 rounds of sectorial searches, 100 cycles of tree-drifting, 100 cycles of ratchet, and 10 rounds of tree fusing, with the following parameters: for sectorial searches we set the minimum size of sectors to 5 and used random sector selections and 100 cycles of constraint-based selections with a minimal fork of 5. For tree-drifting we explored trees with a maximum difference in absolute fit of 5 and a maximum difference in relative fit of 0.1. All other settings were left at their default values.

To further explore the tree space, the MPTs obtained underwent an additional round of TBR (tree bisection and reconnection) algorithm. We used both equal weighting (EW) and implied weighting (IW) with $K = 15$. Other k values have been explored, but do not produce any difference from the value 15. The strict consensus trees of the maximum parsimony analysis are provided in Figure S2.

Bayesian inference. The dataset was re-analysed in MrBayes v3.2.7a, performing a non-clock analysis (Ronquist *et al.* 2012), and then the maximum compatibility tree (MCT) was time-scaled in R (v4.3.1; R Core Team 2023), with the packages: strap (v1.6.1; Bell & Lloyd 2015); ape (v5.8; Paradis & Schliep 2019); paleotree (v3.4.7; Bapst 2012); and geoscale (v2.0.1; Bell 2022). First and last appearance data were taken from the Paleobiology Database (PBDB; https://paleobiodb.org/) (Appendix S8). The character evolution followed the Mk model (Lewis 2001) and the values were sampled from a gamma distribution. The analysis sampled 10 000 000 generations per run, sampled with the Metropolis coupled Markov chain Monte Carlo (MCMCMC) method for four runs of four chains per run. The initial burn-in was set at 25%. Convergence of independent runs and stationarity were assessed using the program Tracer v1.7.1 (Rambaut *et al.* 2018) considering an effective sample size (ESS) of ≥200 to be informative. The analysis was carried out on the online platform CIPRES. To visualize the synapomorphies, the MCT was manually set to be imported into TNT v1.6 (Appendix S4). The branch for Mammalia was added manually to indicate the relationship between these early diverging mammaliaform taxa of interest, and later mammalians.

Institutional abbreviations. IRSNB, Institut Royal des Sciences Naturelles, Bruxelles, Belgium; ML, Lourinhã Museum, Lourinhã, Portugal; NHMD, Natural History Museum of Denmark, University of Copenhagen, Denmark; Pal./CHQ, Paleontology division of Central Headquarters, Geological Survey of India, Calcutta, India.

SYSTEMATIC PALAEONTOLOGY

Clade MAMMALIAFORMES Rowe 1988
Order DOCODONTA Kretzoi 1946
Family DOCODONTIDAE Simpson 1929
Genus *Nujalikodon* nov.

LSID. https://zoobank.org/NomenclaturalActs/67782a45-88a2-40c3-8dec-6d374e29dfb1

Derivation of name. Named after Nujalik, the goddess of hunting on land in Inuit mythology.

Type species. Nujalikodon cassiopeiae.

Diagnosis. As for type and only known species.

Nujalikodon cassiopeiae sp. nov.
Figures 1, 2

LSID. https://zoobank.org/NomenclaturalActs/ca2c8fe9-d1c4-4a2a-a758-eac9a167dd91

Derivation of name. Named for its cusp pattern resembling the arrangement of the stars in the constellation Cassiopeia.

Holotype. Nujalikodon cassiopeiae (NHMD 1184958), partial right dentary containing one complete molar and the roots of a second tooth.

Diagnosis. Nujalikodon cassiopeiae shares several key features with docodontans, such as elongated anteroposterior lower molars and an anterior pseudotalonid basin formed by cusps a, b and g, with a triangular arrangement of cusps g–a–c. The labial row has taller cusps, with cusp a being the largest, although in *Nujalikodon* it is positioned closer to the centre of the tooth than in most docodontans. The lingual cusp row consists of smaller cusps, including a distinct anterior cusp g and a potentially larger posterior cusp c. The anterior cusp e is distinct, while cusp c, although fractured, appears larger at the base than cusp g, and cusp b tilts slightly anteriorly. Additionally, *Nujalikodon cassiopeiae* possesses a well-defined talonid cusp d and a strong a–d crest that curves posterolingually from the labial face of cusp a. It lacks an a–b crest. As with most docodontans, *Nujalikodon cassiopeiae*'s enamel is free of pits or ornamentation.

Type locality. Sandstone sediment from a burrow infill, associated with dark mudstones with intense bioturbation, Rhætelv Formation, Kap Stewart Group, exposed at a mountain ridge near Lepidopteriselv, Greenland.

Stratigraphic level. Triassic–Jurassic boundary; Clemmensen *et al.* 2021.

Description. Nujalikodon cassiopeiae is known from a partial right dentary measuring 6.55 mm in length. The specimen remains in the matrix, with only the labial side observable to the naked eye. The fragment belongs to the middle portion of the dentary, and there is one complete molar, including roots and crown, the roots of a second tooth anterior to this, and two empty alveoli anterior to this (Fig. 1).

