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New mammaliaform from the Upper Triassic of Kap Stewart Group of East Greenland

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NEW MAMMALIAFORM FROM THE LATE TRIASSIC OF KAP STEWART GROUP OF EAST GREENLAND

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"You are not a paleontologist by chance..."

The Dinosaur Hunter

ABSTRACT

The earliest mammaliaforms (the group that includes Mammalia) emerged in the Late Triassic. Due to a lack of fossils from this time period, many questions remain regarding their origin and emergence. Greenland provides pivotal evidence for the earliest mammaliaforms, and the landmass's position between Europe and the Americas provides key biogeographical information. Within Greenland's fossil record, mammaliaforms have been found exclusively in the Fleming Fjord Formation. A new specimen, NHMD 1184958, is the first mammaliaform identified from the Kap Stewart Group, which spans the Late Triassic to Early Jurassic boundary. This specimen comprises an incomplete dentary with a single preserved molar (m2?), and was previously attributed to the order Docodonta. However, it was not fully prepared and studied until now. For this thesis, specimen NHMD 1184958, was manually prepared, and fully digitally visualized using micro CT scans, to reveal details of its anatomy. It was described, and comparisons made with known early mammaliaforms groups, to assess its taxonomic placement. This specimen somewhat resembles the French early mammaliaform *Delsatia*, suggested to be an early docodontan, as well as posessing features also seen in members of the clade Docodonta, especially the British docodont *Dobunnodon*. A phylogenetic analysis incorporating most known genera of docodontans was performed to determine the phylogenetic position of NHMD 1184958. Results place it as a basal member of Docodonta, or close sister taxon, closer than other proposed early docodontans such as *Delsatia, Gondtherium* or *Tikitherium*. This would make NHMD 1184958 one of the oldest known docodontans, pushing the origin of the group back to the Late Triassic. Its presence in Greenland supports the proposal that docodontans have their origins in the region that now includes Europe and Greenland, and later dispersed across the rest of Laurasia. This specimen provides important new anatomical characters that help us understand the emergence of docodontan dental complexity, a key feature for the clade that set the scene for their impressive diversification in the Middle to Late Jurassic.

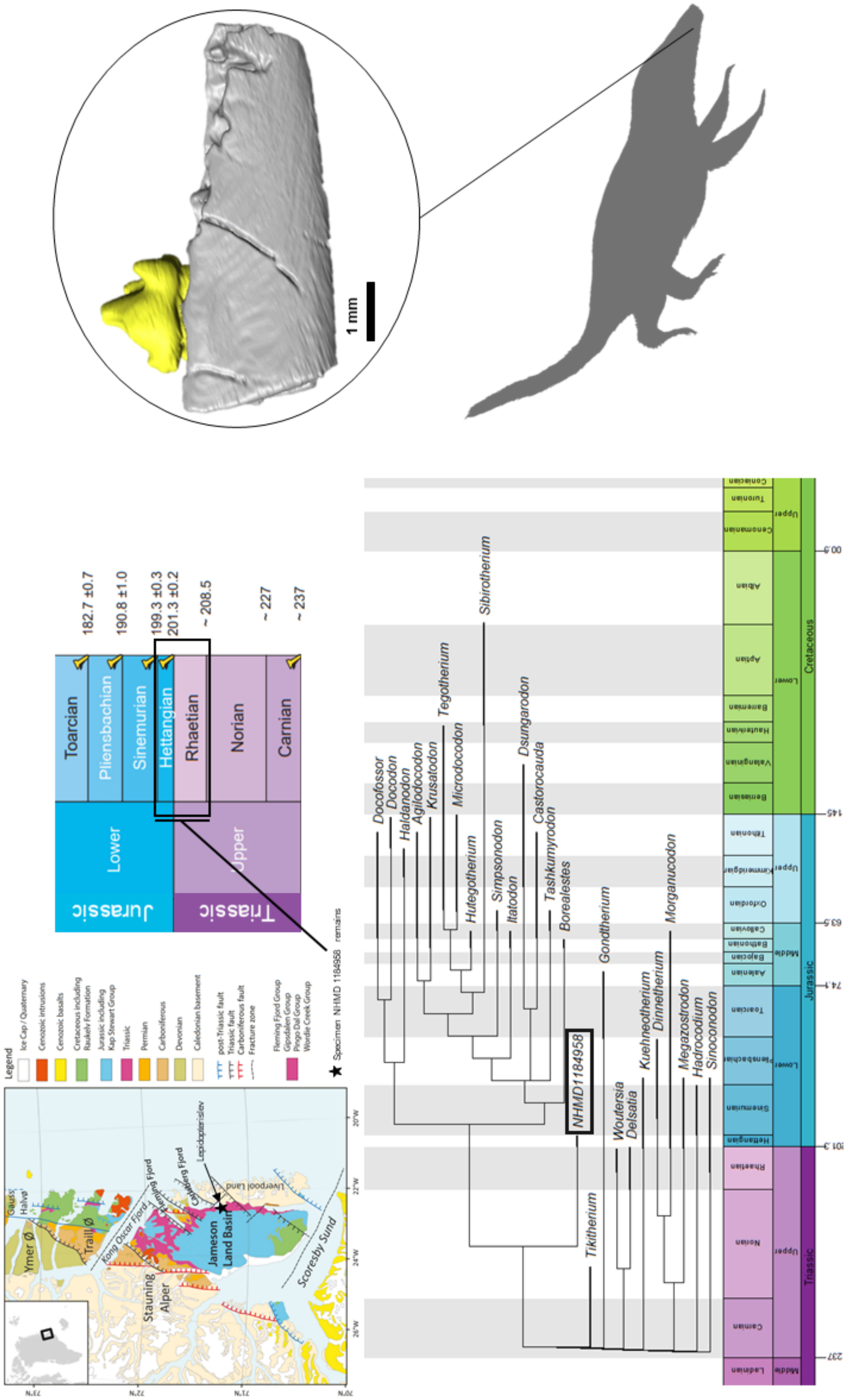
Keywords: Mammaliamorpha, Jameson Land Basin, Rhatelv Formation, Taxonomy, Image segmentation, Phylogeny.

RESUMO

Os primeiros mammaliaformes (o grupo que inclui Mammalia) surgiram no Triássico Superior. Devido à falta de fósseis deste período, muitas questões permanecem quanto à sua origem e aparecimento. A Gronelândia fornece provas fundamentais acerca dos primeiros mammaliaformes, e a posição da massa terrestre entre a Europa e as Américas fornece informações biogeográficas importantes. No registo fóssil da Groenlândia, os mammaliaformes foram encontrados exclusivamente na Formação Fleming Fjord. Um novo espécime, NHMD 1184958, é o primeiro mammaliaforme identificado no Grupo Kap Stewart, que abrange o limite do Triássico Superior ao Jurássico Inferior. Este exemplar compreende um dentário incompleto com um único molar preservado (m2?), e foi anteriormente atribuído à ordem Docodonta. No entanto, não foi totalmente preparado e estudado até agora. Para esta tese, o espécime NHMD 1184958, foi preparado manualmente e totalmente visualizado digitalmente com recurso a microtomografias, para revelar detalhes da sua anatomia. Foi descrito e foram feitas comparações com grupos conhecidos de mammaliaformes, para avaliar sua localização taxonómica. Este espécime assemelha-se um pouco ao mammaliaforme francês *Delsatia*, sugerido como sendo um dos primeiros docodontes, e para além disso possui características também vistas em membros do clado Docodonta, especialmente no docodonte britânico *Dobunnodon*. Uma análise filogenética incorporando a maioria dos géneros conhecidos de docodontes foi realizada para determinar a posição filogenética de NHMD 1184958. Os resultados colocam-no como um membro basal de Docodonta, ou táxon-irmão, mais próximo do que outros docodontes propostos, como *Delsatia*, *Gondtherium* ou *Tikitherium*. Isso faria do NHMD 1184958 um dos mais antigos docodontes conhecidos, recuando a origem do grupo ao Triássico Superior. A sua presença na Gronelândia apoia a proposta de que os docodontes têm a sua origem na região que hoje inclui a Europa e a Gronelândia, e posteriormente dispersaram pelo resto da Laurásia. Este espécime fornece novos caracteres anatómicos importantes que nos ajudam a compreender o surgimento da complexidade dentária dos docodontes, uma característica chave para o clado que preparou o cenário para a sua impressionante diversificação no Jurássico Médio ao Superior.

Palavras-chave: Mammaliamorpha, Jameson Land Basin, Formação Rhatelv, Taxonomia, Segmentação de imagens, Filogenia.

GRAPHICAL ABSTRACT



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INSTITUTIONAL ABBREVIATIONS

NHMD, Natural History Museum of Denmark, University of Copenhagen, Copenhagen, Denmark; ML, Lourinhã Museum, Lourinhã, Portugal

IRSNB, Institut royal des Sciences naturelles, Bruxelles, Belgique

SNP, locality of Saint-Nicolas-de-Port, France (collection MNHN)

Pal./CHQ-009, Paleontology division of Central Headquarters, Geological Survey of India, Calcutta

1. INTRODUCTION

1.1. Mammaliaformes and their molar diversity

Mammaliaformes is a clade within the broader clade Mammaliamorpha. They exhibit a global distribution in the fossil record, dating back to the Late Triassic period, approximately 220 million years ago (Jenkins *et al.* 1997; Kielan-Jaworowska *et al.* 2004). Mammaliaformes is a monophyletic group, originating from probainognathan cynodonts, and their sister group is disputed but is argued to be Tritylodontidae (Figure 1), Brasilodontidae, or Trithelodontidae (Kemp, 2005; Rougier *et al.* 2021). Mammaliaforms comprise the last common ancestor of *Morganucodon* (Morganucodonta), and all other mammals, including crown-mammals (Rowe, 1988). They are united principally by the presence of the dentary-squamosal joint (Martin, 2018). The first Mesozoic mammaliaforms were very small in size; the smallest currently known have only 1.2 cm skull length, and are estimated at 2 g of body mass (e.g. *Hadrocodium*; Novacek, 1997; Luo *et al.* 2001; Kemp, 2005), and most were not much larger than 4.25 cm skull length, not exceeding 800 g (e.g. *Castorocauda;* Ji *et al.* 2006).

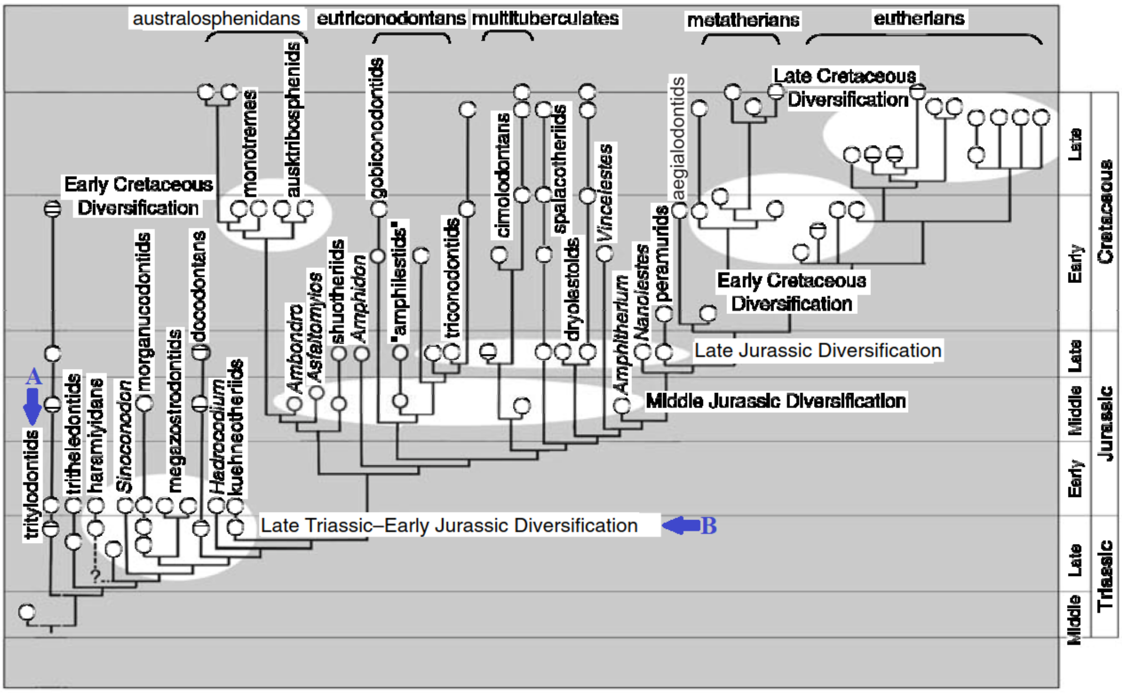

Figure 1. Temporal distribution and relationships between clades of Mesozoic mammaliaforms. A, represents one of the proposed sister groups to the Mammaliaformes, the family Tritylodontidae; B, represents the increase in diversification of mammaliaforms at the Triassic-Jurassic boundary (modified after Kielan-Jaworowska *et al.* 2005).

Mammaliaforms are also characterized by diphyodonty, in which milk or deciduous dentition is replaced by an adult or permanent generation of dentition (Weller, 1968; Nowotny *et al.* 2001). This single replacement allowed for more precise occlusion of the upper and lower tooth crown, and aided the development of complex occlusions and multirooted molar teeth (Crompton, 1972; Sulej *et al.* 2020). Mammaliaform teeth are also distinguished by the presence of prismatic enamel: continuous bundles of similarly oriented crystallites that extend from the dentin-enamel junction to the enamel surface, which help in the distribution of bite force (Carter, 1990; Line and Novaes, 2017).

Differences in dental crown morphology in different genera from the Late Triassic to the Early Jurassic indicate that their dietary diversification was an important factor in the early evolution of mammaliaforms (Figure 2; Luo *et al.* 2015; Padian, 2015). The molars of early mammaliaform groups such as morganucodontans, kuehneotheriids, haramiyidans, and docodontans differ in terms of morphology (Kielan-Jaworowska *et al.* 2004; Kemp, 2005; Martin, 2018). As their molars developed different structures and functions, this was linked to changes in their diet underpinning the evolutionary diversification of many clades (Kielan-Jaworowska *et al.* 2004; Jenkins *et al.* 1997; Martin, 2018). While the first haramiyidans in the Triassic had complex tooth crowns and were adapted to an omnivorous/herbivorous diet, their contemporaries, the morganucodontans and kuehneotheriids, had triconodont teeth with a triangular arrangement of cusps, and had a more insectivorous/carnivorous diet (Debuysschere *et al.* 2015; Morales-García *et al.* 2021). Despite being superficially similar-looking small insectivores, analyses of the teeth and jaws of these genera have revealed ecological specializations even at this early stage in evolution: for example, *Morganucodon* was more specialised at processing hard foods, while *Kuehneotherium* had dentition and a jaw shape more suitable for soft foods (Gill *et al.* 2014; Conith *et al.* 2016).

In the last twenty years, it has become clear that as well as small terrestrial insectivorous taxa, many Mesozoic mammaliaforms were ecologically diverse, with some capable of gliding, swimming, digging or climbing (Kielan-Jaworowska *et al.* 2004; Luo, 2007; Chen and Wilson, 2015; Martin, 2018). Many of the most ecologically diverse taxa belonged to the clade Docodonta. Docodonta was an early-diverging Mesozoic mammaliaform group with undisputed fossil taxa ranging from the Middle Jurassic to Early Cretaceous. Their most unique features were their relatively complex set of molars, characterised by molar teeth whose crowns had developed complex occluding surfaces (Kemp, 2005; Luo and Martin, 2007). The complexity of docodont molars is thought to be directly linked to their ecological complexity. It is therefore important to understand the emergence of the docodontans clade, and how the first mammaliaforms in the Triassic and Jurassic were related, since this information can give us new data about the emergence of ecological diversity in mammaliaforms as a whole.

1.1.1. Early taxa and their uncertain placement

Some Mesozoic mammaliaforms have uncertain taxonomy and phylogenetic placement. This section addresses some of the taxa and families that still generate doubts among specialists about their phylogenetic positioning. Knowing more precisely their evolutionary location helps us understand how mammal ecological and taxonomic variety originated, as well as the larger trend of their evolution.

The ‘Symmetrodonta’ are one of the groups whose composition and position are uncertain. Researchers in recent years have concluded that this group does not represent a true taxonomic group as was originally proposed, but is paraphyletic, including several unrelated branches in the phylogenetic tree of mammaliaforms (Luo *et al.* 2002; Kielan-Jaworowska *et al.* 2004; Martin *et al.* 2020). Despite this, this name is still used by some researchers to refer to some taxa, such as spalacotheriids (e.g. Martin *et al.* 2020) and zhangheotheriids (e.g. Meng, 2014; Averianov *et al.* 2013). Only isolated teeth, incomplete jaws, and rare fragments of postcranial material from the Upper Jurassic and Early Cretaceous have been assigned to ‘Symmetrodonta’ (Kemp, 2005). Morphologically, their molars are symmetrical with a simple occlusal pattern of cusps arranged in a reversed triangle, with the absence of a well-developed talonid (Figure 2B; Kielan-Jaworowska *et al.* 2004; Martin *et al.* 2020). They present an angulation of the main molar cusps (A/a, B/b, C/c) and a very small D/d cusp. The upper and lower molars of symmetrodontan mammaliaforms are arranged in alternating inverted triangles: cusps A/a are positioned lingually on the upper part and labially on the lower part. Occlusion occurs by embrasure occlusion, in which one upper molar occludes between two lowers (Figure 2B; Martin et al. 2020).

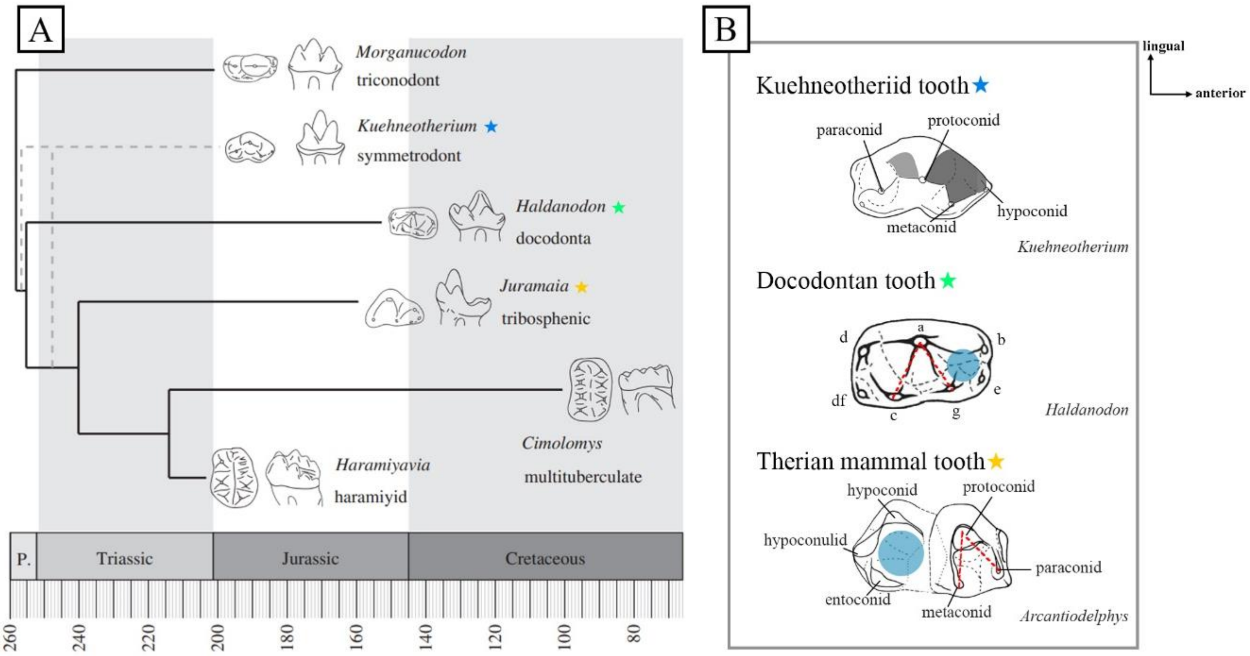

Figure 2. Diagram showing the diversity and morphological lower molar differences of Mesozoic mammaliaforms. A, Mesozoic diversification of the major mammaliaform families and associated lower molar morphologies; B, Systematic character variation of lower molars in three main groups of mammaliaforms (Kuehneotheriidae (symmetrodont), Docodonta and Theria). The blue circle symbolizes the pseudotalonid/talonid basin, while the red dashed line indicates the degree of triangulation between the main cusps. (Phylogenetic tree adapted from Conith *et al.* 2016, Kuehneotheriid tooth adapted from Williamson *et al.* 2014, Docodontan tooth adapted from Luo and Martin, 2007, Therian mammal tooth adapted from Vullo *et al.* 2009).

Mammaliaforms with symmetrodont molars include some of the oldest known representatives of the clade. Initially, the concept of ‘Symmetrodonta’ included members from the Late Jurassic to Lower Cretaceous, corresponding to distant relatives of ‘eupantotherians’, although there were doubts regarding their morphology (Simpson 1925, 1928, 1929). Later, researchers added more primitive taxa from older geological ages (e.g., Kermack *et al.* 1968; Sigogneau-Russell and Hahn, 1995), therefore expanding this group’s range from the Late Triassic to the Late Cretaceous.

Symmetrodontan teeth are distinguished by the obtuse-angular molars of kuehneotheriids and tinodontids (>80-90º, Li and Luo, 2006; Averianov *et al.* 2013) and the acute-angular molars of spalacotheriids (Martin *et al.* 2020). The ’symmetrodont’ pattern probably evolved repeatedly among mammaliaforms (Kielan-Jaworowska *et al.* 2004; e.g. Pascual *et al.* 2002), possibly representing a transitional state between the molar structure of in-line cusps of the ‘triconodonts’, and the more complex molars of the tribosphenic mammals and their precursors among the ‘eupanthotheres’ (Crompton and Jenkins, 1967; Martin *et al.* 2020).