Few morphologically characteristic structures are visible in the dentary. There is a fracture on the lingual side of the dentary posterior to the preserved molar, another fracture lies across the posterior alveolus of the adjacent tooth (containing preserved roots only), and another at the anteriormost part of the dentary, all of them running dorsoventrally through the body of the dentary (Fig. 1A–D). On the labial side, a fracture runs diagonally across two of the alveoli. The ends of the dentary are broken, exposing empty alveoli (Fig. 1I–J).

There are no structures preserved in the dentary that are diagnostic of a particular taxonomic group. The alveoli are labiolingually compressed and separated by U-shaped notches of similar size, as seen in the earliest mammaliaforms including docodontans. The labial walls of the alveoli are thicker than the lingual walls. The anterior alveoli are damaged, but the size of the alveoli decreases anteriorly, as to be expected for the roots of premolar teeth. Anterior to the complete molar (described below), two broken roots are present inside the alveoli (Fig. 1B–C, E–G). The ventral apex of these roots, and those of the more complete neighbouring molar, have a slight posterior curvature.

Lingually, a groove is visible on the posterior side at the base of the dentary below the possible m2, which seems to be the remnants of a morphological feature (Fig. 1D). The Meckel's sulcus is present on the medial surface of the dentary below m2 in other mammaliaforms, including in *Docodon* and *Haldanodon* (Rougier *et al.* 2014; Schultz *et al.* 2019; Martin & Schultz 2023). The Meckel's sulcus withdraws posteriorly during ontogeny in *Haldanodon* (Schultz *et al.* 2019), therefore if this feature in *Nujalikodon cassiopeiae* corresponds to the anterior tip of Meckel's sulcus, it may indicate a relatively young adult animal. There is a slight concavity in the anteriormost part of the lingual side of the dentary, which continues posteriorly, terminating below the position of what we identify as the m1 (Fig. 1D). This appears to be a weak mandibular symphysis. These characteristics support the interpretation of *Nujalikodon cassiopeiae* as representing the middle portion of a right dentary.

The single preserved molar tooth is likely to be an m2 based on its size, depth of the alveoli, and position in the dentary. In docodontans, as in many other early mammaliaforms, the depth of molar roots in the dentary increases anteriorly from the ultimate molar to the m2 position, then decreases anteriorly from the m2 to p1 (e.g. Panciroli *et al.* 2019, figs 3–6). The diameters of the alveoli in the preserved molar of *Nujalikodon cassiopeiae* are larger than the rest of the tooth row, and the diameters of the alveoli in the tooth row shrink anteriorly (Fig. 1G–H). This supports our interpretation of the preserved molar as an m2. The anteriormost preserved alveoli in *Nujalikodon cassiopeiae* are significantly smaller than the rest, indicating that this may represent the ultimate premolar position.

In occlusal view, the m2 in *Nujalikodon cassiopeiae* is anteroposteriorly elongated and slightly labiolingually compressed (Fig. 2A–B). There is a cingulid on the posterior part of the tooth, below two main cusps (identified as cusps c and d) (Fig. 1A, D). A cingulid has been identified on the lingual side of the molars in other docodontans (Luo & Martin 2007), supporting our identification of this as the lingual aspect of *Nujalikodon cassiopeiae*.

Nujalikodon resembles most docodontans (e.g. *Borealestes*, *Krusatodon*, *Castorocauda*, *Itatodon* and *Haldanodon*) in having a taller labial row of cusps, aligned anteroposteriorly with the greatest cusp a (although cusp a is much closer to the middle of the tooth in *Nujalikodon*, see below) (Fig. 1A–B). In comparison, the lingual row has smaller cusps with a distinct anterior cusp g and a posterior cusp c, which, although broken in NHMD 1184958, appears larger than cusp g (see below). The molar possesses an anterior pseudotalonid basin formed by cusps a, b and g, and has cusps g–a–c in a triangular arrangement of *c.* 100°, comparable to docodontans such as *Itatodon* (*c.* 110°); *Dobunnodon* (*c.* 100°) and to the early mammaliaform *Delsatia* (*c.* 90°). Like the majority of docodontans, *Nujalikodon*'s molar tooth enamel does not have pits or ornamentation.

In *Nujalikodon cassiopeiae*, cusp a is located approximately in the median axis of the tooth (linguolabially), which is more lingually positioned than in most other docodontans, but similar to *Dobunnodon* and *Dsungarodon* and the putative docodontan *Delsatia*. Cusp a is conical, rounded labially, and slightly convex lingually with a faint dorsoventral protuberance on the lingual face (Fig. 2A–B, D). Cusp g in *Nujalikodon cassiopeiae* is about two-thirds the height of cusp a. It is positioned anterolingual to cusp a, and aligned with cusp c.

The base of cusp c is positioned posterolingually in relation to cusp a. Cusp c is broken at the base, making it difficult to judge its size, but the width of the base suggests it is smaller than cusp a and slightly larger than cusp g, resembling *Tegotherium*, *Dsungarodon* and *Tashkumyrodon*. The distance between cusp c and cusp g is similar to *Dobunnodon* and *Itatodon*. Cusp b is about one-third of the height of cusp a, and is tilted slightly anteriorly (Fig. 1D), as in *Borealestes* and *Krusatodon*, as opposed to the more upright orientation in *Dsungarodon* or *Simpsonodon*. This well-defined talonid cusp d is similar to *Dobunnodon*, *Itatodon* and *Delsatia*. A smooth df cusp is visible on the posterolingual cingulid. Cusp e is situated on the anteriormost part of the molar and is distinct anteriorly (Fig. 1A, D), resembling *Borealestes*. It is similar in size to cusp d.