Among the earliest taxa with a symmetrodont tooth arrangement are *Woutersia* and *Delsatia*, both Late Triassic in age, and the family Kuehneotheriidae, which is Late Triassic–Early Jurassic in age (Martin *et al.* 2020). The taxonomic placement for these taxa and families is currently uncertain. Woutersiidae is represented by the single genus *Woutersia*, known only by isolated upper and lower molariforms from two localities in France (Sigogneau-Russell and Hahn, 1995). Specimens assigned to this genus show variability in size, general proportions and the degree of development of the talonid (Sigogneau-Russell, 1983; Sigogneau-Russell and Hahn, 1995). This variability can be explained by variations in morphological characteristics along the tooth row (Averianov and Lopatin, 2006).

Sigogneau-Russell (1983) first classified *Woutersia* as a member of the Kuehneotheriidae family. Later, Sigogneau-Russell and Hahn (1995) attributed this genus to a monotypic family. Both publications claim that *Woutersia* shares many characteristics with the Docodonta order, implying that the docodontans descended from Woutersiidae (or a Woutersiid-like ancestor) in some way. In Sigogneau-Russell and Godefroit (1997), *Woutersia* has been classified as a "Symmetrodont". According to Butler (1997), *Woutersia* should be considered a docodontan.

Delsatia is represented by three isolated molars and two possible premolar teeth, from the Late Triassic of France (Sigogneau-Russel and Godefroit, 1997). Despite being initially placed within the clade Docodonta by Sigogneau-Russel and Godefroit (1997), more recent studies do not support this hypothesis (e.g. Luo and Martin, 2007), placing it as a putative relative of Docodonta (Figure 3).

Kuehneotheriidae (named for *Kuehneotherium*) have a wider geographic distribution, being found in localities such as continental Europe, Britain, Greenland, and possibly India (*Kotatherium*, see Prasad and Manhas, 1997) (Debuysschere, 2017; Martin, 2018). The first remains assigned to *Kuehneotherium* were discovered in Wales, being represented mostly by isolated teeth and a few fragments of jaws (Kermack *et al.* 1968). The discovery of this key material resulted in understanding the evolution of the earliest mammaliaforms. Teeth from this genus were also discovered in the Norian of England (proposed to be Rhaetian according to Whiteside and Marshall, 2008) (Fraser *et al.* 1985). A total of 10 teeth from the late Norian to early Rhaetian age of Greenland were assigned to *Kuehneotherium* sp. (Jenkins *et al.* 1994).

The phylogenetic position of *Kuehneotherium* has been widely discussed and is still uncertain (Kermack *et al.* 1968; Kielan-Jaworowska *et al.* 2004). Crompton and Jenkins (1967) attributed this genus to “symmetrodonts”. Although Kermack *et al.* (1968) opted to place *Kuehneotherium* in Amphitheria, in the ‘pantotheres’. The discovery of other basal mammals that predate *Kuehneotherium* on the geological time scale led to the relocation of this genus in the clade Holotheria (Luo *et al.* 2002). The clade Holotheria includes animals with the main and accessory molar cusps arranged in a triangle configuration. The placement of *Kuehneotherium* in Holotheria is regarded as unstable since determining the features of a species based on the limited fossil evidence available is challenging (Luo *et al.* 2002).

Tikitherium is a close relative to Docodonta. This extinct genus of mammaliaform was found in the Carnian (Late Triassic) of India. *Tikitherium copei* Datta, 2005, is represented by only an upper left molar (Datta 2005), which showed several derived features that are similar to other early mammaliaform dentitions: including a complex crown morphology, prominent cingula, and three roots. This tooth stands out on its own as it represents the geologically oldest mammaliaform representative that has such complex dental specialization (Datta, 2005).

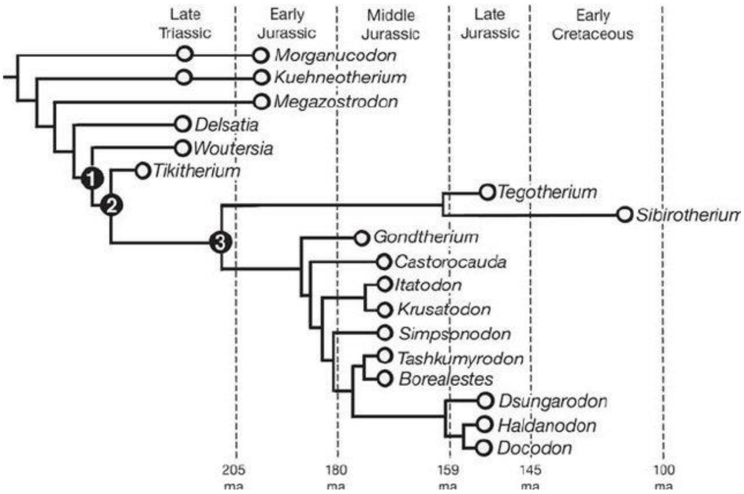

Figure 3. Previously proposed phylogenetic relationships and stratigraphic distributions of docodont genera and their putative relatives. Node 1- clade (Docodonta + *Tikitherium*) + *Woutersia*; Node 2- Clade Docodonta + *Tikitherium*; Node 3- Docodonta (from Luo and Martin, 2007).

In 1997, Sigogneau-Russell and Godefroit identified *Delsatia rhupotopi* Sigogneau-Russell and Godefroit, 1997 as a member of the Docodonta. Although this species shares morphological similarities with *Woutersia* (it was discovered in the same location in Saint-Nicolas-Port, France), its key distinguishing feature is a cute angulation of molar cusps. Butler (1997) proposed that *Delsatia* should be classified as a "Symmetrodont," agreeing with Sigogneau-Russell and Godefroit (1997) that the docodontans must have evolved from ancestral mammaliaforms with a triangulated cusp structure.

Given the strong similarities and co-occurrence of the genera *Delsatia* and *Woutersia*, Kielan-Jaworowska *et al.* (2004) hypothesized that, based on their similar lower molar structure, the discovered molars found to date belong to the same taxon and that the discrepancies discovered correlate primarily to changes in the position of the molars.

1.1.2. Origin and Diversification of Docodonta

One of the most important clades of early mammaliaforms is Docodonta, which exhibits remarkable ecomorphological diversity for such an early-diverging branch of mammaliaforms. Docodonta is a monophyletic order that prevailed from the Middle Jurassic to the Early Cretaceous, diversifying in the Early to Middle Jurassic (Kielan-Jaworowska *et al.* 2004; Luo and Martin, 2007). This order is present in the fossil record of Laurasia, that is, present-day North America, Europe and Asia (Sigogneau-Russell, 2003; Martin and Averianov, 2004; Ji *et al.* 2006; Luo *et al.* 2015a; Meng *et al.* 2015). The majority of docodontans are represented primarily by isolated fossil jaws and teeth (see Kielan-Jaworowska *et al.* 2004; and references therein; e.g. Maschenko *et al.* 2002; Sigogneau-Russell, 2003; Martin and Averianov, 2004; Pfretzschner *et al.* 2005; Averianov *et al.* 2010; Schultz *et al.* 2017; Lopatin *et al.* 2020; Martin *et al.* 2020), but more recent discoveries, particularly from China and Scotland, comprise almost complete preserved skeletons, often in articulation (e.g. Luo *et al.* 2015; Meng *et al.* 2015; Panciroli *et al.* 2021). The body mass of members of this order is variable, ranging from some small taxa the size of a mole, such as *Docofossor* (approximately 13–17g; Meng *et al.* 2015), to *Castorocauda,* a much larger mammal the size of a platypus (approximately 500-800g; Figure 4; Ji *et al.* 2006; Luo and Martin, 2007; Luo *et al.* 2015b).

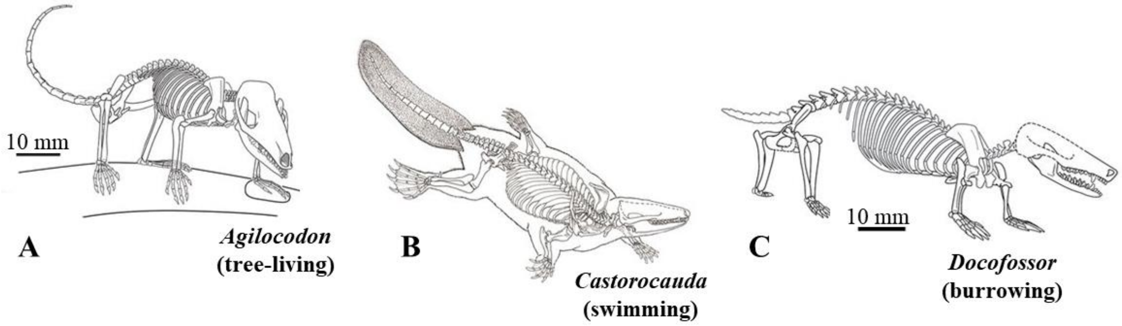

Figure 4. Docodont ecological and morphological variation. A, *Agilodocodon* as an arboreal mammaliaform. B, *Castorocauda* as a semi-aquatic mammaliaform. C, *Docofossor* as a fossorial and subterranean docodont (Modified from Meng et al. 2015).

The name "Docodonta" meaning "beam tooth", refers to the molar complexity of this order, when compared to other early mammaliaforms (Luo and Martin, 2007). One of the distinct characteristics of docodontans in relation to their contemporaries is the highly complex cusp and crest pattern of their teeth (Luo and Martin, 2007). This pattern is called "pseudotribosphenic" because it is similar to the tribosphenic molar morphology that emerged later in Mammalia. Docodontans are the most early-diverging mammaliform lineage with occlusion between a crushing basin (named the pseudotalonid) on the lower molars, and a locking cone (the cusp Y) on the upper molars (Figure 6; Butler, 1997; Luo and Martin, 2007; Schultz *et al.* 2017).

One of the most startling things about the docodontans is their range of ecological specialisations. This included arboreal taxa (*Agilodocodon* [Meng *et al.* 2015]), semi-aquatic (*Castorocauda* [Ji *et al.* 2006] and possibly *Haldanodon* [Martin, 2005]) and fossorial (*Docofossor*; Luo *et al.* 2015b) lifestyles (Figure 4). It has been suggested that the docodontans' complex dentition is linked to their ecological specializations (Meng *et al.* 2015; Martin *et al.* 2020; e.g. Luo and Martin, 2007). Members of Docodonta exhibit molar tooth morphologies that facilitate crushing, shearing, and grinding (e.g., Sigogneau-Russell, 2003; Pfretzschner *et al.* 2005; Luo and Martin, 2007), including possible omnivorous-faunivorous diets (Kielan-Jaworowska *et al.* 2005), specializations for piscivory (Ji *et al.* 2006), and even vermivory (Luo *et al.* 2015). All of these ecomorphological differences show that this order was highly diverse, especially compared to other Jurassic mammaliaforms (Figure 7; Ji *et al.* 2006; Luo, 2007; Luo and Martin, 2007; Meng *et al.* 2015; Luo *et al.* 2015b). The ecological diversity present in this clade is similar to that of extant therian mammals of similar body masses (Luo and Martin, 2007; Luo, 2007; Meng *et al.* 2015).

Docodontan skulls bear many similarities to other groups of early mammaliaforms, such as morganucodontans, in having a long, low profile and long snout (Figure 4). They retain many plesiomorphic characteristics such as: small, separate nares with the posterior border of the nares formed by a large septomaxilla; nasal bones that extend posteriorly above thick lacrimals; frontal and parietal bones that are flat and wide; and no postorbital process forming the posterior edge of the eye socket (Lillegraven and Krusat, 1991). Docodontans are characterized by an elongate jaw, or dentary, which articulates with the skull via the dentary-squamosal joint, as seen in all mammaliaforms. They retain post-dentary bones, still connected to the dentary, which lies within a postdental trough positioned medially at the posterior of the dentary. In addition to the postdental bones, the Meckel's cartilage is also present, extending anteriorly along the medial side of the dentary within the Meckel's groove, or sulcus (Figure 5A; Luo, 2011). In early mammaliaforms such as docodontans, the middle ear is connected anteriorly to the medial surface of the dentary by a long ossified Meckel's Cartilage, sitting within the Meckel's groove (Figure 5A; Luo and Manley, 2020). Through ontogeny there is a change in Meckel's sulcus in docodontans: in juveniles the groove extends to the mandibular symphyseal region, and it retreats posteriorly as the animal matures and reaches adulthood (Figure 4 in Schultz *et al.* 2019; Panciroli *et al.* 2019).

The lower tooth row of adult docodontans presents variability depending on the taxon, consisting of between 2-4 incisors, a single double-rooted canine, 4-5 premolars, and up to 7 molars (Luo and Martin, 2007; Martin, 2018; e.g. Schultz *et al.* 2017; Panciroli *et al.* 2019). Although the docodontan dentary is not very morphologically varied, the complexity of their molars provides a great deal of information for systematic analysis (Luo and Martin, 2007).

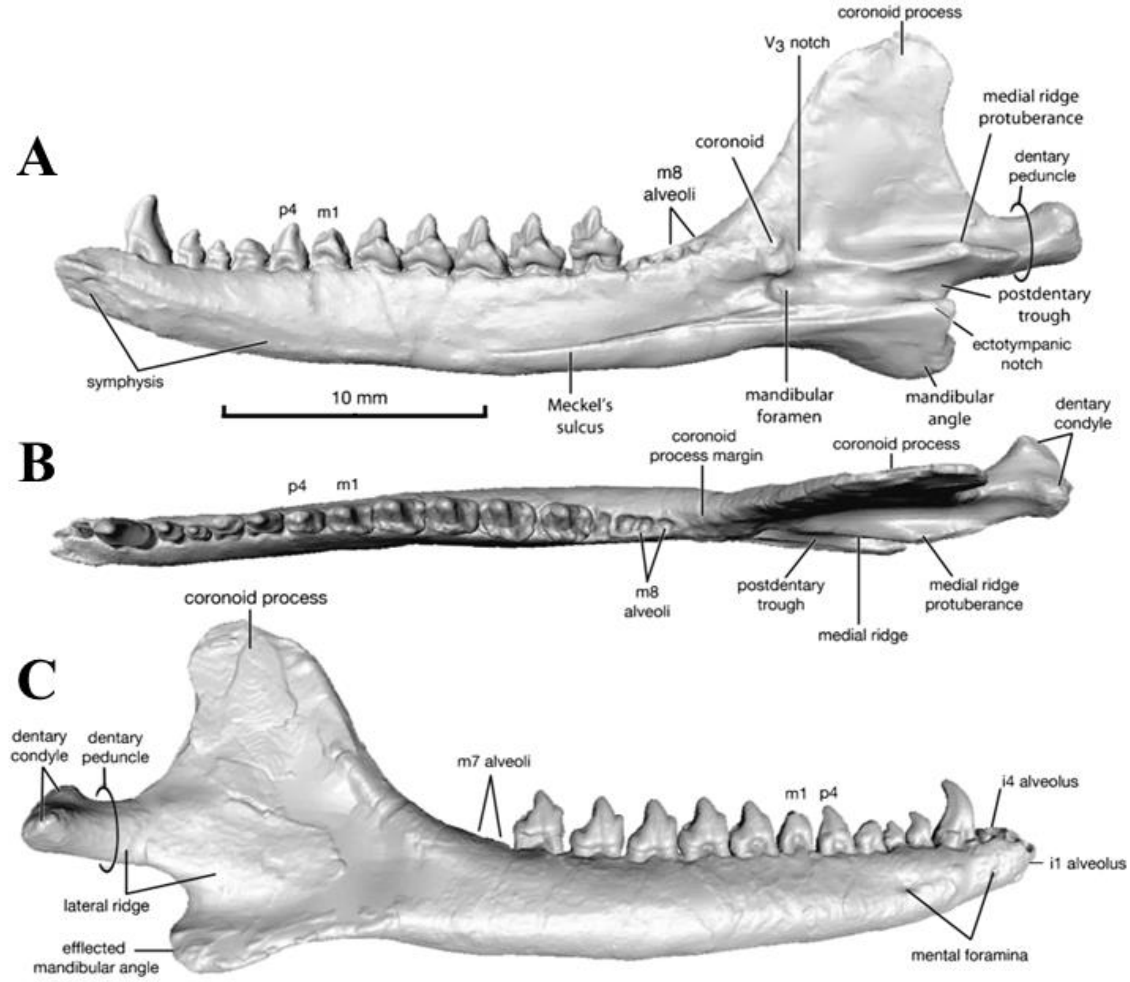

Figure 5. Mandibular structure of *Docodon.* A, lingual view. B, occlusal view; C, labial view (Modified from Schultz *et al.* 2019).

Over the years, debates have arisen regarding the nomenclature and homology pertaining to docodontan molar structures, particularly the attribution of cusps (e.g.: Butler, 1997; Jenkins, 1969; Krusat, 1980; Sigogneau-Russell, 2003). For several years, researchers followed the nomenclature established by Butler (1997), making their own modifications (e.g.: Maschenko *et al.* 2002; Pfretzschner *et al.* 2005; Ji *et al.* 2006; Hu *et al.* 2007; Lopatin *et al.* 2007, 2009; Luo and Martin, 2007; Averianov *et al.* 2010; Martin and Averianov, 2010; Martin *et al.* 2010; Luo *et al.* 2015; Meng *et al.* 2015; Rougier *et al.* 2015). A purely descriptive cusp nomenclature was proposed by Kermack *et al.* (1987) and utilized and expanded by others (Sigogneau-Russell, 2001 and Sigogneau-Russell, 2003). Luo and Martin (2007) then modified Butler's nomenclature, and this is now widely used today (e.g. Schultz *et al.* 2017), with some modifications (e.g. Panciroli *et al.* 2019). There is also a modified nomenclature established by Averianov *et al.* (2010), which employs slightly different terms for cusp df ('dd') and includes cusp b. See Table 1 for an overview of terminology.

Table 1. Docodontan homology and terminology of lower molar structure

Homology and terminology of lower molar structure			
Butler (1997); Pfretzchner *et al.* (2005)	Sigogneau-Russell (2003); Kielan-Jaworowska et al (2004)	Luo and Martin (2007)	Molar Structure and terminology used in this thesis* (defined in figure 6)
cusp a	main cusp	cusp a	cusp a
cusp b	mesiolabial cusp	cusp b	cusp b
cusp c	distolingual cusp	cusp c	cusp c
cusp d	distolabial talonid cusp	cusp d	cusp d
cusp e	Cuspule	cusp e / mesiolingual cingulid cuspule	cusp e
cusp df	lingual talonid cusp	docodont cusp f / distolingual cingulid cuspule	cusp df
cusp g	mesiolingual cusp	cusp g	cusp g
		a-b crest / anterior crest	a-b crest
		a-c crest / postero-oblique crest	a-c crest
	posteromain crest		a-d crest
	anteromain crest	a-g crest / antero-oblique crest	a-g crest
	anterobasal crest		b-g crest
	Crescent		b-e crest
		c-d crest / Transtalonid crest	c-d crest
	posterior crest		c-f crest
	Cingulum	d-f crest / Posterior-cingulid crest	d-f crest

*The molar structures were labeled according to Panciroli *et al.* (2019) terminology, where cusps were designated using letters and abbreviated crests were identified based on their connections to the cusps. In addition, topographical descriptors are included in the nomenclature to indicate their specific position on the tooth. This nomenclature system combines alphabetic terms introduced by Butler (1997) and the simplified descriptive definitions used by Panciroli *et al.* (2019).

In occlusal view, the upper molars of docodontans are subtriangular or figure-eight in shape. Upper molars have up to four main cusps: A, C, X and Y (Figure 6A). The lower molars are mesioposteriorly longer than they are linguolabially wide. They have up to seven cusps approximately arranged in two rows - lingual and labial. The labial row includes the largest cusp, cusp a, which lies between cusps b (slightly smaller than cusp a and more anterior in position) and cusp d (smaller than cusp a, and positioned posteriorly). The lingual row is usually offset from the labial and has up to two larger cusps; cusp g (anterior position) and cusp c (posterior position), and some additional cusps. Additional cusps can include cusp e (anterior to cusp g and lingual to cusp b), and cusp df (also called "docodont cusp f" or cusp dd, posterior to cusp c and lingual to cusp d) (Figure 6B; Luo and Martin, 2007). The cusps are often connected by crests, including four crests between cusp a and the other main cusps (crests a-b, a-g, a-c and a-d). In most docodontan genera, there are also crests connecting cusp b to other cusps: b-g crest, and b-e crest (Figure 6B; Luo and Martin, 2007). The pattern and presence of crests and cusps differ between docodontan genera, and is one of the principal ways in which genera and species are diagnosed (Figure 7).

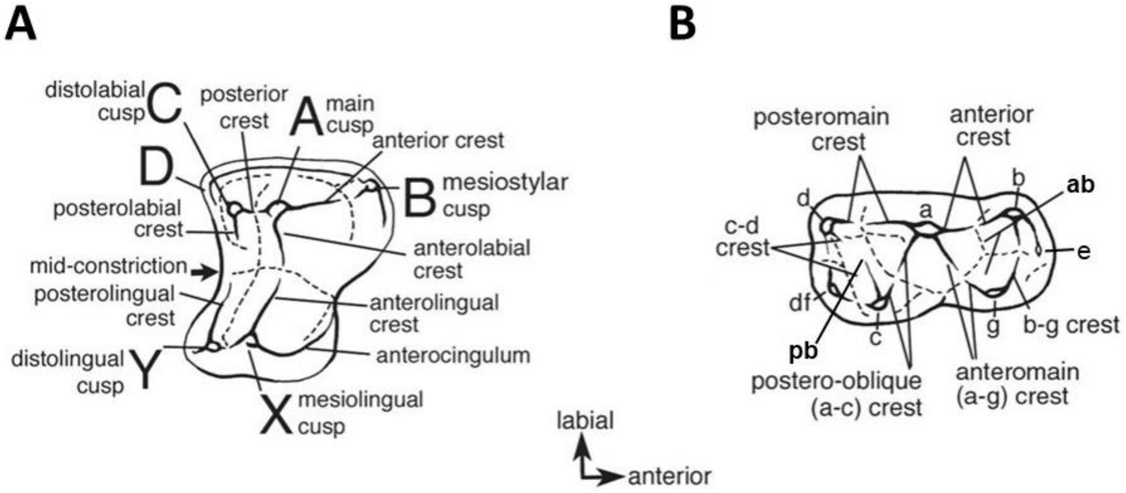

Figure 6. Diagram showing the terminology of docodont molar structures. A. Upper molar of *Docodon*; B. Lower molar of *Borealestes* (modified from Luo and Martin 2007). Single letters represent cusps. The anterior basin (ab) and posterior basin (pb) are represented in bold according the definition of Hu *et al.* (2007).

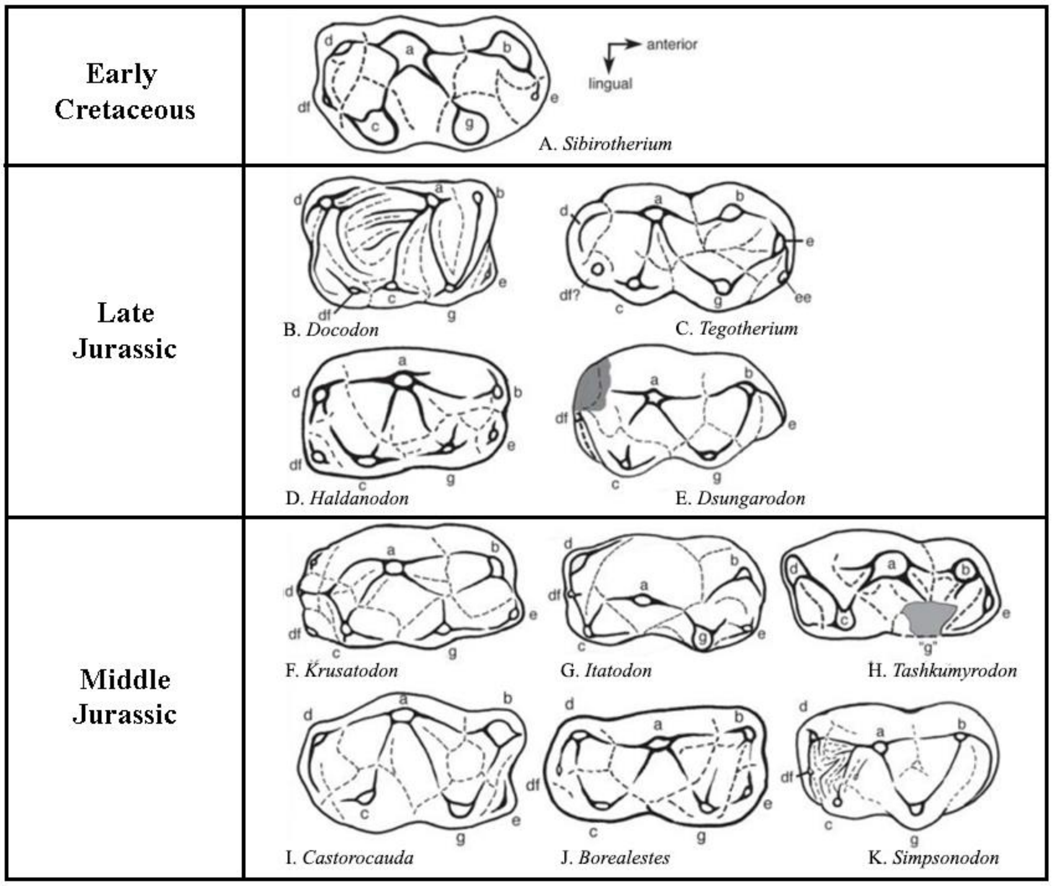

Figure 7. Morphological variation of lower molar cusps among some members of the order Docodonta. Taken from Luo and Martin (2007); article references with original versions of specimen drawings: Luo and Martin (2007).

Within the mammaliaformes, the order Docodonta is one of the most early-diverging (Figure 1; Rowe, 1988; Luo, 2007; Rougier *et al.* 2014). Docodonta evolved before the origin of crown mammals (Mammalia), and are more closely related to crown mammals than other mammaliaforms such as *Morganucodon* and *Sinoconodon* (Wible and Hopson, 1993; Luo *et al.* 2002; Martin, 2005, 2008). Although their overall position within Mammaliaformes has remained relatively stable in large-scale phylogenetic analyses (e.g. Luo and Martin, 2007; Panciroli *et al.* 2021), there is still uncertainty regarding the following:

1) What are the affinities of putative early docodontans, such as *Woutersia*, *Delsatia*, and *Tikitherium*?
2) What are the phylogenetic relationships within Docodonta, particularly of proposed sub-groups?

The answers to both of these questions have profound implications for understanding the macroevolutionary patterns of mammals and the crucial role of ecomorphological diversification among mammaliaforms during the early Mesozoic. Part of the challenge is a lack of fossil material for the earliest docodontans and the scarcity of postcranial material.

1) What are the affinities of putative early docodontans, such as *Woutersia*, *Delsatia*, and *Tikitherium*?

Researchers propose that Docodonta has its origins among the mammaliaforms from the Late Triassic and Early Jurassic. The oldest taxa proposed to belong to this order are three genera of late Triassic "symmetrodont-like" mammaliaformes *Delsatia* (from France), *Woutersia* (from Europe) and *Tikitherium* (from India) (Figures 1 and 8; Butler, 1997; Datta, 2005; Luo, 2007; Luo and Martin, 2007; Abdala *et al.* 2018).

According to Butler (1997) and Martin and Averianov (2004) the European mammaliaform *Woutersia* is closely related to docodontans. Woutersiidae is represented solely by the anterior genus which lived during the Late Triassic period. It exhibits distinct docodontan features, including a main cusp a, lingually placed cusp c, cusp b positioned labially, and well-developed cusps e, g, and d. It has three main crests, a-c, a-b, and b-e (Figure 8; Sigogneau-Russel, 1983; Sigogneau-Russel and Hahn, 1995).

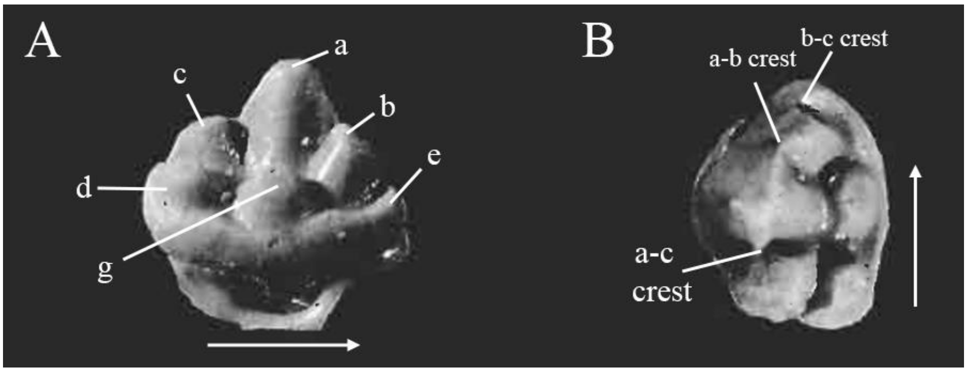

Figure 8. Diagnostic dental features of holotype *Woutersia butleri* (lower right molar SNP 517), from the quarry of Saint Nicolas de Port, France, ?early Rhaetian. A, lingual view; B, occlusal view. Dark arrows point to the anterior (modified from Sigogneau-Russell and Hahn, 1995).

According to Sigogneau-Russell and Godefroit (1997), *Delsatia* should be included within the Docodonta order, being considered the earliest known genus of the order. This genus shares morphological similarities with *Woutersia*, its key distinguishing feature being an acute angulation of molar cusps. *Delsatia* presents similar features compared to the morphology of docodontans, among them are: lateral pinching of cusp a, the presence of an angulated crest between cusp a and the postero-lingual cusp (cusp c), and another crest between the latter and d (Figure 9; Sigogneau-Russell and Godefroit, 1997).

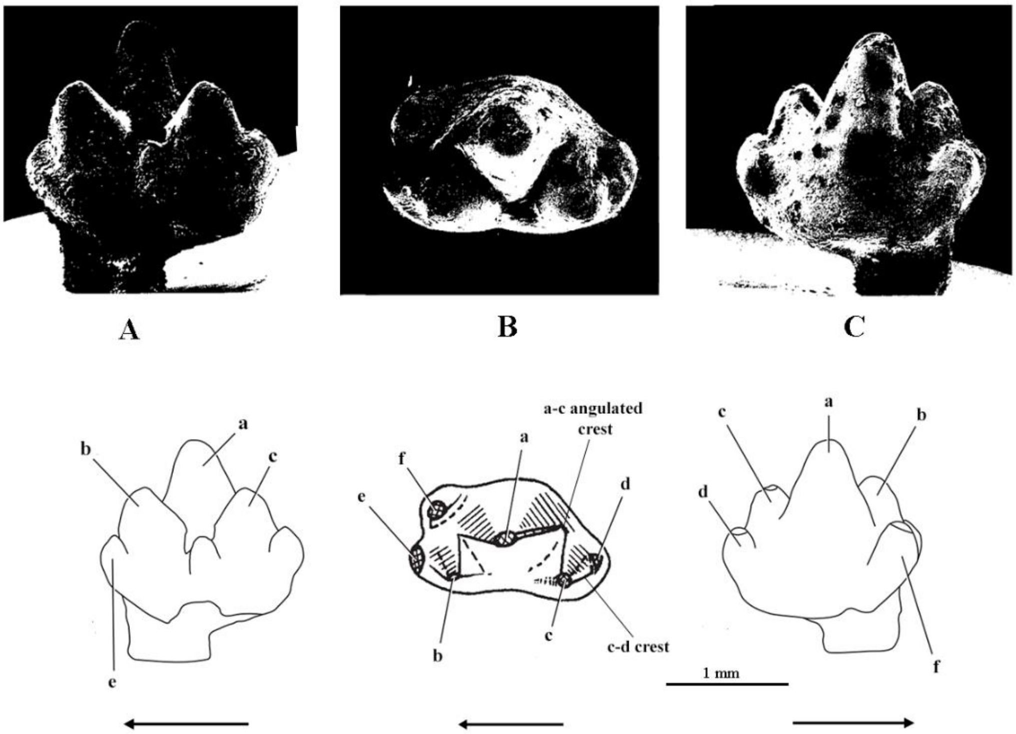

Figure 9. Holotype *Delsatia rhupotopi* (lower right molar IRSNB M1831) and diagnostic dental features. A, lingual view; B, occlusal view; C, labial view. The dark arrows point to anterior (modified from Sigogneau-Russell and Godefroit, 1997 and Kielan-Jaworowska *et al.* 2004).

The genus *Tikitherium*, known only from an upper left molar, displays several docodont-like features, placing it as a putative relative of this order (Luo and Martin, 2007). These features include the few wear facets on the lingual side of the molar, the anteroposterior elongation on the lingual part of the crown, the development of some of the wear surfaces, and the overall shape (Figure 10; Datta, 2005).

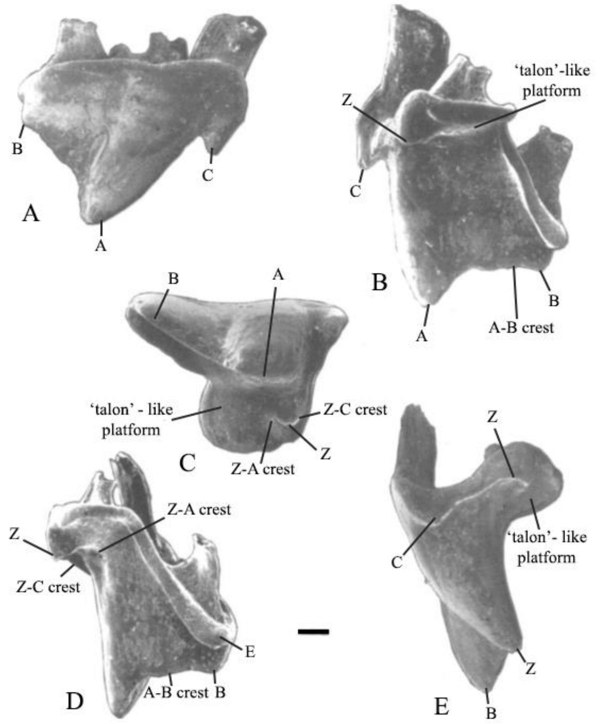

Figure 10. *Tikitherium copei*, upper left molar Pal/CHQ-009. A, labial view; B, lingual view; C, occlusal view; D, anterolingual view; E, posterolingual view (modified from Datta, 2005).

The oldest undisputed docodontans include *Borealestes* and *Krusatodon* from Scotland (Waldman and Savage, 1972; Panciroli *et al.* 2020), and *Hutegotherium* and *Itatodon* from Russia (Averianov *et al.* 2005), all from the Bathonian, Middle Jurassic. This leaves a gap of approximately 40 myr between the proposed earliest docodontans (*Woutersia*, *Delsatia* and *Tikitherium*), and their undisputed earliest members, during which the early evolution of the clade Docodonta presumably took place. Martin and Averianov (2004) proposed a theoretical model for the progression of docodont lower molar development from the 'triconodont' *Woutersia*, which included a hypothetical ancestral intermediate stage exhibiting four additional crests (d-f, c-d, a-g, and g-b) and an additional cusp f (Figure 11). These features would therefore have been present in subsequent docodont lineages, with some species later modifying or losing their crests (Martin and Averianov, 2004). Despite this, Martin and Averianov did not consider *Woutersia* to be part of the Docodonta due to the absence of an a-g crest, which they considered a synapomorphy for the group.

2) What are the phylogenetic relationships within Docodonta?

It has been proposed that Docodonta be split into the subgroups, Euramerican, and Asian docodontans (Martin and Averianov, 2001, 2004). Euramerican docodontans were proposed to have a small or absent cusp e, and a reduced b-e crest (Martin and Averianov 2004). This group initially included *Borealestes*, *Haldanodon* and *Docodon*, and they were thought to most closely represent the ancestral stage hypothesized by Martin and Averianov (2004; Figure 11). They proposed *Simpsonodon* to be a side branch of the Euramerican docodontans, possibly sharing a common ancestor with *Borealestes* (Martin and Averianov 2004: p200). The Euramerican docodontans have subsequently been assigned to the family Docodontidae, in which all docodontans were previously placed (Kielan-Jaworowska *et al.* 2004).

Asian docodontans were suggested to possess distinct morphological features in comparison to the Euramerican ones. These features include the retention of cusp e, the absence of the b-e and e-g crests, and the reduction of the b-g crest (Figure 11). These features are seen in *Tegotherium* and *Sibirotherium,* although another Asian docodontan, *Tashkumyrodon,* has a b-g crest on cusp b. All three of these taxa have an incomplete but well-developed crest a-d that is longitudinally oriented, similar to the a-b crest. Another distinctive feature proposed for Asian docodontans is that the cusps a and b are more distanced from one another than in Euramerican docodontans (excluding *Simpsonodon*). Martin and Averianov (2004) suggested *Sibirotherium* represents an intermediate position between *Tashkumyrodon* and *Tegotherium*, similar to the position of the Euroamerican genus *Simpsonodon* within that clade. They supported the erection of the family Tegotheriidae (Tatarinov, 1994) for *Tegotherium, Sibirotherium* and *Tashkumyrodon,* diagnosed by an enlarged pseudotalonid, large cusp g, well-developed cusp e and crests b-e, e-g, and f-c, and absence of crests b-g and c-d (Figure 11; Maschenko *et al.* 2002; Martin and Averianov, 2004).

Authors' perspectives differ on the exact phylogenetic position of docodontans, as well as their relationships. Averianov together with other authors (e.g. Martin and Averianov, 2004; Averianov and Lopatin, 2006; Averianov *et al.* 2010), who focus on Russian material, tend to place docodontans in several families, such as the Tegotheriidae, Simpsonodontidae, and Docodontidae. Their phylogenetic matrices are based on tooth and dentary characteristics scored principally for docodontans and their closest outgroups. Zhou and Meng and co-authors (e.g Meng *et al.* 2015; Zhou *et al.* 2019), on the other hand, rarely assign their Chinese docodontans to a family, and their material is often analyzed within a phylogenetic matrix that includes postcranial characters for a wide range of mammaliaforms, including the small number of docodontan taxa for which postcrania are known. Finally, Panciroli *et al.* (2019, 2020) adapt both phylogenetic matrices offering tooth and dentary features as well as postcranial evidence for docodontans and other outgroups. However, their findings do not support all of the previously suggested docodontan families.

There are still unanswered questions concerning phylogenetics within the order Docodonta. Future fossil finds may shed light on current docodontan connections, and their origin.

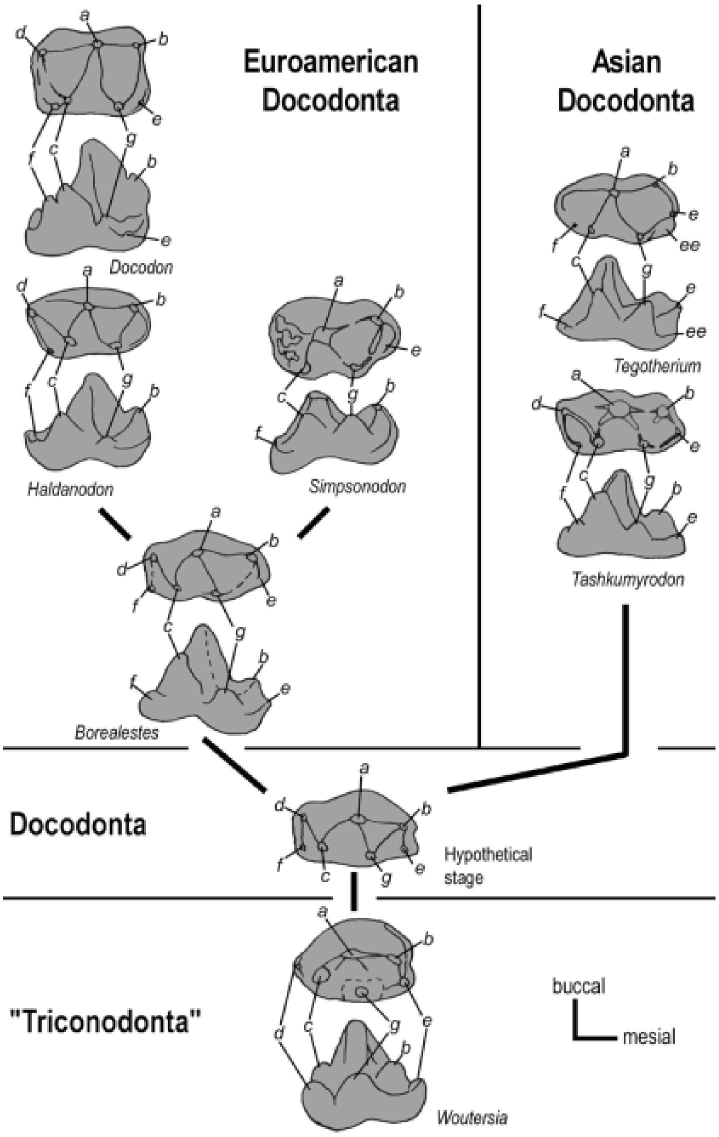

Figure 11. Proposed lower molar evolution of Docodonta, related to the morphology of the Symmetrodont *Woutersia* (from Martin & Averianov, 2004).

1.2. Greenland Mammaliaforms: previous discoveries

Several fragmentary skeletal fossils and isolated mammaliaform teeth have been found in Greenland from the Fleming Fjord Formation, all of them from the Tait Bjerg Beds and Carlsberg Fjord Beds in the Ørsted Dal Member (Table 2; Jenkins *et al.* 1994, 1997; Clemmensen *et al.* 2016, 2020). These date from the Middle Norian to the early Rhaetian. In total, five mammaliaforms have been described: *Mitredon cromptoni* (Shapiro & Jenkins, 2001), *Haramiyavia clemmenseni* (Jenkins *et al.* 1997), *Kalaallitkigun jenkinsi* (Sulej *et al.* 2020), *Kuehneotherium* sp. (Jenkins *et al.* 1994) and cf.? *Brachyzostrodon* sp. (Sigogneau-Russell, 1983). Together, these represent some of the most northerly occurring mammaliaform that remains known globally.

Mitredon cromptoni Shapiro & Jenkins, 2001 is known from a partial left dentary preserving three incomplete postcanine teeth (Shapiro and Jenkins, 2001). This cynodont was found in Rhaetian sediments. It is of uncertain taxonomic affinity but shares characters with 'chiniquodonts' including laterally compressed cusps arranged in a longitudinal row and clearly separated from one another (Shapiro and Jenkins, 2001).

Haramiyavia clemmenseni Jenkins et al. 1997 is represented by a partial maxilla with three molariform teeth, from the Rhaetian Tait Bjerg Beds (Jenkins *et al.* 1997). It belongs to Haramiyaviidae (Butler 2000), a proposed outgroup of the eleutherodontids (Luo *et al.* 2015). This specimen has provided key information about early mammaliform taxonomic relationships, and has been used in wider analyses of dietary habits among mammaliaforms (Luo *et al.* 2015; Morales-García *et al.* 2021). When compared to other early mammal relatives' teeth, which are considered to be insectivorous, haramiyids have molars with longitudinal rows of numerous cusps, which occlude alternately between the upper and lower molars. This indicates that they were designed for omnivory or herbivory (Luo *et al.* 2015).

Another haramiyidan from the Upper Triassic of Greenland is *Kalaallitkigun jenkinsi* Sulej et al., 2020, known from a partial dentary preserving a premolar and a molar (Sulej *et al.* 2020). The morphology of its molars was suggested to represent a transitional stage between the triconodont pattern of morganucodontids, and the two-rowed complex pattern found in haramiyidans. In addition, their study led to the conclusion that the resistance of teeth to bite-related stress is linked to the number of roots, with two roots providing greater resistance to stress than just one (Sulej *et al.* 2020).