There is a strong a–d crest, similar to *Dobunnodon*, which is directed posterolabially (Fig. 1A–B). A strong a–c and weaker a–g crest are directed mesially and posteriorly from the apex of cusp a, forming an angle of *c.* 110°, and both have a v-notch. There is no a–b crest, differing from most docodontans, but similar to *Dobunnodon*, in which it is greatly reduced. All of the crests are straight except for the a–d, which begins on the labial face of cusp a, but curves posterolabially (Fig. 2A–B). This is similar to *Dobunnodon*'s a–d crest. There is no b–e crest or a–b crest. Cusp d is connected to cusp a by a distinct and ridge-like a–d crest, and to cusp c by a c–d crest.

Remarks. Overall, *Nujalikodon cassiopeiae* bears a strong resemblance to *Delsatia* in terms of cusp positioning, but it differs in the size of the lingual cusps, the straighter crests, and the presence of a posterior basin, which *Delsatia* lacks. Overall molar morphology, particularly the lingual positioning of cusp a and the well-defined cusp d, aligns *Nujalikodon cassiopeiae* more closely with *Dobunnodon* and *Delsatia*.

Measurements. Molar length: cusp d–b, 1.60 mm; cusp e–df, 1.76 mm; molar width: across cusp c, 0.88 mm; across cusp g, 0.83 mm (Fig. 2C).

RESULTS

Phylogenetic analysis

Phylogenetic analysis recovers *Nujalikodon cassiopeiae* either as an early-diverging basal docodontan, or as a close sister taxon to Docodonta. This indicates a closer relationship to Docodonta than to other early mammaliaforms previously purported to be early diverging docodontans, such as *Delsatia* and *Gondtherium*. The tree topology is broadly similar to that reported by Zhou *et al*. (2019), but with some key differences in taxon placement, and the addition of *Nujalikodon cassiopeiae*.

Maximum parsimony. The EW analysis recovered 316 MPTs (see parameters in Table 1). The overall topology differs from the results of Zhou *et al*. (2019) in the position of some basal mammaliaforms (the strict consensus trees of the maximum parsimony analysis are provided in Fig. S2). *Nujalikodon cassiopeiae* is nested in a polytomy alongside all other non-docodontan mammaliaforms, and *Borealestes*, *Dsungarodon*, *Dobunnodon*, *Castorocauda* and *Tashkumyrodon*. This supports *Nujalikodon cassiopeiae* as being closely related to other early mammaliaforms, including those previously suggested to be basal docodontans, such as *Delsatia* and *Gondtherium*. However, it does not provide resolution on the relationships between these taxa, and places some confirmed docodontan taxa outside of the clade. In this iteration Docodonta is not recovered as a monophyletic group, however, we highlight taxa that are traditionally assigned to this group in the results of the strict consensus trees of the maximum parsimony analysis provided in Figure S2.

The K15, IW analysis recovered three MPTs (see Table 1 for parameters), and the overall topology is in accordance with EW analysis (Fig. S2), but topological resolution is increased, and docodontan taxa previously nested within a polytomy are recovered now as part of Docodonta. *Nujalikodon cassiopeiae* is in a polytomy with only *Gondtherium*, *Dobunnodon* and the rest of Docodonta, while the other taxa form earlier-diverging branches nested outside that clade.

Bayesian inference. The Bayesian inference analysis reached convergence for all parameters (ESS > 200), and the good quality of this analysis is supported by a potential scale reduction factor equal to 1, and an average standard deviation of split frequencies *c*. 0.007. In the MCT, *Nujalikodon cassiopeiae* is recovered as the most basal member of Docodonta, or a close sister taxon (Fig. 3; the MCT showing the posterior probabilities is given in Fig. S3). The position of the clade is supported by the non-preservation of the anterolingual cusp X of the upper molars (char. 7). The Indian taxon *Gondtherium* is sister taxon to *Nujalikodon* + Docodonta, and despite the observed morphological similarities, *Delsatia* forms a further outgroup with *Woutersia*. This supports a closer relationship between *Nujalikodon* and Docodonta than between *Delsatia* and Docodonta.

TABLE 1. Parameters for the maximum parsimony phylogenetic analysis.

	EW	IW
CI	0.545	0.545
RI	0.816	0.816
RCI	0.445	0.445
TL	143	143

CI, consistency index; EW, equal weighting; IW, implied weighting; RCI, rescaled consistency index; RI, retention index; TL, tree length.

DISCUSSION

Systematic affinities of Nujalikodon cassiopeiae

Similarities between *Nujalikodon* and other, coeval mammaliform taxa such as *Morganucodon* and *Woutersia* are limited; for example, the cusp g of *Nujalikodon* is more enlarged, and placed more anteriorly along the lingual cingulid relative to primary cusp a than in either of those taxa (Luo & Martin 2007, fig. 2). *Nujalikodon*'s crests are also straighter, and it has a unique posterior basin. The morphology of the cusps and crests in *Nujalikodon* most closely resembles putative docodontan *Delsatia* (from the Late Triassic), and the definitive docodontan *Dobunnodon* (Middle Jurassic), particularly the more lingual position of cusp a and well-defined cusp d. However, *Delsatia* has equally sized lingual cusps, while *Nujalikodon*'s cusps differ in size (as in docodontans), suggesting a closer affinity to Docodonta for the latter taxon than other early mammaliaform taxa.

Docodontans are united by diagnostic features including lower molars that are elongated longer anteroposteriorly than linguolabially (Luo & Martin 2007), and an anterior pseudotalonid basin formed by cusps a, b and g, arranged in a triangular g–a–c pattern. The labial row contains taller cusps, with cusp a being the largest, although more centrally positioned than in docodontans. The lingual row has smaller cusps, with a distinct anterior cusp g and a potentially larger posterior cusp c. *Nujalikodon* shares these features.

The phylogenetic analyses herein recover *Nujalikodon cassiopeiae* either as an early diverging docodontan, or a sister taxon to Docodonta (Figs 3, S2, S3). The unresolved polytomy of early mammaliaforms and some docodontan taxa recovered in the maximum parsimony EW analysis might be the result of the limited set of characters available for many of these taxa. For instance, 33 out of 57 characters could be scored for *Nujalikodon cassiopeiae* (*c*. 58%), while only 16% of characters can be scored for *Gondtherium* (Appendix S3). Many early mammaliaform taxa are known only from single isolated teeth and associated fragments, offering a limited possibility to score characters.

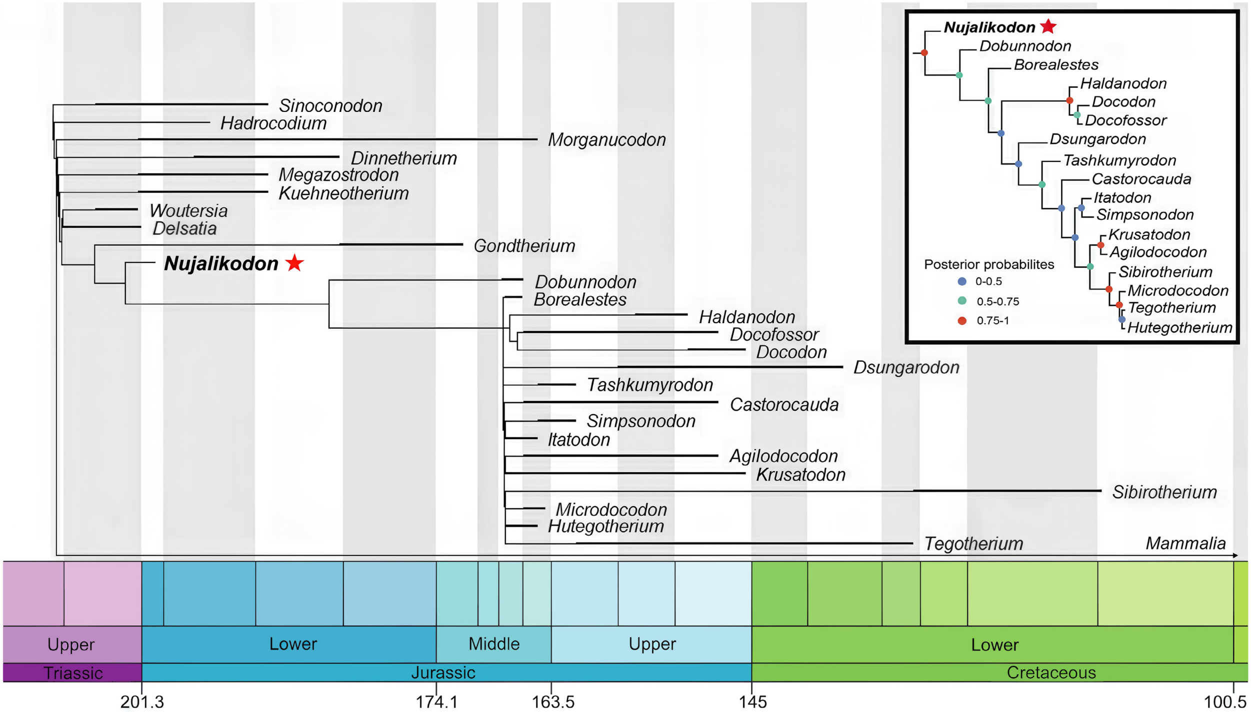

FIG. 3. Time scaled maximum compatibility tree (MCT) from the Bayesian analysis, created with R software v4.3.1 (R Core Team 2023). Top right inset image shows the relationships of *Nujalikodon* and Docodonta in the MCT with posterior probabilities (see Fig. S3 for the full MCT with posterior probabilities). First-to-last appearances are represented by black bars (Appendix S8).