Ten mammaliamorph teeth from the Upper Triassic Greenland have been assigned to *Kuehneotherium* sp. Kermack et al. 1968 and span from late Norian to early Rhaetian age (Jenkins *et al.* 1994; Marzola *et al.* 2018). They were assigned based on the relative size and position of the cusps, as well as the wear facets that record a specific occlusal pattern (Jenkins *et al.* 1994).

A single mammaliamorph tooth was assigned as possibly belonging to *Brachyzostrodon* Sigogneau-Russell, 1983, a morganucodontan mammal also known from Saint-Nicolas-de-Port, France (Sigogneau-Russell. 1983a; Jenkins *et al.* 1994). The sediments where the fossil was extracted correspond to the Upper Triassic (late Norian to early Rhaetian) (Clemmensen *et al.* 2016; Jenkins *et al.* 1994; Marzola *et al.* 2018). The specimen was designated by its very large internal cingular cusp (kuehneocone; see Figure 25D), which is a distinctive feature of the morganucodontids (Jenkins *et al.* 1994).

Table 2. Mammaliaformes found in Greenland's Mesozoic fossil record.

Taxon name	Formation	Member	Time Period	Main Publication/s
Mitredon cromptoni	Fleming Fjord Formation	Ørsted Dal Member (Tait Bjerg Beds)	Late Norian to early Rhaetian	Shapiro and Jenkins (2001)
Haramiyavia clemmenseni	Fleming Fjord Formation	Ørsted Dal Member (Tait Bjerg Beds)	Late Norian to early Rhaetian	Jenkins *et al.* (1997); Luo *et al.* (2015)
Kalaallitkigun jenkinsi	Fleming Fjord Formation	Ørsted Dal Member (Carlsberg Fjord Beds)	Mid-late Norian	Sulej *et al.* (2020)
cf.? *Brachyzostrodon*	Fleming Fjord Formation	Ørsted Dal Member (Two teeth – Carlsberg Fjord Beds; Eight teeth - Tait Bjerg Beds)	Late Norian to early Rhaetian	Jenkins *et al.* (1994)
Kuehneotherium sp.	Fleming Fjord Formation	Ørsted Dal Member (Tait Bjerg Beds)	Late Norian to early Rhaetian age	Jenkins *et al.* (1994)

1.2.1. Geological framework: Late Triassic-Early Jurassic boundary of Greenland

The Jameson Land Basin is located in east-central Greenland (Figure 12A; Clemmensen *et al.* 2016, 2020) and comprises sediments from the Middle Devonian to the Late Jurassic (Jenkins *et al.* 1994; Marzola *et al.* 2018). It contains a thick succession of continental sediments, consisting of the Pingo Dal, Gipsdalen, Fleming Fjord and Kap Stewart groups (Figure 12; Clemmensen, 1980a; Clemmensen *et al.* 1998). The climate was characterized as warm, moist and temperate (Clemmensen *et al.* 1998). The vertebrate fauna found in the Late Triassic deposits of the Jameson Land Basin includes bone fragments, teeth, coprolites and other remains. Evidence of mammaliaforms, batrachians, fishes, sharks, temnospondyls and early archosaurs such as dinosaurs, pseudosuchians and early marine reptiles have been found (Bendix-Almgreen, 1976; Jenkins *et al.* 1994; Jésus *et al.* 2022; Milàn *et al.* 2012; 2016).

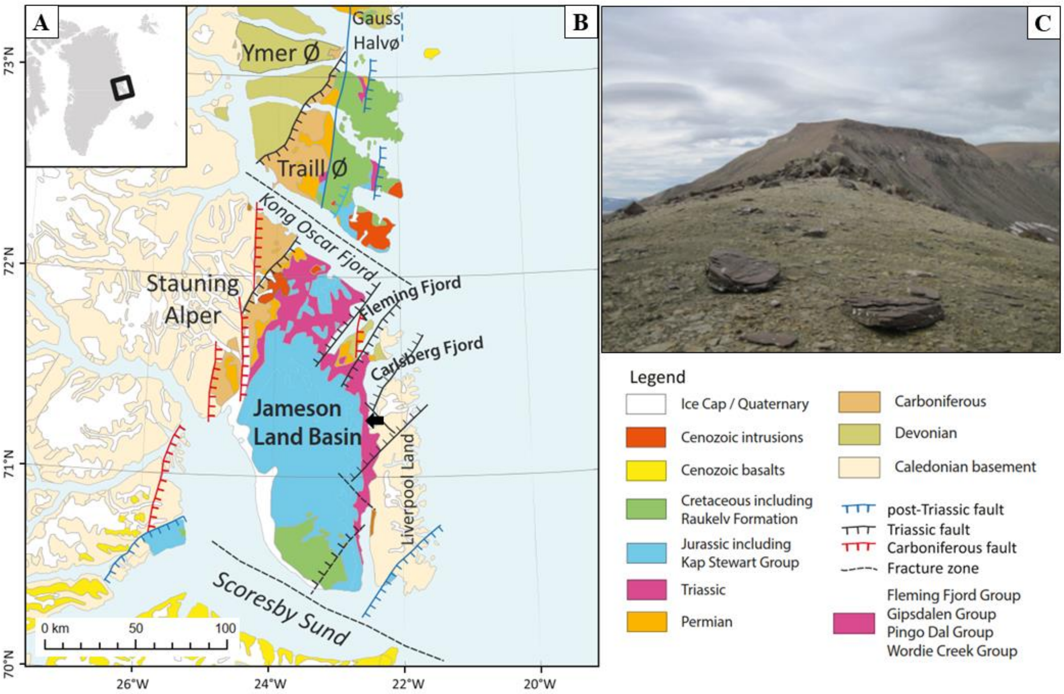

Figure 12. Location of the late Triassic fossil site in east-central Greenland. A, Map that shows the location of the Jameson Land Basin in central East Greenland. B, Section of Lepidopterislev in the Rhætelv Formation of the Kap Stewart Group (black arrow). C, Photograph of the middle part of the Rhætelv Formation at Lepidopteriselv (Modified from Clemmensen *et al.* 2022).

The Kap Stewart Group (originally known as the Kap Stewart Formation) is composed of Upper Triassic to Early Jurassic sediments, dated from Rhaetian to Hettangian ages (Figure 12B; Clemmensen, 1998; Marzola *et al.* 2018; Surlyk, 2003). It is 155-600 m thick, and comprises three formations: in the center of the basin is the Rhætelv Formation, composed of lacustrine claystone rich in organic matter with interspersed sheet sandstones; on the basin margins are the Innakajik Formation composed of alluvial plain sandstone and conglomerate and the Primulaelv Formation overlaid by delta plain sandstones to mudstones (Figure 13A; Clemmensen *et al.* 1998; Surlyk, 2003; Surlyk *et al.* 2021).

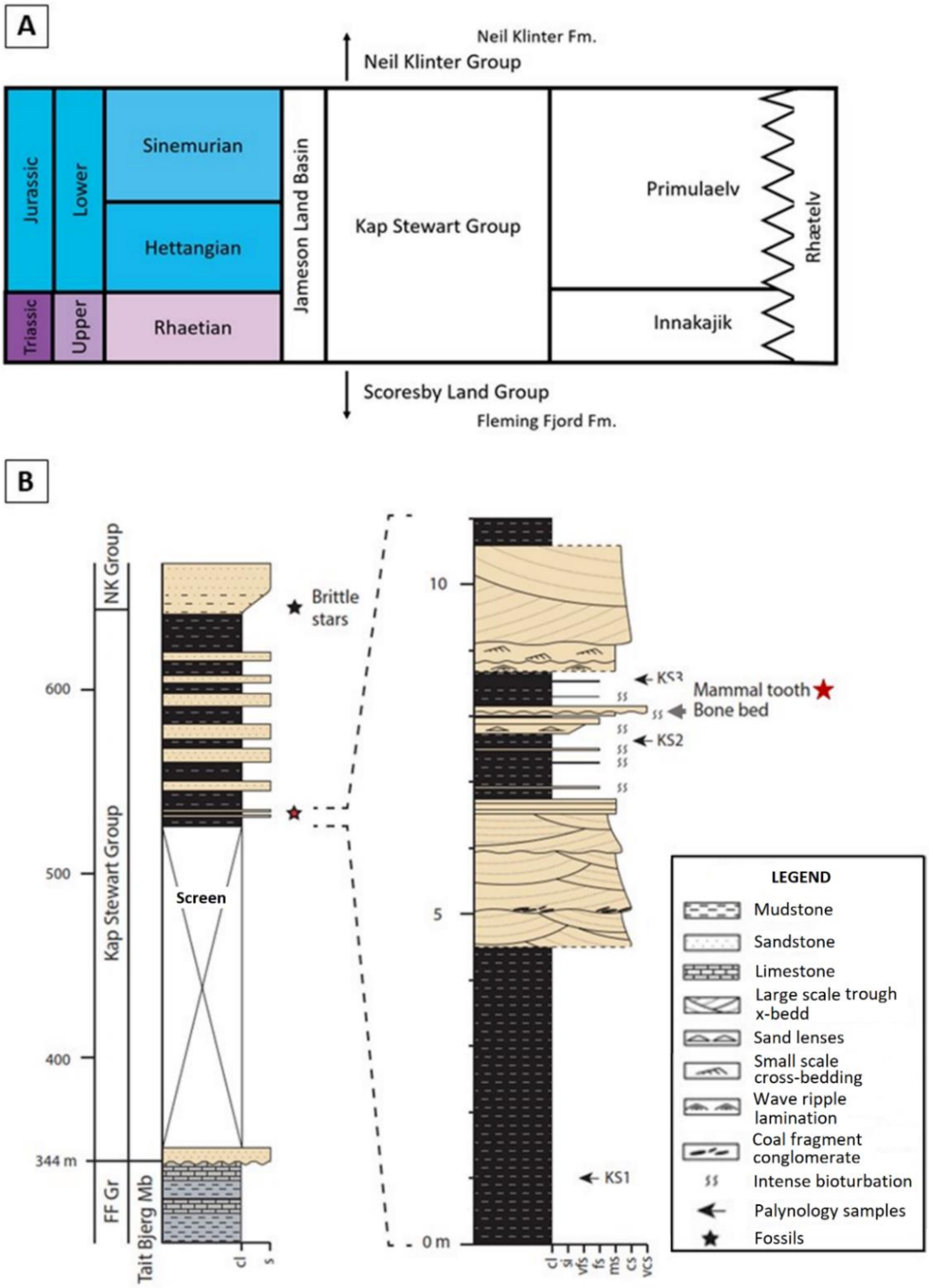

Figure 13. Geological and lithological framework from the Kap Stewart Group. A, General stratigraphical column of the Jameson Land Basin, East Greenland showing the stratigraphic position of the Kap Stewart Group (Modified from Surlyk, 2003 and Clemmensen, 2020).

The Rhaetelv Formation is located on the northeast coast of Jameson Land, at about 344 and 633 m above current sea level (Clemmensen *et al.* 2022). This formation is 300m thick (Clemmensen *et al.* 2021; Surlyk, 2003) and is composed of sediments dating back to the Late Triassic (Rhaetian) to the Early Jurassic (Sinemurian) (Figure 13A; Clemmensen *et al.* 2022). Its lower limit, although difficult to understand, is delimited by red sediments, corresponding to the last dolomitic marlstone of the Tait Bjerg Member, changing to light grey sandstones and dark mudstones of the Kap Stewart Group (Clemmensen 1980b; Clemmensen *et al.* 2022). At 190m above the base of the group is a bone-bearing associated with laminated black mudstones (Figure 13B; Clemmensen *et al.* 2022).

1.2.2. Paleoenvironment of Rhætelv Formation

According to Dam and Surlyk (1993), the sediments that make up the Kap Stewart group were formed by an anoxic lake, dominated by waves and storms (Figure 14). The anoxic conditions dominated in the lower water bodies and at the bottom of the lake during the deposition of muds. More recently, Clemmensen *et al.* (2022) affirmed that the sediments were formed in a lacustrine basin flanked by deltas. Its coarse-grained sediments, of eastern, western and northern origin, were transported forming large deltaic systems (Figure 14). This lake has experienced several short-term fluctuations in water level, largely due to climate change. Long-term variations in sea level have occurred in the Rhaetian, Hettangian and Sinemurian (Figure 15B; Dam and Surlyk 1992, 1993). Palynological analyzes and the existence of fossils of wood fragments and black phytoclasts suggest the existence of forests in the vicinity of the formation environment (Clemmensen *et al.* 2022).

The Rhætelv Formation previously did not have a correct and precise dating for the vertebrate fossil layer, making it difficult to understand the clear definition of the Triassic-Jurassic boundary. Clemmensen *et al.* (2022) conducted palynological studies on the mudstones of the formation, and the age obtained was middle to late Hettangian (Figure 15). According to Haq (2017), at this age, there were two episodes of marine transgressions, the first immediately before 200.8 Ma and the second immediately before 200 Ma. When analyzing the plesiosaur fossil remains found in a thin sandstone bed, Clemmensen *et al.* (2022), concluded that the presence of these bones means that the plesiosaur entered the basin in a period of marine transgression, and *"its bones were eroded from the sediments of the front of the delta during a storm and later deposited in a large inter-distributive bay on the delta plain"*. Thus, by comparison with global sea-level variation, the marine transgression in the Jameson Land Basin corresponded to the second observed transgression (T2) in the Hettangian age, dated to approximately 200 Ma (Figure 15; Clemmensen *et al.* 2022).

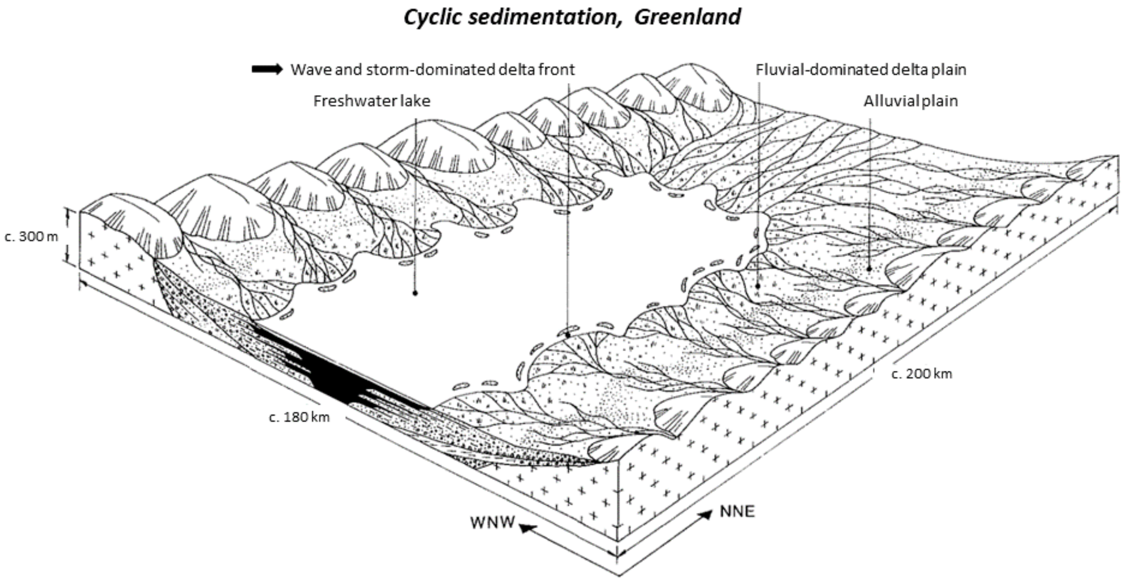

Figure 14. Paleogeographic reconstruction of the Jameson Land Basin during the Rhaetian. The black arrow represents the possible paleoenvironment from which the mammal tooth (see Figure 13) originated (Modified from Dam & Surlyk, 1992).

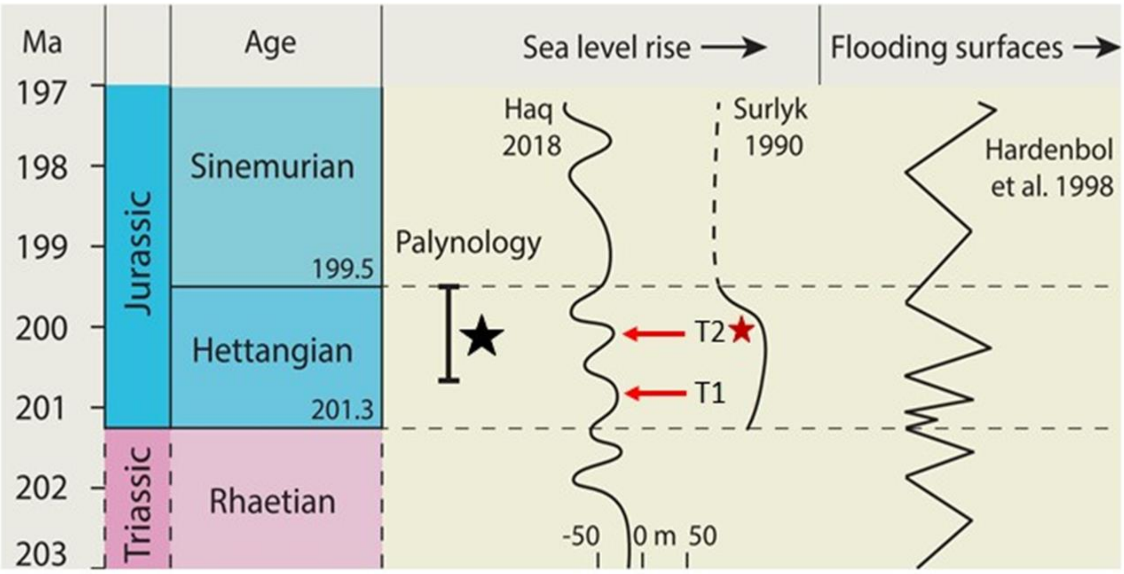

Figure 15. Age interpretation of the studied section by Clemmensen *et al.* (2022) in the middle part of the Rhætelv Formation and its relation with the sea level. The black star represents the age obtained by palynological analysis of the black mudstones by Clemmensen *et al.* (2022). The red arrows represent transgressions at sea level (T1- 1st Transgression; T2- 2nd Transgression). The red star represents the transgression that corresponds to the layer of the fossil under study. Adapted from Clemmensen *et al.* (2022); Dam and Surlyk, (1992).

1.3. Objectives

This thesis focuses on the preparation, analysis, description and study of the material NHMD 1184958, an incomplete dentary with preserved molar, tentatively attributed to Docodonta by Clemmensen *et al.* (2022). The objectives include:

- Preparing the fossil material by removing excess sediment;
- Performing a µCT-scan of the material;
- Digital reconstruction of the µCT data to produce a 3D model of the specimen using Avizo software;
- Describing the morphology of the dentary and dentition, comparing it with other early mammaliaforms;
- Performing a phylogenetic analysis to examine the placement of specimen NHMD 1184958 within the broader mammaliaform phylogeny;
- Examining how NHMD 1184958 informs our understanding of the origin of Docodonta, and the emergence of mammal ecomorphological diversity.

2. MATERIAL AND METHODS

2.1. Specimen NHMD 1184958

Specimen NHMD 1184958 comprises an incomplete right dentary with a single molar and roots of a second tooth (Figure 16). It was found in sandstone sediment within an infilled fossil burrow (Clemmensen *et al.* 2022). The specimen was found during fieldwork in 2016, near the Liasryggen area, in the Kap Stewart Group. It was accessed for preparation and study during its staying at the Lourinhã Museum (ML). At this time, this is the known repository of the specimen. There are several elements dispersed on the surface of the block, such as an ichthyofaunal material which consists of the possible semionotiform scale and a hybodontiform tooth (Appendix I and II). The specimen was cleaned using a needle and a Nexius Zoom Euromex Holland microscope to permit specimen identification and show as much of the crown of the tooth and dentary as possible to understand its morphology (Figure 17). The specimen was not completely separated from the matrix because further preparation was likely to cause damage and loss of stability.

Based on the previous identification of the molar as belonging to the order Docodonta, (Clemmensen *et al.* 2022), the terminology of Luo and Martin (2007) was used for interpreting the molar structure, cusp assignation and definition of the crests and basins. This terminology is based on Butler (1997). For more information on terminology, see Table 1 and Figure 17.

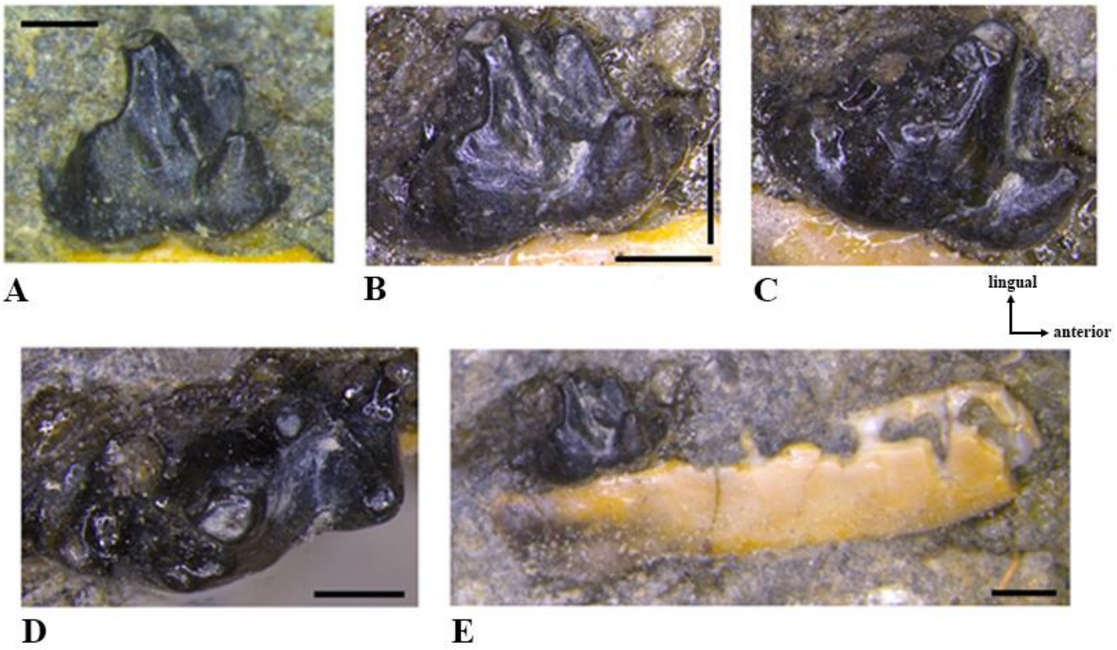

Figure 16. Right lower molar of NHMD 1184958 before and after preparation. A, molar before preparation; B, molar after preparation; C, molar in lingual view; D, molar in occlusal view; E, partial dentary in lingual view, with preserved molar. All scales correspond to 0.5 mm.