The Bayesian analysis returned a more resolved topology which provides greater resolution than the results of the EW and IW analyses. In the MCT *Nujalikodon* is the closest taxon to Docodonta, supporting the interpretation that it is a basal member of this clade (Fig. 3). Within Docodonta, the polytomy between *Microdocodon*, *Hutegotherium* and *Tegotherium* in the maximum parsimony analysis was resolved, resulting in the topology *Microdocodon* + (*Hutegotherium* + *Tegotherium*). In the Bayesian analysis Docodonta consist of two distinct clades: *Haldanodon* + (*Docodon* + *Docofossor*), and all other docodontan taxa in the other, except for *Borealestes*, *Dobunnodon* and *Nujalikodon*, which form, respectively, successive sister taxa, and represent the most basal taxa in the clade.

Implications for docodontan phylogeny

The recognition of *Nujalikodon cassiopeiae* as a docodontan definitively extends the stratigraphic record of this lineage back to the Triassic–Jurassic boundary, making this the oldest occurrence of this group of mammaliaforms. This finding narrows the ghost lineage between putative early docodontans and definitive later taxa from 40 to 33 myr between *Nujalikodon cassiopeiae* and the second oldest docodontan, *Borealestes* (Panciroli *et al.* 2019, 2020). The persistence of this gap is not surprising given the poor preservation potential of small mammaliaforms during the Mesozoic as a whole, and the early Jurassic in particular (Kemp 2005).

Martin & Averianov (2001, 2004) proposed the existence of two distinct radiations within Docodonta: Euroasian docodontans (*Tashkumyrodon*, *Sibirotherium* and *Tegotherium*) and Euroamerican docodontans (*Borealestes*, *Haldanodon*, *Docodon* and *Simpsonodon*). Morphological characters they identified in Eurasian docodontans include a well-developed cusp e, the presence of the b–e and e–g crests, and the reduction of the b–g crest. Martin & Averianov (2001, 2004) suggested that Euroamerican docodontans are characterized by the reduction or loss of cusp e and a strong reduction of the b–e crest. However, phylogenetic analyses that have included subsequent discoveries of new docodontan taxa from the Middle to Upper Jurassic of China, and the Middle Jurassic of Siberia and Scotland, have led to phylogenetic topologies that are significantly different from that of Martin & Averianov (2004) (e.g. Zhou *et al.* 2019; Panciroli *et al.* 2021; Averianov *et al.* 2023). Our analyses including these newer fossils do not support the separation of Eurasian and Euramerican clades (see also Meng *et al.* 2015; Averianov *et al.* 2023). In our analysis *Docofossor* (China), *Docodon* (America and Europe) and *Haldanodon* (Portugal) form a clade. While Martin & Averianov (2001, 2004) regarded *Docodon* and *Haldanodon* as part of the Euroamerican clade, the inclusion of *Docofossor*, an Asian taxon, does not fit this biogeographical picture.

The other main clade in our analysis consists of a mixture of taxa known from the UK (*Simpsonodon* and *Krusatodon*) and Asia (*Agilodocodon*, *Castorocauda*, *Dsungarodon*, *Hutegotherium*, *Itatodon*, *Microdocodon*, *Sibirotherium*, *Simpsonodon*, *Tashkumyrodon* and *Tegotherium*). This does not fit the geographic distribution proposed by Martin & Averianov (2001, 2004) for Eurasian docodontans. They also placed *Simpsonodon* within Euroamerican docodontans, but it is now known from Kyrgyzstan (Martin *et al.* 2010) and Russia (Averianov *et al.* 2010). *Nujalikodon cassiopeiae* shares the well-developed cusp e and absence of the b–e crest proposed as a feature of Eurasian docodontans, but unlike them, the b–g crest in *Nujalikodon cassiopeiae* is not reduced.

Clades proposed within Docodonta, Tegotheriidae, Simpsonodontidae and Docodontidae (Averianov & Lopatin 2006; Averianov *et al.* 2010) also appear unstable. Docodontans placed in Tegotheriidae by other authors include *Tegotherium*, *Krusatodon*, *Sibirotherium* and *Hutegotherium*, based on upper molar characters such as a cusp Z (except *Tegotherium*) and absent A–X crest, and on the lower molars, presence of cusp bb, a large pseudotalonid basin bordered by crests a–b, b–bb, bb–g and a–g, and absent b–g crest. Docodontidae, in which 'Euramerican' *Haldanodon*, *Docodon* and *Borealestes* have been placed (Kielan-Jaworowska *et al.* 2004), is characterized by upper molar characters such as a reduced cusp C twinned with cusp A, and lower molar characters such as a larger cusp b than cusp c, cusp b close to cusp a, and a wide anterolingual cingulid. Finally, Simpsonodontidae includes *Simpsonodon*, and is characterized by lower molar characters such as a large pseudotalonid basin bordered by crests a–b, a–g and b–g, an absent cusp e, wide anterolingual cingulid, crenulations on the posterior side of the lower molariform crowns, and the dentary character of a continuous additional groove located above the Meckelian groove and separated from the more posterior trough for the postdentary bones (Averianov *et al.* 2010).

Our phylogenetic analysis does not support the monophyly of these proposed docodontan groups, but the results are similar to the those of Panciroli *et al.* (2019, 2021). Other authors rarely assign docodontans to specific families (e.g. Meng *et al.* 2015; Zhou *et al.* 2019). We suggest that the evidence does not currently support the monophyly of these groups, but that there may be at least two larger clades within Docodonta, albeit not following the biogeographic Eurasian–Euramerican split previously proposed.

Origin of docodontan molar complexity

The docodontan molar is complex compared with that of other early mammaliaforms. Martin & Averianov (2004) proposed a theoretical model for the development of the docodontan lower molar, suggesting a progression from the 'triconodont' *Woutersia* (which they placed outside of Docodonta due to the absence of the a–g crest) through a hypothetical ancestral stage with four additional crests and an extra cusp f. These features would have been inherited by later docodontan lineages, with some taxa modifying or losing some cusps or crests.

The small or absent cusp e and a reduced b–e crest of proposed Euramerican docodontans, such as *Borealestes*, *Haldanodon* and *Docodon*, were thought to represent the ancestral condition (Martin & Averianov 2004). *Simpsonodon* was considered to represent a side branch of this group (possibly sharing a common ancestor with the oldest known docodontan taxon at that time, *Borealestes*), making the molar morphology of this taxon ancestral for the 'Euroamerican' group (Martin & Averianov 2004, fig. 5). This proposal for the development of the lower molars of Docodonta is partially compatible with the results obtained here. We find *Borealestes* basal to *Haldanodon*; or *Docodon* and *Dobunnodon*, the next successive outgroup, and these two taxa may therefore retain features of the early docodontan molar morphology.

More recently, it has been suggested that the molar features of Docodonta are homologous to those of shuotheriids, placing these groups together in a new clade, Docodontiformes (Mao *et al.* 2024). Shuotheriids have traditionally been interpreted as possessing a cusp arrangement homologous to the tribosphenic molars present in Mammalia, but their cusp arrangement has been reinterpreted as being pseudotribosphenic. The pseudotribosphenic molar is proposed by Mao *et al.* to have developed from a '*Morganucodon*-like ancestor' (i.e. a 'triconodont' cusp arrangement), which is congruous with earlier hypotheses of the evolution of dental complexity for Docodonta (see above; Martin & Averianov 2004).

The position of *Nujalikodon cassiopeiae* suggests that it may be representative of the ancestral docodontan molar. It resembles *Delsatia* (the Upper Triassic taxon from France also proposed to be a basal docodontan; Sigogneau-Russell & Godefroit 1997) in the more lingual position of cusp a. It also shares features with chronologically earliest undisputed docodontan taxa, the Bathonian *Dobunnodon* and *Borealestes*; *Dobunnodon* also has a more lingually placed cusp a, while *Borealestes* shares a distinct anterior cusp e. Shuotheriids such as *Feredocodon chowi* also possess a more lingual central protoconid/cusp a (Mao *et al.* 2024). This supports hypotheses that

Docodonta (and possibly Docodontiformes *sensu* Mao *et al.* 2024) emerged from a triconodontan ancestor, and suggests that cusp a moved to a more labial position through docodontan evolution, as seen in *Nujalikodon*.

Palaeobiogeographical implications & the origin of Docodonta

The discovery of specimen *Nujalikodon cassiopeiae* provides new insights into the palaeogeographical distribution and evolution of Docodonta. This group has an almost exclusively Laurasian distribution (Fig. 4), with fossils from North America, Europe, the UK and Asia, peaking in diversification during the Middle–Late Jurassic (Sigogneau-Russell 2003; Kielan-Jaworowska *et al.* 2004; Martin & Averianov 2004; Ji *et al.* 2006; Luo & Martin 2007; Luo *et al.* 2015; Meng *et al.* 2015).

If included within Docodonta, the exception is *Gondtherium*, which is from the Kota Formation (Middle Jurassic and Lower Cretaceous) in India, which was in the southern hemisphere during the Middle Jurassic (Prasad & Manhas 2007, fig. 27). *Gondtherium dattai* is represented by a single worn upper molar, and was suggested to be a docodontan based on cusp morphology (Prasad & Manhas 2007). If *Gondtherium* is also a basal docodontan it challenges the idea that docodontans were absent from the southern hemisphere. Our maximum parsimony analysis recovers a close relationship between this taxon and Docodonta, and the Bayesian analysis places it as a sister taxon but, as noted earlier, *Gondtherium*'s character scores include a lot of missing data (as do those of another putative docodontan taxon, *Woutersia*). The classification of *Gondtherium* as a docodontan is disputed (Kielan-Jaworowska *et al.* 2004), and the sparse material and the fact that it is an upper molar, makes it difficult to compare directly with *Nujalikodon cassiopeiae*. Instead, it is likely to belong to a different mammaliaform group with superficial similarities to Docodonta.