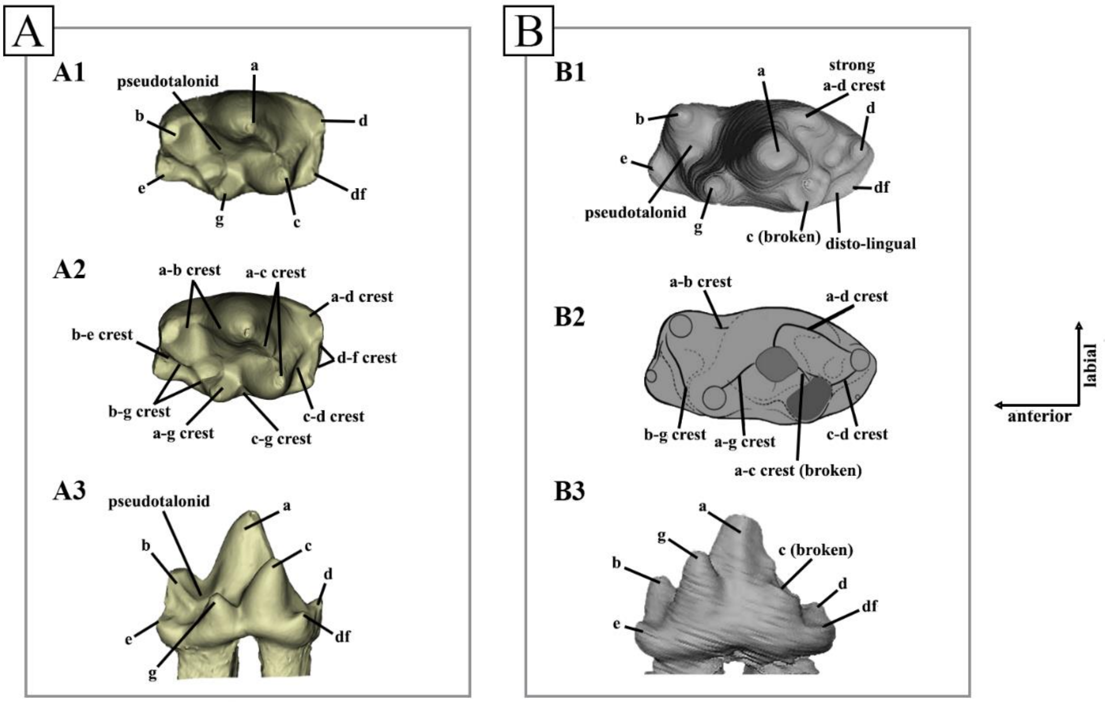

Figure 17. Terminology of molar of a docodontan (*Borealestes*) and comparison with NHMD 1184958. A, lower molar cusp and crest terminology of *Borealestes*: A1 and A2, occlusal view, and A3, lingual view. B, lower molar cusp and crest terminology of NHMD 1184958: B1 and B2, occlusal view, and B3, lingual view. Not to scale. (Adapted from Panciroli *et al.* 2019).

2.2. Digitization and image treatment

Specimen NHMD 1184958 was initially studied using a LEICA M165 C stereo microscope, and photos were taken using a FLEXACAM C1 camera (Figure 17). The images were processed using programs LAS X and Leica LAS X Hardware Configurator. Subsequently, NHMD 1184958 was scanned in Micronsense (Leiria, Portugal) using MicroCT phoenix v|tome|x m with a voxel size of about 83 µm, an acceleration voltage of 200 kV, and a current of 500 µA. This generated 831 DICOM slices (DICOM: Digital Imaging and Communications in Medicine format), and the scan resolution was 15 µm.

Segmentation was performed using the Avizo 2019.1 (Thermo Fisher Scientific), which was obtained via the trial version. Avizo is a general-purpose commercial software application developed for the visualization and analysis of scientific and industrial data. It allows users to visualize, analyze and model various types of 3D datasets. Data and modules are manipulated with various parameters, creating an interactive graphical representation whose output is displayed in a 3D viewer (Figure 18). Segmentation was mostly carried out using the brush selection tool and interpolation. The process took around 54 hours and resulted in the generation of three 3D meshes: the dentary, the tooth, and the vascular canals within the dentary. The 3D meshes were generated using the Generate Surface tool and were treated using the Unconstrained

Smoothing tool with a smoothing extent of 6.16312. Different surface views were created using an opaque dentary and teeth, and a transparent dentary with opaque tooth (Figure 17).

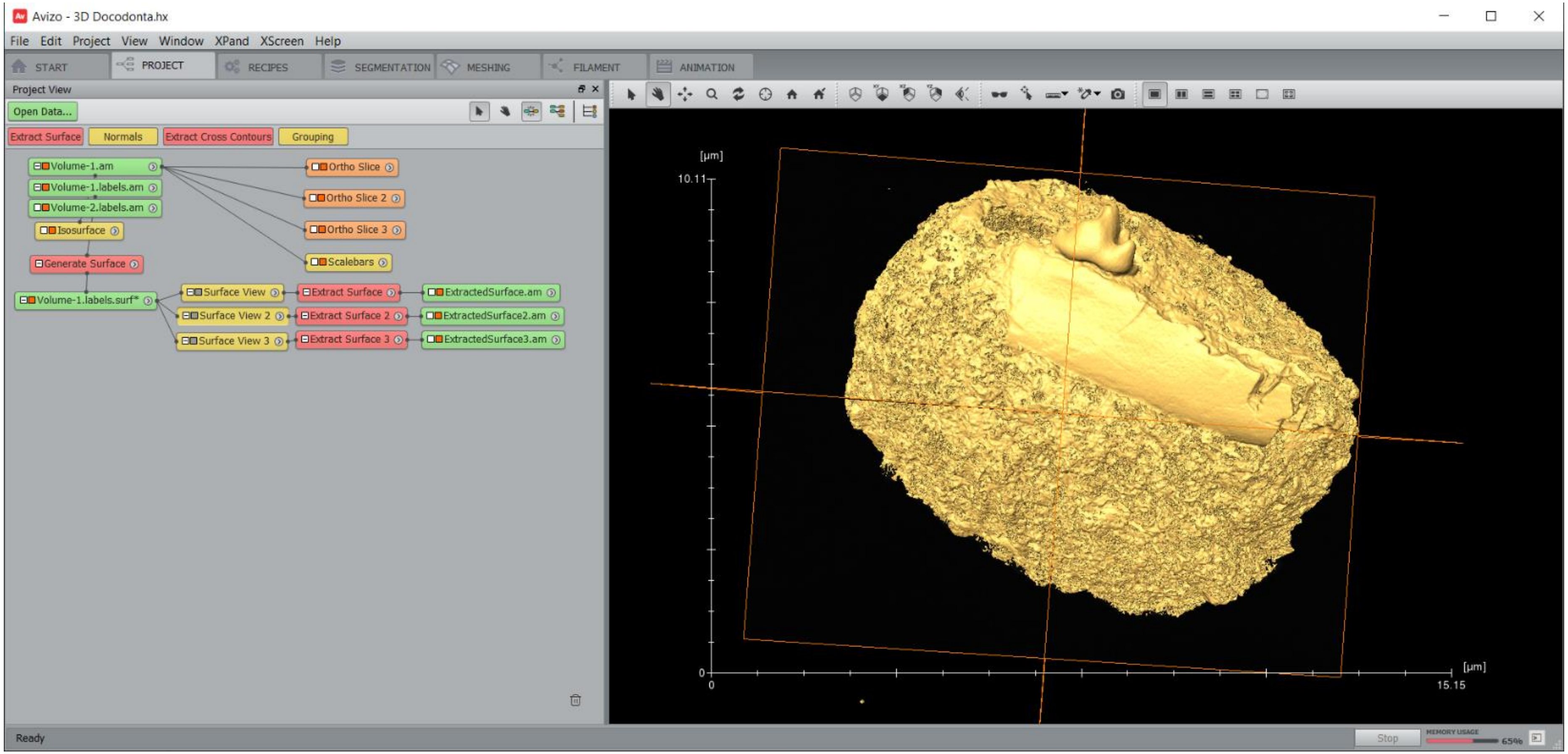

Figure 18. Example of the 3D model of the specimen with software Avizo 2019.1.

Measurements were taken first using a LEICA M165 C Stereo microscope, and later corroborated digitally in Avizo using the Measurement tool. Tooth measurements were performed according to the methodology in Panciroli *et al.* (2019) for lower molars. The length (anteroposterior) was measured from cusp b to cusp d and from cusp e to cusp df, and the width (labiolingual) was measured across cusps c and g (Figure 19). All measurements are in millimeters (see Systematic Paleontology: Measurements). All figures of NHMD 1184958 were arranged using PhotoshopCS6.

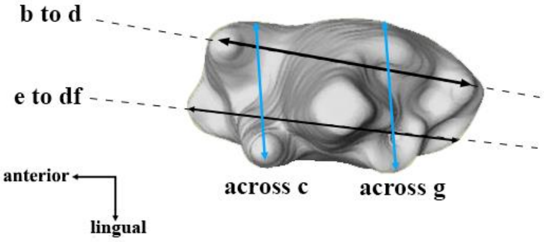

Figure 19. Lower molar measurements. Blue arrows represent linguo-labial measurements and black arrows represent antero-posterior measurements.

2.3. Phylogenetic analysis methodology

The phylogenetic analysis was performed using TNT (Tree Analysis using New Technologies) version 1.25 (Goloboff and Catalano, 2016), with Mesquite version 2.75 (Maddison and Maddison, 1997-2011) initially used to convert the data matrix to NEXUS format. TNT analyzes data sets with discrete and continuous characters (in this case, an array), allowing the user flexibility in phylogenetic analysis or simulation, and creating tree diagrams that can be saved as metafiles (Goloboff *et al.* 2008). According to Giribet (2005), the tree bisection and reconnection (TBR) feature exhibits a significantly reduced computational time compared to another popular software used for phylogenetic analysis, PAUP (Phylogenetic Analysis Using Parsimony). This disparity becomes more pronounced as the data set size increases. TNT permits options for configuring targeted searches via "new technology".

To understand the phylogenetic position of the specimen, a phylogenetic analysis was performed using the character matrix used by Zhou *et al.* (2019). This comprised the most known docodontan genera, plus their nearest putative relatives. The purpose was to understand the position of the new taxon under study, NHMD 1184958, within the phylogeny of early morganucodontan and docodontan mammaliaforms. This matrix was chosen because it comprises mainly dental characters, and it has a greater number of docodonts compared to other matrices (Appendix III). The final data matrix (with NHMD 1184958 added) includes 25 genera scored for 57 binary characters, and is presented in full in Appendix V.

In total, four analyses were carried out: (1) Zhou *et al.*'s (2019) original matrix (which did not include NHMD 1184958), applying the same parameters as the anterior authors ; (2) Zhou *et al.*(2019)'s original matrix with NHMD 1184958 added; (3) Zhou *et al.*(2019)'s matrix with NHMD 1184958 added, but amending character scores 1, 2, 3, 4, 5, 18, 20, 21, 22, 27, 32, 38, 44, 48, 49, 51, 52, 53 and 54 for some docodontans, to correct errors, update scores, or where our interpretation differed from that of the previous authors' (see Appendix IV); (4) as for analysis (3), but using different parameters.

Analysis 4 was performed using a standard search with 1.000 repeats and 200 trees per replication. After the search, the trees were collapsed using the TBR approach. Bremer Supports were calculated using the TBR with 10 in maintain suboptimality. The Bootstrap standard approach was utilized with absolute frequencies and 100 repetitions. We used TNT "stats" tool to obtain the consistency index (CI), homoplasy index (HI), retention index (RI) and rescaled consistency index (RC) for all analyses (Table 3). All the phylogenetic analysis results are presented in Figure 24 (Consensus trees) and Appendix VI-VII (Synapomorphies, Bremer Supports and Bootstrap Standard). The data from TNT were imported into R Studio (version 2023.06.1+524; RStudio Team (2023)), and a time-scaled phylogeny created using the packages strap (Bell and Lloyd, 2015); ape (Paradis and Schliep, 2019); paleotree (Bapst, 2012) and geoscale (Bell, 2015). First and last appearance data was taken from the Palaeobiology Database (PBDB - https://paleobiodb.org/) (Appendix IX).

3. RESULTS

3.1. Systematic Paleontology

Clade MAMMALIAFORMES Rowe, 1988

Order Docodonta Kretzoi, 1946

Family Docodontidae Simpson, 1929

Docodonta indet. (Fig. 17)

Material. NHMD 1184958, partial right dentary containing one complete molar and the roots of a second tooth.

Locality and Horizon. Sandstone sediment associated with dark mudstones with intense bioturbation, Rhætelv Formation, Kap Stewart Group, exposed at a mountain ridge near Lepidopterielv, Greenland.

Description and remarks. NHMD 1184958 represents 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 (Figure 17). 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 (Figure 20).

The specimen is quite fragmented and practically no morphologically characteristic structures are visible in the dentary. A ditch 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 (Figure 20.A5). The Meckel's sulcus is present in the posterior medial zone of the dentary of mammaliaforms (Rougier *et al.* 2014), so this small ditch in the posterior of NHMD 1184958 could correspond to the anterior tip of Meckel's sulcus. In the most anterior zone of the dentary there is a slight concavity compared to the rest of the dentary, which continues posteriorly until below the m1? (Figure 20.A5). This appears to be a weak mandibular symphysis: the fusion zone that occurs between the right and left halves of the dentary in its most anterior part. It divides inferiorly to form a mental protuberance (a bony prominence in the mental region) (Beecher, 1979; Phulari, 2013). These characteristics support the interpretation of NHMD 1184958 as representing the middle portion of the right dentary, and indicate that this is the medial side of the dentary (Figures 17.B3; 20.A1 and 20.A5).

According to Luo and Martin (2007) there is a lingual cingulid in docodontan molars. Analyzing the preserved molar in NHMD 1184958, there is a cingulid on what is here interpreted as the postero-lingual part of the tooth, below the cusps d and c, covered by sediment in the unprepared specimen (Figures 17; 20.A8 and 20.A11). Therefore, we consider the cusp row exposed outside the sediment as the labial (Figures 17 and 20.A4) and that the lingual row corresponds to the one that is covered (Figures 17 and Figure 20.A8) (see 5.2). It should be noted that the a-d crest was designated as being a crest and not a cusp because although voluminous, it is not enough to be considered a cusp (see 5.2).

The dentary fragment has several fractures running through it: on the lingual side there is a fracture posterior to the preserved molar, another across the posterior alveolus of the adjacent tooth (containing preserved roots) and another at the anteriormost part of the dentary, all of them running dorsoventrally through the body of the dentary. On the labial side, another fracture runs diagonally across two of the alveoli. The ends of the dentary are broken, exposing empty alveoli.

There are no structures preserved in the dentary that are diagnostic of a particular taxonomic group. The alveoli are labiolingually compressed and are separated by U-shaped notch widths 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 might be expected for the roots of premolar teeth. Anterior to the complete molar (described below), two broken roots are present inside the alveoli (Figure 20: A2, A4, A6, A8, A9 and A11). The ventral apex of these roots, and those of the more complete neighbouring molar, have a slight anterior curvature.

In occlusal view, the general morphology of the molar tooth in NHMD 1184958 is anteroposteriorly elongated and slightly buccolingually compressed (Figure 21A1-2). It possesses an anterior pseudotalonid basin on the lower molar, formed by cusps a, b, and g, and has cusps g–a–c in a triangular arrangement of approximately 100 degrees, comparable to docodontans such as *Itatodon* (approximately 110 degrees); *Dobunnodon* (approximately 100 degrees) and to the early mammaliaform *Delsatia* (approximately 90 degrees). Like members of Docodonta, the labial row has taller cusps aligned anteroposteriorly with the greatest cusp a (although cusp a is much closer to the middle of the tooth, see below). In comparison, the lingual row has smaller cusps with a distinct anterior cusp g and a possibly bigger posterior cusp c.

Resembles most docodontants, e.g. *Borealestes*, *Krusatodon*, *Castorocauda*, *Itatodon* and *Haldanodon*, in possessing a large cusp a and a posterior basin. Cusp a is located approximately in the median axis of the tooth (linguolabially) and positioned very lingually, a feature that is uncommon within docodontans, but similar to the putative docodontan *Delsatia*, and somewhat similar to *Dobunnodon* and *Dsungarodon*, however the cusp a more lingually positioned in NHMD1184958. It is conical, rounded labially, and slightly convex lingually with a faint dorsoventral protuberance on the lingual face (Figure 21A4).

Cusp c is broken at the base, making it difficult to judge its size, but the width of the broken base suggests to be slightly bigger than cusp g, resembling *Tegotherium*, *Dsungarodon* and *Tashkumyrodon*, and smaller than cusp a. Like the majority of docodontans, but unlike *Simpsonodon*, *Krusatodon*, *Agilodocodon*, and *Docodon,* NHMD1184958's molar tooth enamel does not have pits or ornamentation.

There is a very distinct, strong a-d crest which is directed posterolabially, running around the edge of the tooth to form a ridge. A strong a-c and weaker a-g crest are directed mesially and posteriorly from the apex of cusp a, forming an angle of about 110°, and both have a v-notch. There is no a-b crest, differing from most docodontans, but somewhat 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. This feature is uncommon among docodontans, but is similar to *Dobunnodon*'s a-d crest (Figure 21A1-2).

The cusp g is about 2/3 the height of cusp a. It is positioned anterolingual to cusp a, and aligned with cusp c. The base of the broken cusp c is positioned posterolingually in relation to cusp a. The a-c crest sits dorsoventrally higher than the a-g crest, suggesting that this cusp could have been larger than cusp g, although the diameter of the broken surface of cusp c does not differ much from the diameter of the base of cusp g (Figure 21A3-4). The distance between cusp c and cusp g is similar to *Dobunnodon* and *Itatodon*. This characteristic is apparent in NHMD1184958, even though cusp c is fractured.

Cusp b is approximately 1/3 of the height of cusp a, and is tilted slightly anteriorly, as in *Borealestes* and *Krusatodon,* as opposed to the more upright orientation in *Dsungarodon* or *Simpsonodon*. It is somewhat separated from the rest of the tooth, except for the strong b-g crest. There is no b-e crest nor a-b crest. The pseudotalonid (anterior basin) is relatively deep but very underdeveloped, formed by crests a-g, b-g and the point where the base of cusps a and b meet. 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. This well-defined talonid cusp d is similar to *Dobunnodon, Itatodon* and *Delsatia*. A smooth df cusp is visible on the postero-lingual cingulid. Cusp e is situated on the anteriormost part of the molar and is distinct anteriorly, bearing resemblance to *Borealestes*. It is similar in size to cusp d (Figure 21A1-2).

This molar tooth is likely to be an m2 based on its large size, depth of the alveoli, and position in the dentary. The preserved molar alveoli diameter is bigger than the other alveoli in the tooth row, and the diameter of the alveoli in the tooth row shrink anteriorly. The depth of molar roots within the dentary increases anteriorly from the ultimate molar to the m2 position in docodontans, then decreases anteriorly from the m2 to p1 (eg, Figures 3-6 in Panciroli *et al.* 2019). The m2 roots are therefore deeper in comparison to the other molars, and the alveoli diameter also decreases in the anterior direction from this position in the tooth row. The anteriorly located alveoli in NHMD 1184958 are significantly smaller than the rest, indicating that this may represent the ultimate premolar position (Figure 22).

Measurements. Molar: length (cusp d to b) 1.60 mm; (cusp e to df) 1.76 mm | width: (across cusp c) 0.88 mm; (across cusp g) 0.83 mm.

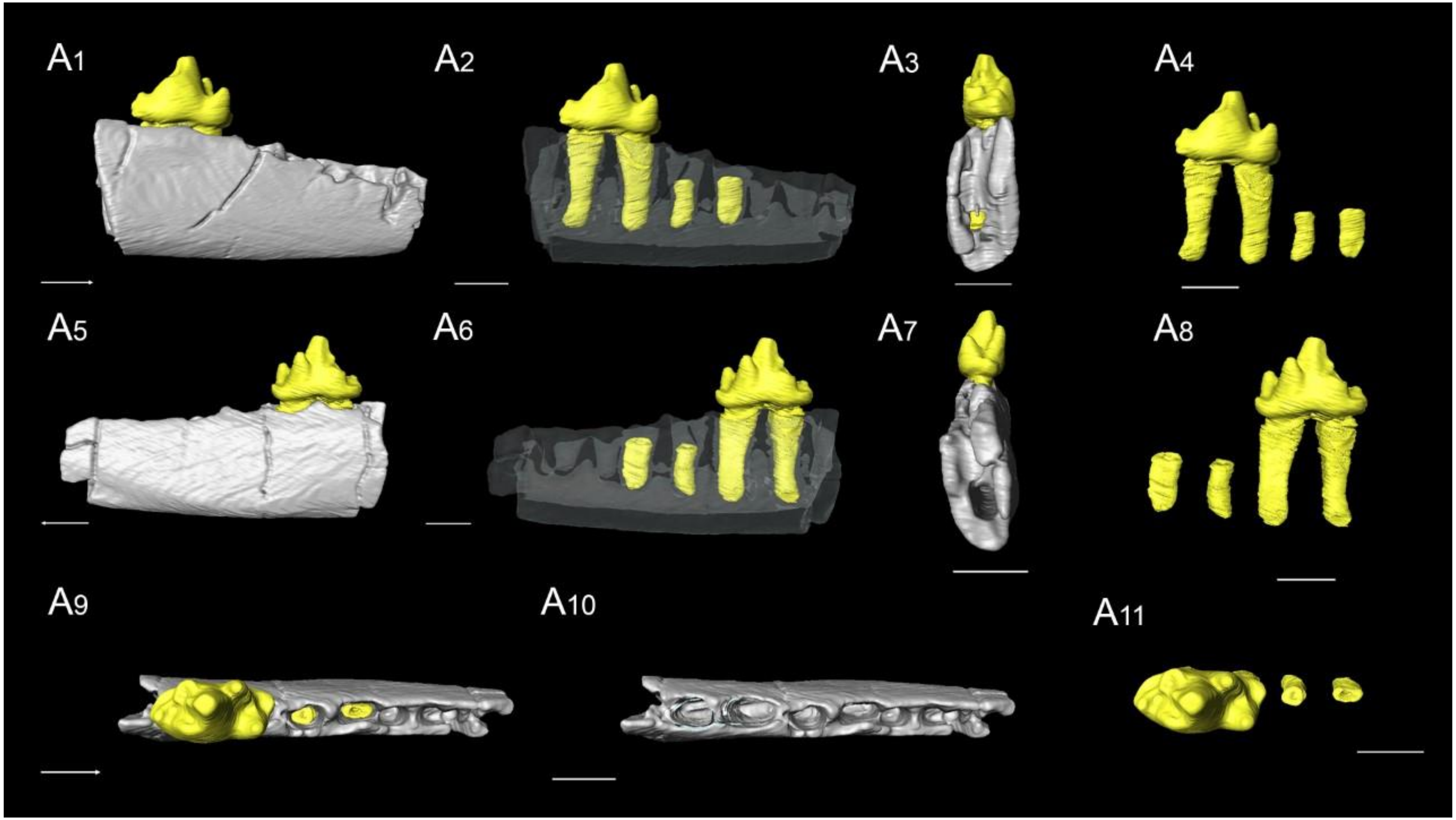

Figure 20. NHMD 1184958 right dentary with associated dentition. A1-2, specimen NHMD 1184958 in labial view; A3, specimen NHMD 1184958 in the most posterior view; A4, molar of NHMD 1184958 in labial view; A5-6, specimen NHMD 1184958 in lingual view; A7, specimen NHMD 1184958 in the most anterior view; A8, molar of NHMD 1184958 in lingual view; A9-10, specimen NHMD 1184958 occlusal view; A11, molar of NHMD 1184958 in occlusal view. Arrows indicate the anterior direction. Scale bar corresponds to 1 mm. The different scales correspond to the same value.

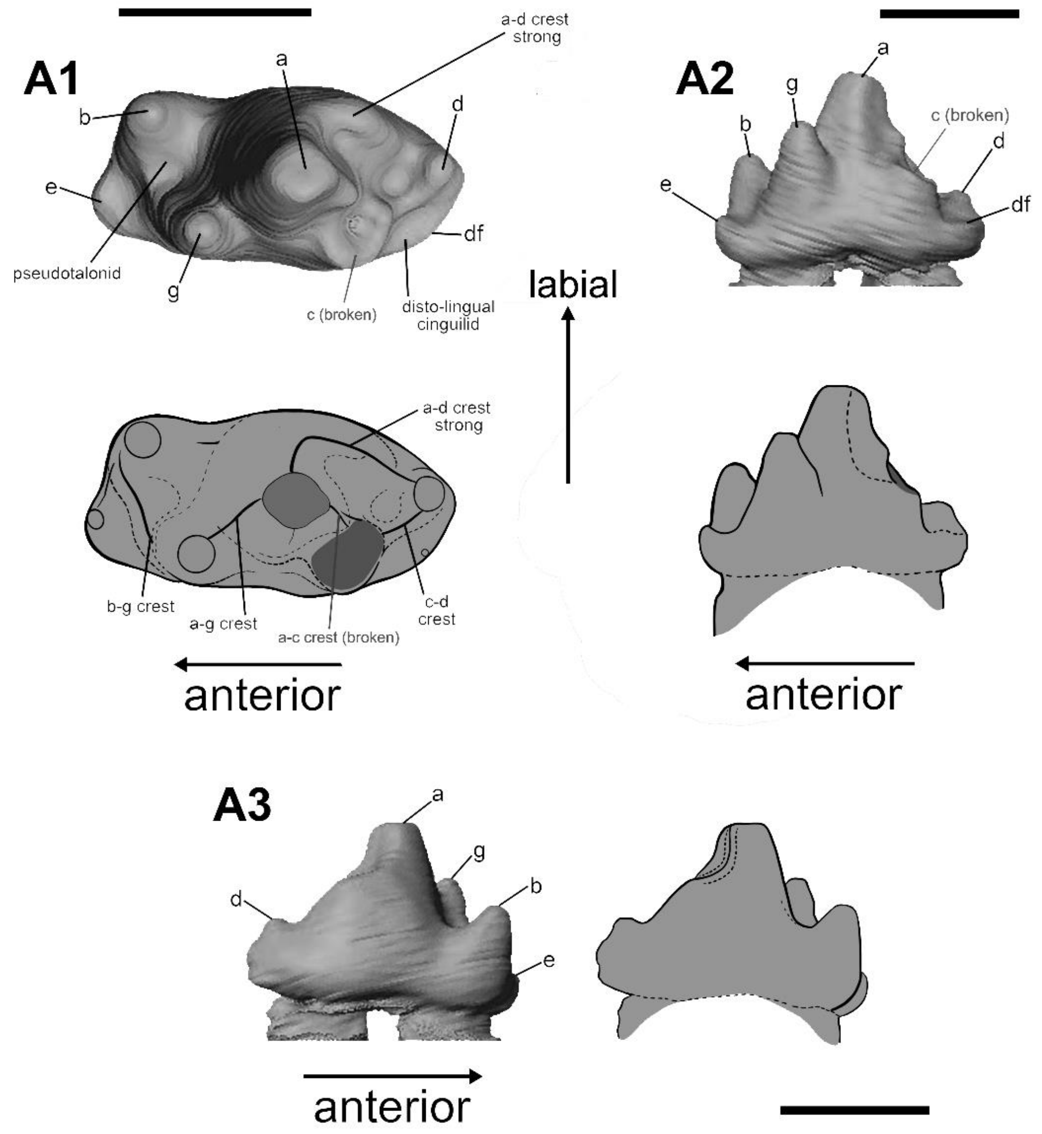

Figure 22. Diagnostic dental features of NHMD 1184958. A1, occlusal view and respective diagrammatic illustration below; A2, lingual view and respective diagrammatic illustration below; A3, labial view and respective diagrammatic illustration below. Darker grey area indicates broken and slight darker grey area indicates wear surface. Letters in grey indicate broken cusps and crests. Scale bars equal 1 mm.

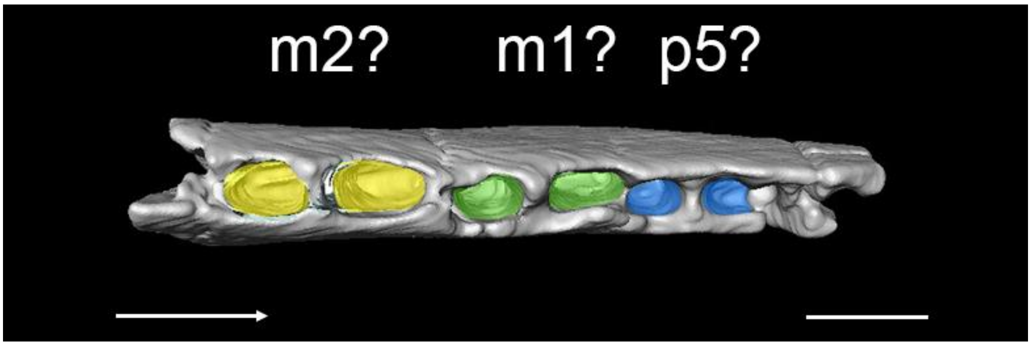

Figure 21. Illustration of roots on the lower right dentary in occlusal view. m2?, 2nd molar (belonging to the specimen); m1?, 1sh molar; p5?, 5th premolar. Scale corresponds to 1 mm.

3.2. Phylogenetic analysis results

Four analyses were carried out. All the recovered topologies do not differ substantially from the topology presented by Zhou *et al.* (2019). The first analysis using the same parameters as Zhou *et al.*'s (2019) original matrix without NHMD 1184958 resulted in 200 MPTs (CI=0.612; RI=0.847) of 129 steps. The second analysis using Zhou *et al.*'s original matrix with NHMD 1184958 added resulted in 200 MPTs (CI=0.590; RI=0.838) of 134 steps. The third analysis of Zhou *et al.*'s matrix with NHMD 1184958 added, but amending character scores for some docodontans (Appendix IV) resulted in 200 MPTs (CI=0.565; RI=0.827) of 138 steps. Finally, the fourth analysis was carried out, changing some of the parameters, and the results are very similar to the third analysis. NHMD 1184958 gave a total of 200 MPTs (Most Parsimonious Trees), with tree length of 134 steps with a Consistency index (CI) of 0.590, homoplasyindex (HI) of 0.410, a Retention index (RI) of 0.838 and a rescaled consistency index (RC) of 0.494 (Table 3).

All the results of the strict consensus gave several polytomies (Figure 24). A large polytomy is visible in all analyzes performed, which includes the basal mammaliaforms *Gondtherium*, *Tikitherium*, *Woutersia*, *Delsatia*, *Kuehneotherium*, *Hadrocodium*, *Dinnetherium*, *Megazostrodon*, *Morganucodon*, and when NHMD 1184958 is added (in analyzes 2, 3 and 4), is included in this polytomy. In the first analysis *Castorocauda* is included in this large polytomy, however, in the remaining analyses, it is nested within Docodonta.

Within Docodonta, the position of some taxa varies between the different analyzes carried out. *Simpsonodon* and *Itatodon* are basal taxa forming a polytomy outside the clades (*Tashkumyrodon* + *Borealestes* + *Dsungarodon* + *Haldanodon* + *Docodon* + *Docofossor*) and (*Agilodocodon* + *Krusatodon* + *Sibirotherium* + *Hutegotherium* + *Tegotherium* + *Microdocodon*). In analyzes 2, 3 and 4 *Tashkumyrodon* + *Borealestes* + *Dsungarodon* + *Itatodon* + *Castorocauda* also form a polytomy. *Haldanodon* + *Docodon* + *Docofossor* are consistently found to form a clade in analysis 2, 3 and 4. Finally, a polytomy composed of *Hutegotherium*, *Tegotherium* and *Microdocodon* was obtained in all analyses, and found as the most derived clade along with *Sibirotherium.*

For a better visual understanding of the phylogeny of the mammaliaforms, with the inclusion of a time scale, a phylogenetic tree was performed in the R software. The trees obtained in TNT were exported to Software R, and the polytomies were resolved by adding the first and last occurrences for each genus. The phylogenetic tree of Docodonta with the addition of NHMD 1184958 is presented below (Figure 23).

The results of the analysis are partially similar to the ones from Zhou *et al.* (2019), which is to be expected since this investigation used a modified version of that matrix. In all analyses NHMD 1184958 is placed in an unresolved polytomy with *Tikitherium* and *Gondtherium*. Pruned trees return the position of NHMD 1184958 either within the Docodonta, or as a sister taxon to Docodonta. The position of some basal mammaliaforms varies from Zhou *et al.* (2019), however the position of Docodonta remains almost the same. In Zhou *et al.* *Woutersia, Delsatia, Kuehneotherium* and *Hadrocodium* are returned as a clade which is an outgroup to Morganucodonta, and all of them are an outgroup to (*Gondtherium* + *Tikitherium* + Docodonta). However, we recover *Woutersia* and *Delsatia* as a clade, being the sister group to (*Gondtherium* + *Tikitherium* + Docodonta). This supports the suggestion that *Woutersia, Delsatia, Gondtherium* and *Tikitherium* are close sister taxa to Docodonta, or may represent basal docodontans.

In this analysis, NHMD 1184958 is found as the closest sister taxa to the clade Docodonta. *Borealestes* is in a more basal position compared to Zhou *et al.* (2019), perhaps reflecting the updated characters re-scored in the present work.

These results support the inclusion of NHMD 1184958 in the clade Docodonta, and the erection of a new genus and species.

The results also suggest there are two main clades of docodontans: one comprising *Docofossor, Docodon* and *Haldanodon* and other comprising all of the other docodontans known (including the taxa proposed by Martin and Averianov (2001, 2004) to be in the Euramerican and the Euroasian clades; see section 5.3).

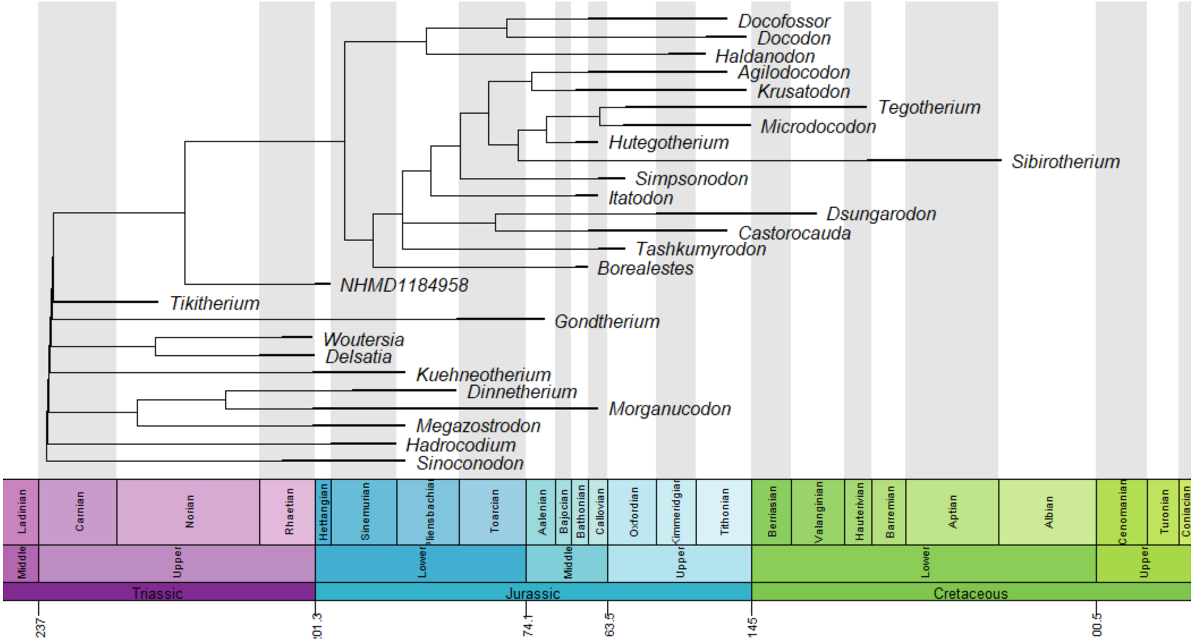

Figure 23. Phylogeny of Docodonta based on the performed phylogenetic analysis, created with R software. Bootstrap standard of 200 trees of 134 steps resulting from parsimony analysis of the data matrix of Zhou et al. (2019), with the addition of NHMD 1184958. First-to-last appearances are represented by black bars (see Appendix IX).

Table 3. Scores for the tree in the phylogenetic analysis. CI, Consistency Index; HI, Homoplasy Index; RI, Retention Index; RC, rescaled Consistency Index.

Length	134
CI	0.590
HI	0.410
RI	0.838
RC	0.494

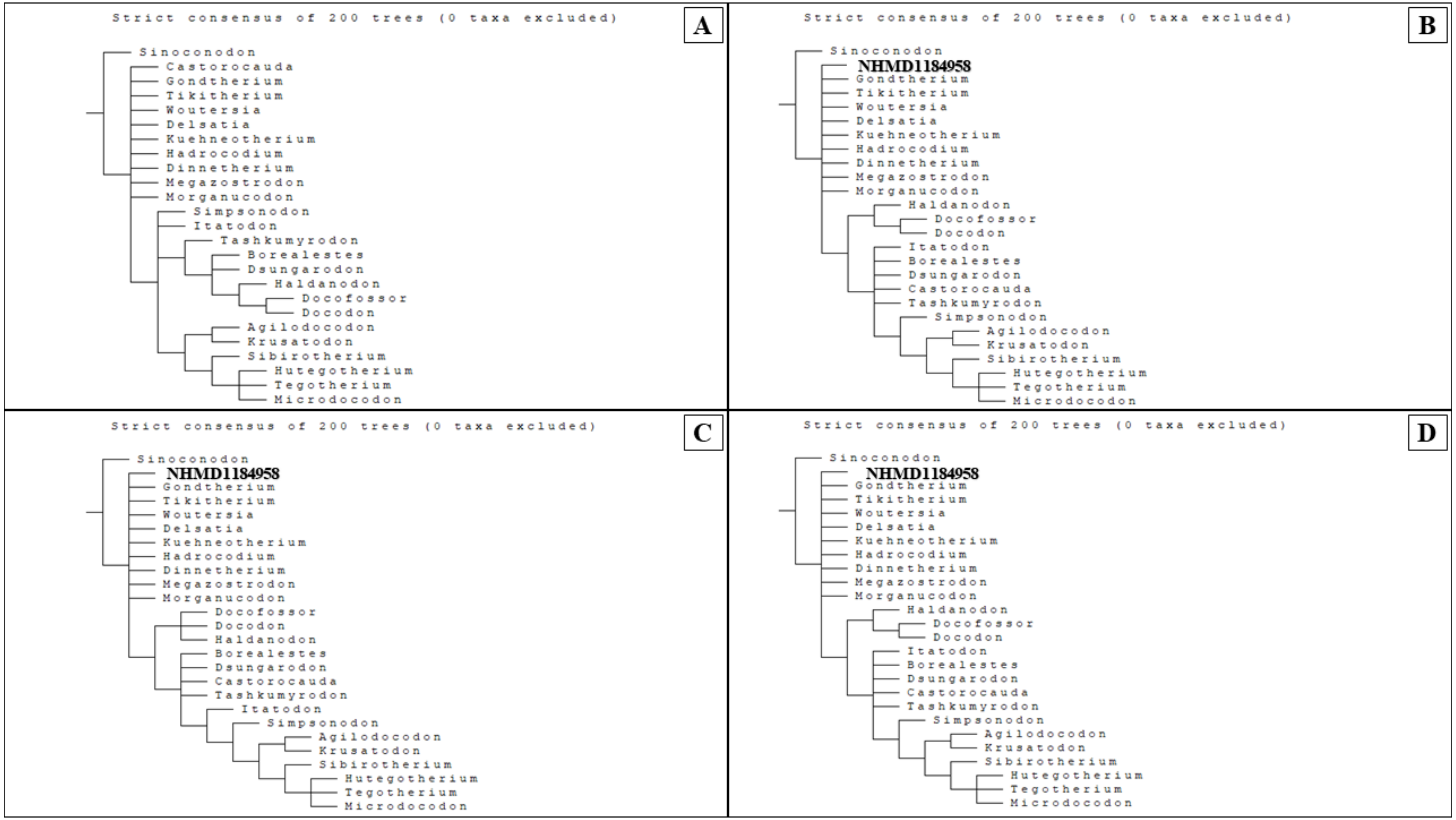

Figure 24. Results strict consensus trees of the specimen NHMD1184958 (A) Zhou *et al.*’s (2019) original matrix; (B) Zhou *et al.*’s (2019) original matrix with NHMD 1184958 added; (C) Zhou *et al.*’s (2019) matrix with the specimen added, but amending character scores (see Appendix IV); and (D) Zhou *et al.*’s (2019) matrix with NHMD 1184958 and amended scores, but using different parameters.

4. DISCUSSION

4.1. Comparisons between the main groups of mammaliaforms

NHMD 1184958 can be excluded from the group of haramiyidans and kuehneotherids due to their different lower molar morphologies. The haramayidan clade is marked by lower molariform teeth with two rows of anteroposteriorly aligned cusps. The lingual row has the highest cusp anteriorly, and cusps successively decrease in height posteriorly. The anterior cusp on the labial side is variable in height, but with a height lower than the A1 cusp, and again, the successive cusps decrease in height (Figure 25. B; Jenkins *et al.* 1997; Luo *et al.* 2015). This morphology is totally different from NHMD 1184958. The kuehneotherid clade has triconodont molars, where the three main cusps constitute a slightly asymmetrical triangle (Cassiliano, 1979; Debuysschere, 2017). The central cusp (a) is the highest, and there are smaller anterior (b) and posterior (c) cusps. The cingulum of the lower molars contains an anterior and a large posterior cusp (Figure 19.C; Cassiliano, 1979). Although more similar to NHMD 1184958 than the haramiyidan tooth morphology, the overall shape and cusps on the cingulum do not resemble NHMD 1184958.

Another group that must be considered for comparison is Morganucodonta. This group of mammaliaformes is subdivided into two families: Morganucodontidae and Megazostrodontidae (Kielan-Jaworowska *et al.* 2005; Luo, 2007). Their triconodont lower molar morphology is characterized by a main row of three cusps, usually with a smaller supplementary fourth posterior cingular cusp and cingular elements on at least one side (Figure 25.D; Kermack *et al.* 1973; Kielan-Jaworowska *et al.* 2005). NHMD 1184958 has main cusps in a triangular occlusal pattern, whereas the main cusps in members of Morganucodonta form a straighter row. Furthermore, the small supplementary cingular cusp with cingular elements present on the posterior side of the tooth in morganucodontans contrasts with NHMD 1184958, which has two quite distinct cusps - the anterior cusp e and posterior cusp df.

Morphologically, NHMD 1184958 shares similarities with the genus *Delsatia* (Figure 25E) – which has also been suggested to be a basal docodontan - concerning the position of the cusps. Unlike *Delsatia*, which has lingual cusps c and b of the same size, NHMD 1184958 presents lingual cusps c and g of different sizes (cusp c appears larger). Like the specimen in study, *Delsatia* has two angular crests that originate on cusps c and b and are linked to the main labial cusp, but in NHMD 1184958 these are both straighter. A third a-d crest curves posterolabially in NHMD 1184958, but is straight and oriented anteroposteriorly in *Delsatia.* In addition, both taxa have a well-developed anterolabial cusp (identified as cusp f in *Delsatia,* but cusp b in NHMD 1184958) and a well-defined talonid cusp d, but the fossil under study, unlike *Delsatia*, has a posterior basin.