During the Late Triassic to Early Jurassic, Greenland was close to what is now Great Britain and France, which could explain the phylogenetic relationship between *Nujalikodon cassiopeiae* and the Upper Triassic *Delsatia* from France (Fig. 4). Their age and location suggests that Docodonta have their origins in Europe–Greenland in the Late Triassic to Early Jurassic, and later dispersed across the northern hemisphere. During the Triassic, Earth's landmasses were united in the supercontinent Pangaea, characterized by warm, uniform climates without polar ice (Benton 2016). Clemmensen *et al.* (1998) observed a European faunal influence between eastern Greenland and Europe during the Late Triassic, corroborated by Sulej *et al.* (2014) and Marzola *et al.* (2018). *Brachyzostrodon* and *Kuehneotherium* are found in both regions (Sigogneau-Russell 1983; Jenkins *et al.* 1994), as are amphibians such as *Cyclotosaurus* and members of Batrachia (Jenkins *et al.* 1994; Jésus *et al.* 2022), and dinosaurs such as *Plateosaurus* (Jenkins *et al.* 1994; Kent & Clemmensen 2021; Beccari *et al.* 2021). At the end of the Triassic, an extensive arid belt covered much of North and South America, Europe and Africa (Benton 2016), potentially explaining the divergence of faunal assemblages between Europe–Greenland and North America around or just after this time. If Docodonta have their origins in Europe–Greenland, then, as Pangaea began to break up at the end of the Triassic this may have created further physical barriers to their southward spread.

The separation of the 'Euroamerican' and 'Eurasian' docodontans was proposed to be related specifically to the formation of the Turgai Strait, which separated Europe and Asia at various times between the Bathonian and Oxfordian (Golonka *et al.* 1996; Martin & Averianov 2001, 2004). Relatively plesiomorphic taxa, such as *Borealestes*, *Haldanodon* and *Docodon*, were restricted to Europe and North America (*Docodon victor* and *Docodon apoxys* identified in the USA, and *Docodon hercynicus* recently discovered in Germany), whereas docodontans in Asia diversified (Averianov & Lopatin 2006; Luo 2007). Although our phylogenetic analysis does not support this palaeogeographic split of Docodonta, changes taking place at the end of the Triassic and Early Jurassic clearly influenced the distribution of taxa overall. The presence of *Delsatia*, *Nujalikodon* and basal docodontans *Borealestes* and *Dobunnodon* in Europe and Greenland and representing the earliest docodontans, supports a Europe–Greenland origin for the group in the Late Triassic to Early Jurassic (Fig. 5).

CONCLUSION

Nujalikodon cassiopeiae is the first mammaliaform discovered in the Rhætelv Formation of the Kap Stewart Group in central East Greenland. Being Hettangian in age, it is

FIG. 4. Jurassic to Early Cretaceous palaeogeography, showing locations of docodontan fossils and NHMD1184958. Geochronological map adapted from the Paleobiology Database (https://paleobiodb.org/navigator/). Docodonta silhouette from PhyloPic (https://www.phylopic.org/; Elis Newham, *Haldanodon*, CC0 1.0).

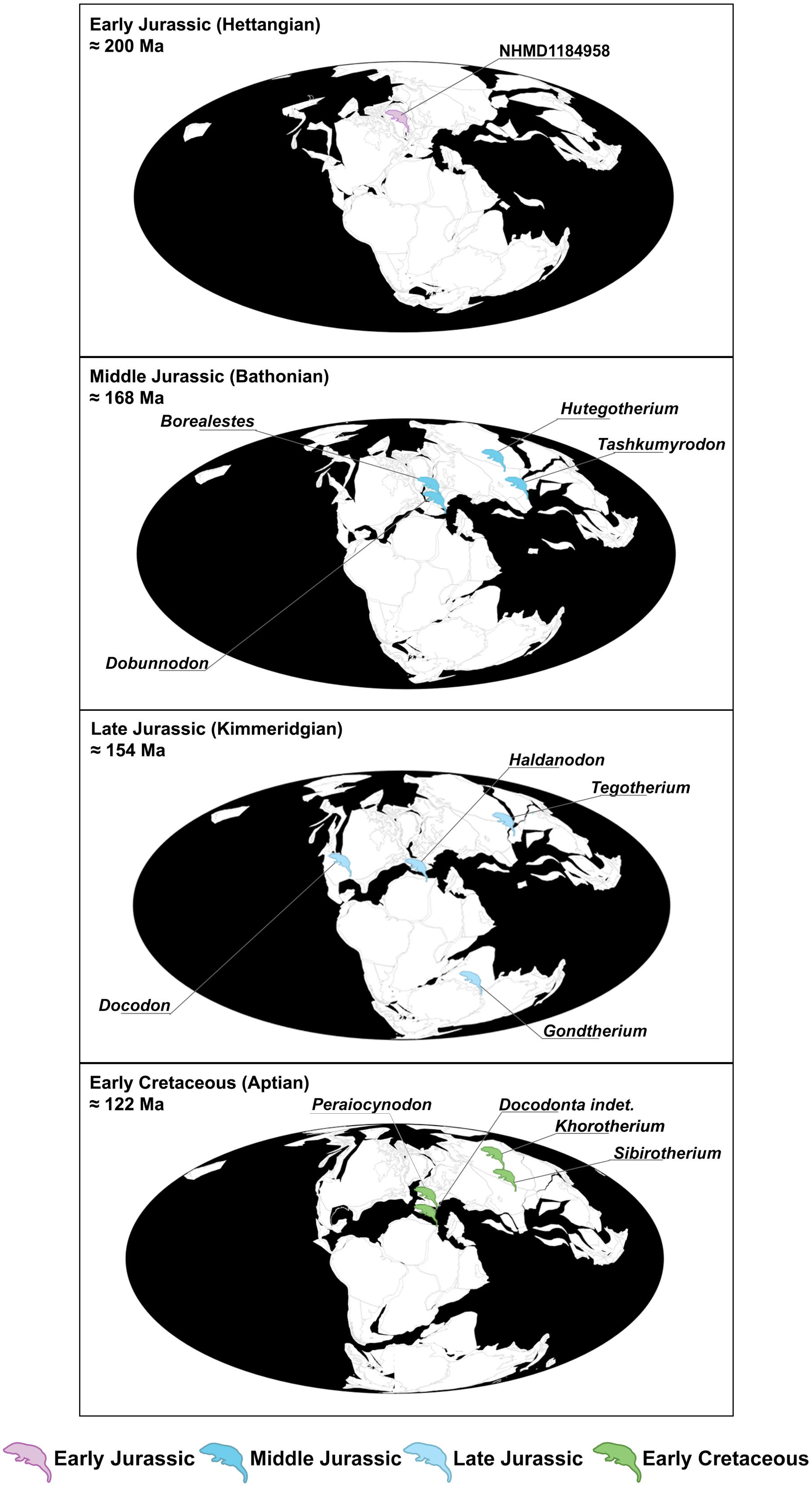
Early Jurassic (Hettangian)
≈ 200 Ma
NHMD1184958
Middle Jurassic (Bathonian)
≈ 168 Ma
Borealestes
Hutegotherium
Tashkumyrodon
Dobunnodon
Late Jurassic (Kimmeridgian)
≈ 154 Ma
Haldanodon
Tegotherium
Docodon
Gondtherium
Early Cretaceous (Aptian)
≈ 122 Ma
Peraiocynodon
Docodonta indet.
Khorotherium
Sibirotherium
Early Jurassic
Middle Jurassic
Late Jurassic
Early Cretaceous