NHMD 1184958 presents the most morphological similarities with members of Docodonta. Currently, the order Docodonta includes at least 21 genera, including: the Middle Jurassic *Borealestes* (Waldman and Savage, 1972), *Simpsonodon* (Kermack *et al.* 1987), *Krusatodon* (Sigogneau-Russell, 2003), *Tashkumyrodon* (Martin and Averianov, 2004), *Itatodon* (Lopatin and Averianov, 2005), *Dsungarodon* (Pfretzschner *et al.* 2005), *Castorocauda* (Ji *et al.* 2006), *Hutegotherium* (Averianov, Lopatin, Krasnolutskii and Ivantsov, 2010), *Agilodocodon* (Meng *et al.* 2015), *Docofossor* (Luo *et al.* 2015) and *Dobunnodon* (Panciroli *et al.* 2021); the Late Jurassic *Haldanodon* (Kühne and Krusat, 1972), *Docodon* (Marsh, 1881), and *Tegotherium* (Tatarinov, 1994); and the Early Cretaceous *Sibirotherium* (Maschenko, Lopatin and Voronkevich, 2002). According to Luo and Martin (2007), the lower molars of docodontans are longer antero-posteriorly than linguo-labially, as in NHMD 1184958. The cusps are arranged in two anteroposterior 'rows' (although the cusps may be slightly offset): lingual and labial; the labial row has taller cusps aligned anteroposteriorly with the greatest cusp a (although cusp a is much closer to the middle of the tooth), while the lingual row has smaller cusps with a distinct anterior cusp g and a posterior cusp c.

The morphology of the cusps and crests in NHMD 1184958 most closely resembles *Delsatia* and *Dobunnodon*, particularly the lingual position of cusp a and well-defined cusp d. These taxa come from the Late Triassic (lower Rhaetian) of France and Middle Jurassic (Bathonian) of England, respectively, and are thought to sit at a more primitive position within the docodontan phylogeny (see 5.3). Geologically, *Delsatia* is older than NHMD 1184958 by approximately 7.2Ma (Sigogneau-Russel and Godefroit, 1997) and *Dobunnodon* is younger than NHMD 1184958 by approximately 33 Ma (Panciroli et al. 2021). During the Triassic to Jurassic, the regions where these three taxa were found were geographically relatively close, at times separated by the shallow Tethys Sea (PBDB - https://paleobiodb.org/)**.** At some point between the Late Triassic and Middle Jurassic, these landmasses might have been connected, allowing mammaliaforms to disperse (see 5.4).

According to Schultz *et al.* (2019), the extent of the Meckel's sulcus (which is located on the medial side of the dentary) varies through ontogeny in docodontans. Younger individuals have a prominent Melckel's sulcus in the symphyseal zone, while this sulcus retreats posteriorly along the dentary with the increasing of age. In NHMD 1184958, the symphysis ends ventral to the possible m1, and what is here interpreted as the anterior extent of the Meckel´s sulcus, terminates ventral to the possible m2 (Figure 22.A5). Comparing the positioning of the symphysis in relation to Meckel's sulcus in *Docodon* (Schultz *et al.* 2019: fig 4) with NHMD 1184958, it is possible to speculate that NHMD 1184958 may represent a late juvenile to sub-adult animal.

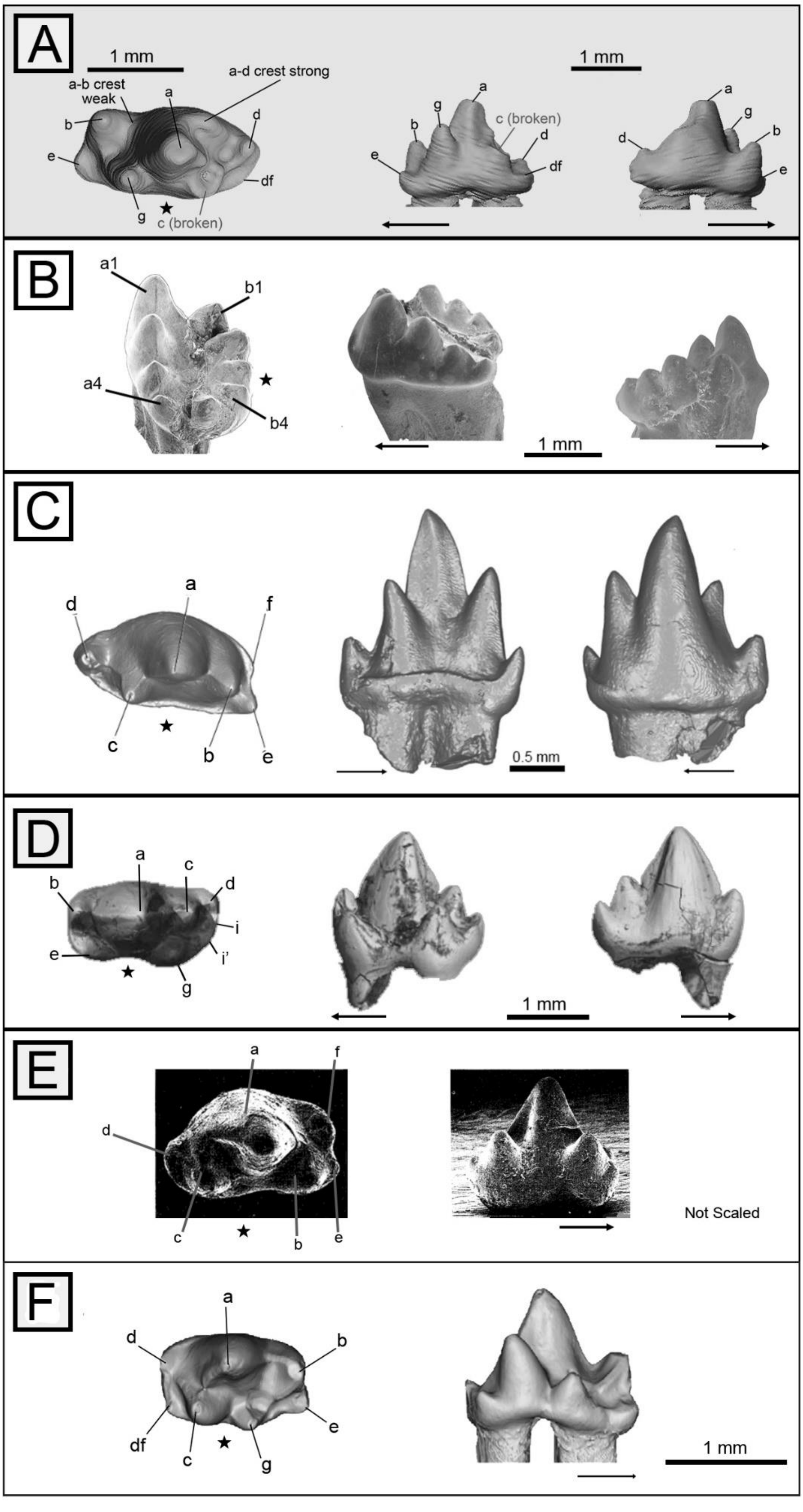

Figure 25. Comparison between NHMD 1184958 and diagnostic dental features of different groups of early mammaliaform. A, NHMD 1184958 possible m2? in occlusal, lingual and labial views; B, *Haramiyavia* lower m3 in a posterior occlusal, lingual and labial views (modified from Luo *et al.* 2015); C, *Kuehneotherium* lower m3 in occlusal, lingual and labial views (modified from Martin *et al.* 2020); D, *Brachyzostrodon coupatezi* Sigogneau-Russell, 1983 right lower molariform in occlusal, lingual and labial views (modified from Debuysschere *et al.* 2014); E, *Delsatia rhupotopi* Sigogneau-Russell and Godefroit, 1997 left lower molar in occlusal and lingual views (modified from Sigogneau-Russel and Godefroit, 1997); F, *Borealestes serendipitus* Waldman and Savage, 1972 right m2 in occlusal and lingual views (modified from Panciroli *et al.* 2020). The black stars represent the lingual side of the molar. The arrows point to the anterior side of the molar.

4.2. Alternative interpretations

Other interpretations of the dental morphology were considered when analyzing NHMD 1184958. They are listed below, with justifications for not having been followed.

Alternative Interpretation 1: This first approach, depicted in Figure 26B, is similar to the one subsequently adopted in this study (Figure 26A), which identified specimen NHMD 1184958 as a right dentary with preserved molar. However, it differs in the arrangement of molar cusps: cusp d and cusp df. In Alternative Interpretation 1 cusp d is interpreted as cusp df, and the a-d crest is interpreted as an incipient cusp d. (Figure 26B).

According to Nelson (2014), a cusp is characterized as a pyramidal elevation located on the occlusal surface of the teeth. There is no such visible elevation at this location on the tooth, nor does it appear that there would be an elevation in that location that had subsequently been worn away. The crest lacks the volume or width expected of a cusp. Altogether, this means it cannot be considered to be a cusp. This conclusion is supported both by the digital reconstruction from the micro CT data and by microscopy (Figure 17). Furthermore, no other early mammaliaform is known to have a cusp d located antero-labially to the main cusp in this position, which further supports the decision not to adopt this interpretation.

Alternative Interpretation 2: Another approach considered when studying NHMD 1184958, was that important characters for morphological characterization, such as Meckel's sulcus, might not be visible in the micro CT data. If what is interpreted as the posterior of mandibular symphysis was instead the anteriormost portion of the Meckel's sulcus, NHMD 1184958 would be identified as a lower left dentary, with the anteriormost part of the dentary being where the molar is located (Figure 26C). The preserved molar would then be mirrored, and the cusps would have different designations: cusp e would become the cusp df; the cusp c would become cusp g; and cusp d would be cusp b (Figure 26C). Occlusally, the size of the alveoli decreases in size along its length. The preserved molar, due to its large size, may correspond to a second (m2) or third molar (m3), so the preserved tooth positions may represent the sequence of molars m2, m3 and m4 if it was a right dentary, but would be m3, m4 and m5 if it was a left dentary. If it was a left dentary, analyzing the dentary in medial view it is possible to see a depression at the tip of the dentary (most posterior part), which would coincide with the position of the 4/5th molar (Figure 20.A5). Since Meckel's sulcus in different ontogenic states can be reabsorbed up to the position of the 4th molar, we would then interpret this individual as senescent. Additionally, if the specimen was a left dentary, then the molars would be progressively smaller towards the posterior of the tooth row, and the dentary would be slenderer (dorsoventrally shallower and mediolaterally narrower) towards the posterior portion of the tooth row – neither of these traits are commonly seen among mammaliaforms.

However, Alternative Interpretation 2 was not followed since the more posterior molars of docodonts exhibit a posterior curvature in the root apices, with molars m4 and m5 having the most pronounced curvature. And, in this specimen, there is no noticable curvature (Figure 20.A6). Also, the morphology of the region below the empty alveolus is more congruent with that of the posterior portion of the mandibular symphesis, as seen in other docodontans (see figure 3 in Panciroli *et al.* 2019).

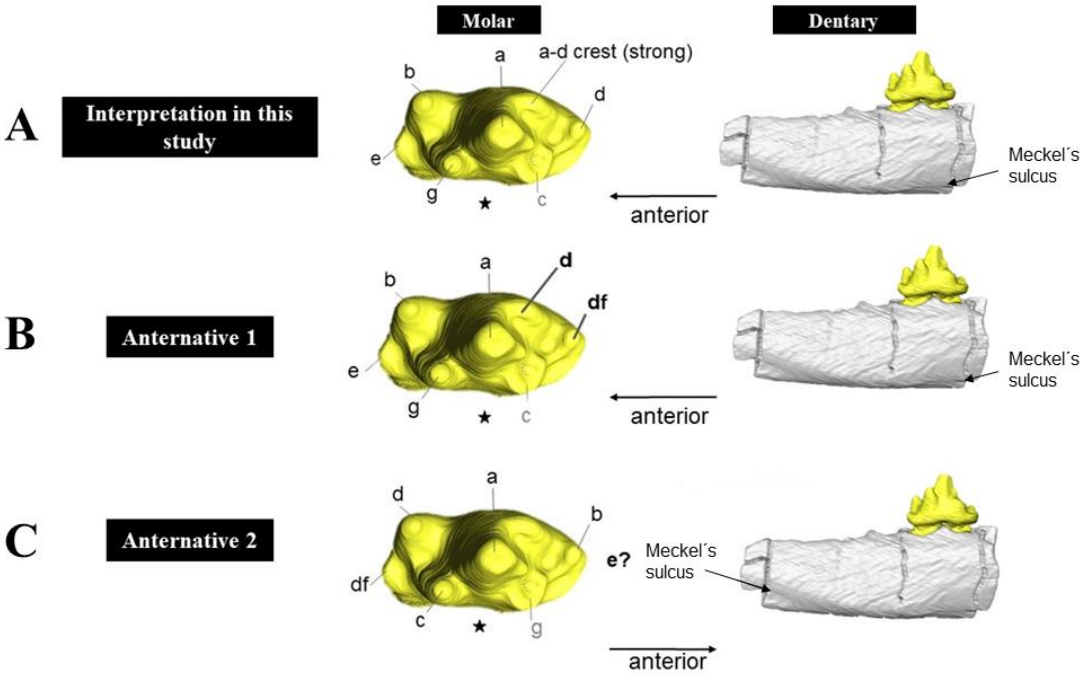

Figure 26. Dentary and molar morphology of specimen NHMD 1184958 interpretations considered for the thesis. A, the interpretation in this study, representing a right dentary; B, Alternative 1, as a right dentary with df cusp; C, Alternative 2, NHMD 1184958 as a left dentary and cusps reinterpretaed accordingly (The black stars correspond to the lingual side of the molar).

4.3. Phylogeny and erection of a new genus

Specimen NHMD 1184958 possesses a distinct set of characteristics that support the interpretation that specimen NHMD 1184958 belongs to the order Docodonta: the presence of an anterior pseudotalonid on the lower molar, formed by cusps a, b, and g; the presence of cusps b-a-c in a triangular arrangement; and the molar being elongated anteroposteriorly. The results of the phylogenetic analysis also support the suggestion that NHMD 1184958 – along with several other early mammaliforms - is a close sister taxon to Docodonta, or may represent a basal docodontan (Figure 23). The results not only place NHMD 1184958 at the base of the docodontan clade, but they do not put it in a sister relationship with any other docodontan, supporting the interpretation that it does not belong to an existing docodontan genus. Also, the results do not place it in a sister-taxon relationship with any of the other early mammaliaforms included in the phylogenetic analysis, not even *Delsatia*. In fact, the results place NHMD 1184958 on a huge unresolved polytomy that includes the basal mammaliaforms *Gondtherium, Tikitherium, Woutersia, Delsatia, Kuehneotherium, Hadrocodium, Dinnetherium, Megazostrodon, Morganucodon*. That might be attributed to the scarcity of mammaliaform fossils for analysis, and the limited set of characters available for analysis. For example, only 33 out of 57 characters could be scored for NHMD 1184958 (aprox. 58%), as it is known only from a single tooth and a fragmentary dentary (see Appendix X). Therefore, the scoring of 24 characters is still unknown, and the percentage of unassigned characters is 42% which is to be expected that it might have an effect on our results. The mandibular characters and upper molar characteristics are important for understanding the relationships between mammaliaforms and, in this case, many of the fossils found are recognized by a single tooth and/or very fragmentary material, not allowing a complete character scoring. If further material (mandibular and upper molar material) similar to NHMD 1184958 is discovered, it will be possible to do a fuller scoring of the characters, potentially altering the obtained results.

The position of NHMD 1184958 with these basal mammaliaforms taxa further supports our proposal that it is a separate genus. Furthermore, there is a huge temporal gap between NHMD 1184958 and the rest of the docodontans (at least 33 Ma). This led us to assume that the specimen is unlikely to belong to any docodontan genera, as genera do not usually persist for such huge time periods. Overall, we conclude that this taxon is separated from all the others at the genus level.

The results of the phylogenetic analysis are generally in agreement with the study of Zhou *et al.* (2019), but differ from the tree of Panciroli *et al.* (2021) in the placing of several taxa. These changes are likely the result of using a different software (TNT instead of PAUP), and some different character scores.

Authors in prior studies, such as Martin and Averianov (2001, 2004), have proposed the existence of two distinct radiations within Docodonta: Euroamerican docodontans (*Borealestes*, *Haldanodon*, *Docodon*, and *Simpsonodon*) and Euroasian docodontans (*Tashkumyrodon*, *Sibirotherium*, and *Tegotherium*). These have latterly been placed in several families, within Docodonta, including Tegotheriidae, Simpsonodontidae, and Docodontidae (see below) (Averianov and Lopatin, 2006; Averianov *et al.* 2010). However, the characteristics presented to separate these lineages appear unstable. For Martin and Averianov (2001, 2004), the separation of the two clades (Euroamerican and Euroasian docodontans) could be related to the formation of the Turgai Strait, which separated Europe and Asia at various times between the Bathonian and Oxfordian (Middle/Late Jurassic; Golonka *et al.* 1996). According to Martin and Averianov (2001, 2004), morphological features such as the well-developed cusp e, the presence of the b-e and e-g crests (not present in Euramerican docodontans found to date) and the reduction of the b-g crest are characteristic in Eurasian docodontans. They suggest Euroamerican docodontans are characterized by the reduction or loss of cusp e and strong reduction of b-e crest.

Results of the phylogenetic analysis including NHMD 1184958 do not support the erection of two clades within Docodonta. *Docofossor*, *Docodon* and *Haldanodon* were returned as belonging to a clade, originating from Asia, North America and Europe, respectively. The result is similar to Martin and Averianov (2001, 2004) regarding the *Docodon* and *Haldanodon* set, however, included in this clade is also *Docofossor*, an Asian and not a Euro-American docodontan. The other main clade comprises a mixture of taxa from the United Kingdom (e.g. *Borealestes*, *Simpsonodon*, *Krusatodon*) and Asia (e.g. *Agilodocodon*, *Castorocauda*, *Dsungarodon*, *Hutegotherium*, *Itatodon*, *Microdocodon*, *Sibirotherium*, *Simpsonodon*, *Tashkumyrodon*, *Tegotherium*). In Martin and Averianov (2001, 2004) *Tashkumyrodon*, *Tegotherium* and *Sibirotherium* form the clade of Asian docodontans, however in our results, the clade comprises a bigger number of taxa and with a wide geographic distribution, which includes not only Asian but also European docodontans. Furthermore, in our results, the bigger main clade has *Simpsonodon*, which in Martin and Averianov's would correspond to a Euroamerican docodontan instead. Therefore, since each clade has individuals with a high geographic distinction, in the present study we cannot support the existence of two main radiations of docodontans: Euroamerican docodontans and Euroasiatic docodontans.

Furthermore, the results obtained are not compatible with Martin and Averianov´s assessment of the morphological development of Docodonta lower molars (Figure 11). They suggested two main clades comprising (*Borealestes* + *Haldanodon* + *Docodon*) + *Simpsonodon* as one group, and (*Tashkumyrodon* + *Tegotherium* + *Sibirotherium*) as another (Martin and Averianov 2004: fig 4). They suggested that these groups each had independent molar evolution, and that *Borealestes* represented the ancestral molar morphology for the 'Euroamerican' group (Martin and Averianov 2004: fig 5). This proposal for the development of the lower molars of Docodonta is not compatible with the results obtained here, especially the resolved phylogenetic tree (Figure 23), particularly as the position of *Borealestes* is not found to be basal to that of *Haldanodon* or *Docodon*. *Borealestes* might still represent a basal docodontan, but not in the sequence implied by Martin and Averianov. The position of NHMD 1184958 however, supports the suggestion that it could be representative of the ancestral docodontan molar.

Compared with proposed Euroasian docodontans, the first two features - well-developed cusp and absence of the b-e crest - are similar to our specimen. The reduction of the b-g crest is not similar to NHMD 1184958, since in the specimen b-g crest is not reduced. On the other hand, not all the characters proposed for Euroamerican docodontans seem to be consistent with the fossil material, as our specimen has a distinct cusp e, contrary to the characteristics discussed above for Euroamerican docodontans.

The hypothesis regarding the existence of several families within Docodonta, including the Tegotheriidae, Simpsonodontidae, and Docodontidae (Averianov and Lopatin, 2006; Averianov *et al.* 2010) also appears unstable. According to Averianov and Lopatin (2006), a progressive development of docodonts may have been restricted to Asia, while Europe and North America were inhabited by relatively plesiomorphic taxa such as *Borealestes, Haldanodon,* and *Docodon*. The separation of docodontans into families is based on data obtained from phylogenetic analyses. Tegotheriid docodontans include *Krusatodon*, *Tegotherium*, *Sibirotherium* and *Hutegotherium*, characterized by a cusp Z on upper molariform teeth (except *Tegotherium*), crest A-X absent, cusp bb on the lower molariform teeth, a large pseudotalonid basin bordered by crests a-b, b-bb, bb-g, and a-g, and crest b-g absent. Docodontidae includes *Haldanodon*, *Docodon* and the stem docodontid *Borealestes*, characterized by cusp C reduced and twinned with cusp A, cusp b larger than cusp c, cusp b approximated to cusp a, and a wide anterolingual cingulid. Simpsonodontidae includes *Simpsonodon*, characterized by a large pseudotalonid basin bordered by crests a-b, a-g, and b-g, and absent cusp e, a wide anterolingual cingulid, crenulations on the posterior side of the lower molariform crowns, and a continuous additional groove above the Meckelian groove and separated from the more posterior trough for the postdentary bones (Averianov *et al.* 2010).

Concerning the hypothesis of docodontan families, a thorough re-evaluation of the characteristics proposed as defining each family is required (this is outwith the scope of this project). The results obtained in our phylogenetic analysis do not support the suggested docodontan families proposed by Averianov and Lopatin (2006) and Averianov *et al.* (2010) because the monophyly of these groups is also not shown in the obtained results.