FIG 5. A pair of *Nujalikodon cassiopeiae* enjoying a peaceful sunset in the Rhætelv Formation, Greenland. Credit: Pedro Andrade, used with permission (CC BY NC 4.0).

the oldest confirmed member of Docodonta. Its presence suggests at least an Early Jurassic origin for Docodonta, and probably represents the ancestral molar morphology of docodontans, perhaps derived from a 'triconodont' pattern. This provides insight into the evolution of their complex dentition, which contributed to their Middle Jurassic ecomorphological diversification.

The presence of *Nujalikodon cassiopeiae* in central East Greenland, coupled with other basal docodontan taxa from the Upper Triassic and Middle Jurassic of Europe, suggests that Docodonta originated in Europe–Greenland and later dispersed across the northern hemisphere. The specimen's location also reinforces previous suggestions of faunal links between East Greenland and Europe during the Late Triassic (e.g. Clemmensen *et al.* 2016), which continued into the Early Jurassic. The similarities between *Nujalikodon* and *Delsatia* from France, as well as Middle Jurassic docodontans from Great Britain, are consistent with the proximity of Greenland to these regions during the Late Triassic to Early Jurassic, facilitating dispersal.

We find support in our phylogenetic analysis for two main clades within Docodonta but not the previously proposed Euramerican and Eurasian docodontan clades; although biogeography clearly influenced the distribution of taxa in pivotal ways. We also find limited support for the sub-clades erected within Docodonta, suggesting that further work is needed to resolve relationships within the group.

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Author contributions. **Conceptualization** S Patrocínio (SP), E Panciroli (EP), VD Crespo (VDC); FM Rotatori (FMR); **Data Curation** SP, EP; **Formal Analysis** SP, FMR, EP, O Mateus; **Investigation** SP, EP; **Methodology** SP, FMR, EP; **Project Administration** SP; **Software** SP, EP, FMR; **Supervision** SP, EP, VDC; **Validation** SP; **Visualization** SP; **Writing – Original Draft Preparation** SP, EP, VDC, LB Clemmensen (LBC); **Writing – Review & Editing** SP, EP, VDC, FMR, LBC, J Milán.

DATA ARCHIVING STATEMENT

Data for this study are available in MorphoSource (https://doi.org/10.17602/M2/M702614; https://doi.org/10.17602/M2/M702877), Morphobank: (http://morphobank.org/permalink/?P5871) and the Dryad digital repository (https://doi.org/10.5061/dryad.w0vt4b92g). This published work and the nomenclatural acts it contains, have been registered in ZooBank: https://zoobank.org/References/1ed67841-5ea5-40da-b8b8-ce1b175d866f

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SUPPORTING INFORMATION

Additional Supporting Information can be found online (https://doi.org/10.1002/spp2.70022):

Appendix S1. Docodontan homology and terminology of lower molar structure.
Appendix S2. Digitalization and image treatment (includes Fig. S1).
Appendix S3. Data matrix used in this analysis.
Appendix S4. Systematic character list for docodontans and outgroups.
Appendix S5. Cross-referencing and re-interpretation of characters in taxa from the matrix of Zhou *et al.* (2019).
Appendix S6. Phylogenetic analysis (includes Figs S2–S4).
Appendix S7. R code for phylo tree.
Appendix S8. Matrix of first and last chronological appearances of mammaliaform taxa.
Appendix S9. Comparison between percentage (%) of characters scored by taxon.

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