There remains a scarcity of more complete skeletal material, and although the dentition and dentaries themselves are a great source of morphological information for mammaliaforms, with high complexity and variety across the different species, additional traits from the rest of the skeleton would assist with taxon separation and phylogenetic placing. Until recently, the oldest docodontan was the Middle Jurassic *Borealestes*. Specimen NHMD 1184958, coming from the Triassic-Jurassic border, and being phylogenetically placed near the base of Docodonta, may now represent the oldest known docodontan.

4.4. Paleogeographic implications and the origin of Docodonta

The discovery of NHMD 1184958 and its placement at the base of Docodonta has implications for our understanding of mammal evolution, as well as the paleogeographical context for the Kap Stewart Group. Docodontans from the Middle Jurassic have previously been recovered from China, Russia and the United Kingdom (e.g. Ji *et al.* 2006, Martin and Averianov, 2004, Panciroli *et al.* 2019, 2021; Lopatin and Averianov, 2005; Sigogneau-Russel, 2003; Meng *et al.* 2015). Specimen NHMD 1184958 will add Greenland to the list of docodonts, but significantly predates all previously known specimens (by 33 Ma), being from the Triassic-Jurassic boundary. The next docodontan specimens are from the Middle Jurassic (Bathonian) to Early Cretaceous (Aptian) (Luo and Martin, 2007), so their origin must have occurred earlier, which is consistent with this discovery from Greenland.

According to Martin and Averianov (2004), there should be a hypothetical stage for the origin of this very diverse order from the paraphyletic "Triconodonta". NHMD 1184958 has some morphological similarities with other early mammaliaforms from the Late Triassic, such as *Delsatia*. In the phylogenetic analysis obtained, NHMD 1184958 is also close to basal mammaliaforms such as *Gondtherium* and *Tikitherium*. Therefore, NHMD 1184958 may possess features representative of the ancestral or transitional stages between the earliest Late-Triassic to Early-Jurassic mammaliaforms, and Docodonta.

Geographically, the location of NHMD 1184958 supports Clemmensen *et al.* (1998) hypothesis of European faunal influence between eastern Greenland and Europe during the Late Triassic, which was later corroborated by other researchers (Sulej *et al.*, 2014; Marzola *et al.*, 2017). Both geographical locations share common faunas such as early mammaliaforms like *Brachyzostrodon* and *Kuehneotherium* (Sigogneau-Russell, 1983; Jenkins *et al.*, 1994), amphibians such as *Cyclotosaurus* and members corresponding to Batrachia (Jenkins *et al.*, 1994; Jésus *et al.*, 2022), and dinosaurs such as *Plateosaurus* (Jenkins *et al.*, 1994; Kent and Clemmensen, 2021; Beccari *et al.* 2022).

During the Triassic, the Earth´s landmasses were fused, forming the supercontinent Pangaea. The climates were warm and uniform, without the presence of polar heats. A broad arid belt extended over most of North and South America, Europe, and Africa (see Figure 1 in Benton, 2016), which may be an explanation for the divergence of faunal assemblages between Europe-Greenland and North America at the end of the Triassic. The absence of docodontans in the Southern Hemisphere /Gondwana (besides *Gondtherium*) might be related to the presence of the aforementioned arid climatic belt during the Triassic. This type of arid climate probably acted as a barrier for the dispersal of early mammaliaforms from northern to Southern latitudes, thereby promoting their diversification within regions situated north of the equatorial zone (e.g. Europe, Asia, North America). Furthermore, at the end of the Triassic, Pangaea began to split up (Benton, 2016), creating physical impediment, obstructing the southern ward passage of docodontans and, thereby, allowing their diversification predominantly in regions situated north of the equator.

The majority of docodontans have been discovered in localities north of the Equator (both presently, and in the geological past), except *Gondtherium* which was discovered in the Kota Formation in India (which was located south of the Equator in the Middle Jurassic) (Figure 27; Prasad and Manhas, 2007). *Gondtherium dattai* Prasad and Manhas, 2007 was a mammaliaform that lived between Middle Jurassic and Early Cretaceous (approximately 167.3-127.2 Ma). Was classified as a docodontan based on the tooth cusps from a single worn and fragmentary molar tooth (Prasad and Manhas, 2007). However, its classification has been disputed by several researchers (Kielan-Jaworowska *et al.* 2004), in part because of the lack of fossil material, and thus its exact identity is still unknown. If this genus represents a primitive member of Docodonta, it contradicts the idea that docodontans only diversified throughout Laurasia and were not able to disperse throughout the southern hemisphere. On the other hand, if this taxon might not be a docodontan, it’s position in the southern hemisphere supports the interpretation that it belongs to a different early mammaliaform group.

Docodont fossils are not currently known from Africa, South America or Australia. They have a wide Laurasian distribution, having been found in North America, Europe, the United Kingdom, and Asia, with a peak in diversification during the Middle/Late Jurassic. Their dispersal and evolution are currently unclear. The Greenland mammaliaform, NHMD 1184958, shares features with docodontans from the Middle Jurassic of Great Britain and with *Delsatia* from France (Figure 27). Greenland was positioned close to what is now Great Britain and France during the Late Triassic-Early Jurassic, making it possible for this group to disperse, and perhaps explaining the similarities between NHMD 1184958 and British docodontans and *Delsatia* (Figure 27).

Despite the small amount of material discovered, the newly described NHMD 1184958, provides novel information on the phylogeny of early mammaliaforms, and the evolution and distribution of mammaliaforms in the Late Triassic to Early Jurassic. Based on tooth morphology, we can imply it is a new genus, and its location in Greenland supports the proposal that docodontans have their origins in Europe-Greenland, and later dispersed across Laurasia. Future discoveries of cranial and post-cranial material would allow a more thorough examination, and provide critical characters to further clarify its phylogenetic placement and the early origins of the diverse docodontan clade.

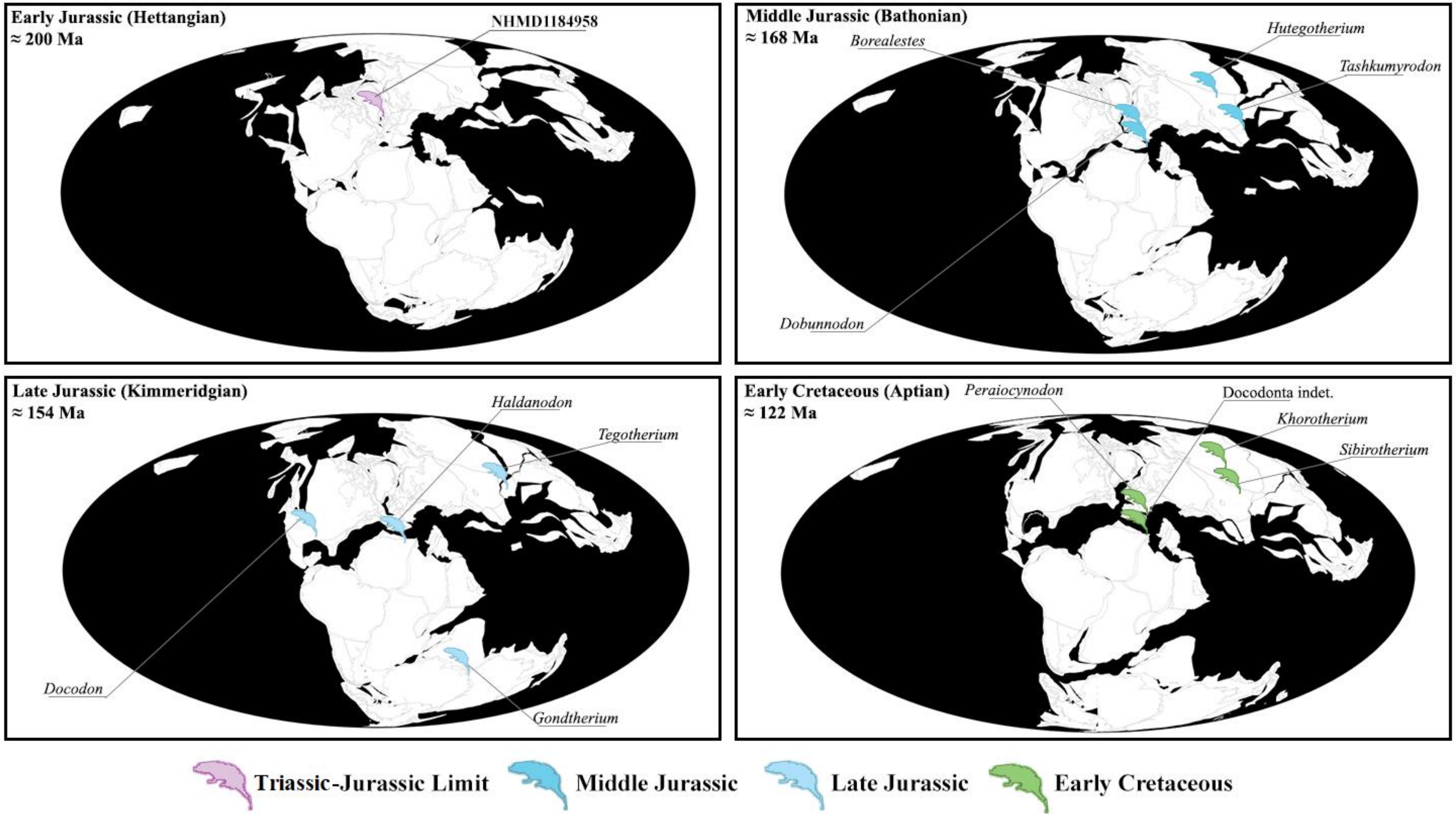

Figure 27. Early Jurassic to early Cretaceous paleogeography, with locations of Jurassic docodonts and the Greenland specimen. Mammal icons mark the location of each specimen; the purple color represents the Triassic/Jurassic limit specimen; dark blue the Middle Jurassic specimens; light blue the Late Jurassic specimens; green the Early Cretaceous specimens (Geochronological Map adapted from PaleoBiologyDataBase; Docodonta Icon adapted from PhyloPic; see Appendix XII for bibliography of the Docodonta ocurrences).

Figure 28. Illustration of NHMD 1184958 in life, found in Kap Stewart Group, Central East Greenland (by Pedro Andrade).

5. CONCLUSION

A new mammalian specimen, NHMD 1184958, is not only the first mammaliaform found in Kap Stewart Group in central East Greenland (Late Triassic – Early Jurassic), but is potentially the oldest known member of Docodonta – one of the most ecologically diverse early diverging mammaliaforms clades.

Although only comprising a partial dentary with a single preserved molar, it provides diagnostic features sufficient for the erection of a new genus and species and some are congruent with previous studies aiming to characterise the ‘ancestral’ molar of early docodontans. This provides a baseline for the emergence of their morphological complexity – the pseudotribosphenic molar – which is thought to have helped unlock their ecological complexity and led to their subsequent diversification in the Middle to Late Triassic.

The results obtained through phylogenetic analysis place NHMD 1184958 as a basal docodontan or close sister taxon, closer to Docodonta than other early mammaliaforms previously suggested to be basal docodontans, such as *Delsatia*, *Gondtherium* and *Tikitherium*. Some inconsistencies (polytomies) can be attributed to the scarcity of mammaliaform fossils for analysis.

This discovery sheds light on the origin and dispersal of the Docodonta, supporting that docodontans have their origins in Europe-Greenland, and later dispersed across Laurasia. NHMD 1184958, as a member of Docodonta and representing the oldest docodontan ever found, provides compelling evidence that the origin of the order may have occurred earlier, in the Late Triassic. Geographically, the location of NHMD 1184958 supports Clemmensen *et al.*'s (1998) hypothesis of European faunal influence between eastern Greenland and Europe during the Late Triassic. The Greenland mammaliaform shares features with docodontans from the Middle Jurassic of Great Britain, and with *Delsatia* from *France*. Furthermore, Greenland was positioned close to what is now Great Britain and France during the Late Triassic-Early Jurassic, making it possible for this group to disperse, and explaining the similarities between NHMD 1184958 and British docodontans and *Delsatia*.

Although the origin and dispersal of Docodonta remains uncertain, NHMD 1184958 adds a significant new datapoint to the story of their emergence. Further discoveries from Greenland may provide more evidence, and finally resolve the pattern of evolution for this compelling group of early mammaliaforms.

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7. APPENDIX

Appendix I - Possible semionotiform scale found in the sandstone sediment block of Rhaetelv Formation, Kap Stewart Group.

Appendix II - Hybodontiform tooth found in the sandstone sediment block of Rhaetelv Formation, Kap Stewart Group.

Appendix III - Systematic Character List for Docodontans.

Character matrix based in Zhou *et al.* (2019), which followed Meng *et al.* (2015), with modifications (see below). Character 58 was omitted in Zhou *et al.* (2019) original matrix, therefore it was not accounted for in this analysis.

Characters and Scores for NHMD 1184958

1. Shape of the angular region (character state revised from 11- Meng *et al.* 2015):
(0) Pointed mandibular angle (two sides of the angular process forming an angle of 90 degrees and smaller)
(1) Obtuse mandibular angle (two sides of the angular process forming an angle of greater than 90 degrees)
(2) Rounded angular region
(?) Unknown
NHMD 1184958 = ? (not preserved)

2. Angular process of the mandible with an efflected ventral crest:
(0) Absent
(1) Present
(?) Unknown
NHMD 1184958 = ? (not preserved)

3. Mandible angular region – receiving structure for ectotympanic:
(0) Medially facing concavity for ectotympanic
(1) Posteriorly facing groove for ectotympanic
(?) Unknown
NHMD 1184958 = ? (not preserved)

4. Meckel’s groove to ventral margin of mandible:
(0) Convergent to the ventral margin
(1) Parallel to ventral margin
(?) Unknown
NHMD 1184958 = ? (not preserved)
5. Replacement dental lamina (Crompton’s groove; visible along the lingual alveolar margin of last molars):
(0) Present
(1) Absent
(?) Unknown
NHMD 1184958 = ? (not preserved)

6. Transversely widening of upper molars:
(0) Present
(1) Absent
(?) Unknown
NHMD 1184958 = ? (not preserved)

7. Antero-lingual cusp X of upper molars:

(0) Absent
(1) Cusp X present with wear facets present on the labial side of the cusp
(?) Unknown
NHMD 1184958 = ? (not preserved)

8. Transverse antero-lingual and antero-labial crests between cusp A and cusp X on anterior molars:
(0) Absent
(1) Present and complete
(?) Unknown
NHMD 1184958 = ? (not preserved)

9. Transverse antero-lingual and antero-labial crests between cusp A and cusp X on posterior molars:
(0) Absent
(1) Present and complete
(?) Unknown
NHMD 1184958 = ? (not preserved)

10. Cusp Y (=upper postero-lingual cusp):
(0) Absent or indistinctive
(1) Present as a distinctive cusp
(2) Present, as crest aligned in antero-posterior line
(?) Not preserved
NHMD 1184958 = ? (not preserved)

11. Size and development of cusp C (postero-labial cusp) and its separation from cusp A (antero-lingual cusp):
(0) Cusp C present and enlarged
(1) Reduced cusp C twinned with cusp A
(?) Not preserved
NHMD 1184958 = ? (not preserved)

12. Posterior transverse crest extending from the postero-labial cusp (C) to the posterior cingulum:
(0) Absent
(1) Present
(?) Unknown
NHMD 1184958 = ? (not preserved)

13. Presence of cusp E separated from cusp B on posterior upper molars:
(0) Present
(1) Cusp E present and in labiolingual alignment with cusp B
(2) Absent
(?) Unknown
NHMD 1184958 = ? (not preserved)

14. Constricted waist between the labial part and the lingual part of upper molars:
(0) Absent

(1) Present
(?) Unknown
NHMD 1184958 = ? (not preserved)

Lower Molar Characteristics
15. Cusp c on lingual cingulid and in alignment with antero-lingual cusp g (antero-lingual):
(0) Absent
(1) Present
(?) Unknown or Not Applicable
NHMD 1184958 = 1

16. The a-c v-notch crest (postero-main crest of Sigogneau-Russell, 2003):
(0) Absent
(1) Present
(?) Unknown
NHMD 1184958 = 0

17. Presence vs. absence and size of cusp g (antero-lingual) (lower molars in occlusal and lingual views):
(0) Absent
(1) Small
(2) Distinctive, opposite to primary cusp a
(3) Distinctive, anteriorly positioned
(4) Anteriorly placed and hypertrophied (to the same size as or larger than cusp c)
(?) Not preserved
NHMD 1184958 = 3

18. Cusp c to cusp g size ratio (lower molars in lingual view):
(0) Cusp c much larger than cingular cusp g
(1) Sub-equal to the anterolingual cusp g
(?) Unknown or Not Applicable
NHMD 1184958 = 1

19. Development of pseudotalonid:
(0) Absent
(1) Present and its anterior-border by b-g crest
(2) Present and its anterior-border by b-e crest
(3) Present but cusp b is much taller than g so the pseudotalonid appears to be lingually open
(?) Unknown
NHMD 1184958 = 1

20. Raised a-g crest:
(0) Absent
(1) Present or lower

(2) Raised, with v-notch
(?) Not preserved
NHMD 1184958 = 2

21. Crest b-g:
(0) Absent, or weakly developed
(1) Present
(?) Unknown or Not Applicable
NHMD 1184958 = 1

22. The c-d crest in the posterior basin – presence/absence and alignment:
(0) Absent
(1) Present, c-d crest or c-f-d crests straight
(2) Present, c-d crest angled
(?) Unknown or Not Applicable
NHMD 1184958 = 1

23. Crest extending from cusp c to cusp df or the cusp df position (lower molars in occlusal view):
(0) Absent
(1) Present
(?) Unknown or Not Applicable
NHMD 1184958 = 0

24. Placement of cusp d (modified from Sigogneau-Russell 2003: character 7; Luo and Martin 2007 Character 16; assuming homology of the morganucodontan cusp d to docodontan cusp d) (lower molar in occlusal view):
(0) Labial position (in alignment with a-b crest, or nearly so)
(1) Median placement (nearly halfway along the transverse width of posterior crown)
(?) Unknown or Not Applicable
NHMD 1184958 = 0

25. Posterior Cusp d-f (=cusp dd of Hu *et al.* 2007) (lower molars in occlusal view):
(0) Absent
(1) Present
(?) Unknown or Not Applicable
NHMD 1184958 = 1

26. Folding enamel (on either upper or lower) (Sigogneau-Russell, 2003: character 5; Luo and Martin 2007 Character 17, scored on the posterior face of lower cusp a or lingual face of upper cusps A-C):
(0) Absent or weakly developed
(1) Present
NHMD 1184958 = 0

27. Connecting structure of cusps a and d (modified from Luo and Martin 2007 character 19; Hu *et al.* 2007, Character 14):
(0) Not connected
(1) Incomplete

(2) Connected by a crest with a v-notch
(?) Unknown or Not Applicable
NHMD 1184958 = 1

28. Alignment of posterior crest of cusp a toward cusp d (postero-main crest of Sigogneau-Russell 2003; as defined in Luo and Martin 2007 character 18) (lower molars in occlusal view):
(0) Present and straight
(1) Present and angled
(?) Unknown or Not Applicable
NHMD 1184958 = 1

29. The b-g crest: Crest between the antero-labial cusp and antero-lingual cusps:
(0) Absent
(1) Present, as a v-shaped valley
(2) Present and continuous
(?) Not preserved or Not Applicable
NHMD 1184958 = 1

30. Size of cusp e:
(0) Present and distinctive
(1) Reduced
(?) Not preserved or Not Applicable
NHMD 1184958 = 0

31. Anterolingual cingulid (width would be related with presence/absence of cusp e) (lower molars in occlusal view):
(0) Narrow or absent
(1) Wide
(?) Not preserved or Not Applicable
NHMD 1184958 = 1

32. Antero-lingual line-like cingulid extending from cuspule e or an equivalent position:
(0) Connected to cusp g
(1) Extending posteriorly to below the cusp g
(2) Absent or limited to the anterior part of the tooth
(?) Not preserved or Not Applicable
NHMD 1184958 = 2

33. Size ratio of cusp b and cusp a:
(0) Large, well separated by a notch from cusp a
(1) Small, approximated to cusp a
(?) Not preserved or Not Applicable
NHMD 1184958 = 0

34. Cusp b position:
(0) Close to cusp a (cusp b is close to cusp a)
(1) Well-separated from cusp a by a deep notch
(?) Not preserved or Not Applicable

NHMD 1184958 = 1

35. The “docodont cusp f” (Postero-lingually positioned as defined by Martin and Averianov 2004: figs 3 and 5, and differing from antero-labially positioned cusp f; Luo and Martin 2007 character 24):
(0) Absent
(1) Present
(2) Present and crest-like
(?) Not preserved or Not Applicable
NHMD 1184958 = 1

36. The “standard cuspule f” (antero-labially positioned, as defined by Kielan- Jaworowska *et al.* 2004: fig. 5.9: ‘anterolabial cusp’):
(0) Absent
(1) Present
(?) Not preserved or Not Applicable
NHMD 1184958 = 0

37. The b-e crest:
(0) Absent
(1) Present and continuous from cusp b to the cingulid
(2) Present, as a part of the pseudotalonid rim
NHMD 1184958 = 0

38. Anterior basin:
(0) No basin
(1) Small concavity
(2) Pseudotalonid basin
(?) Unknown
NHMD 1184958 = 1

39. Posterior basin:
(0) Absent
(1) Present
(?) Unknown
NHMD 1184958 = 1

40. Width ratio of anterior basin vs. Posterior basin (modified from Hu *et al.* 2007 character 21, measured at the level of cusps/crests on occlusal surface):
(0) Posterior basin narrower than anterior basin
(1) Posterior basin wider than anterior basin
(?) Not applicable
NHMD 1184958 = 0

41. Interlock of lower molars:
(0) No interlock
(1) d-b-e interlock
(2) d – ‘standard-‘f’-e interlock

(3) d-e overlap
(4) d-b overlap
(?) Not preserved
NHMD 1184958 = 2

42. Placement of lower cusp e:
(0) Lingual position (lingual to the median axis of the lower molar)
(1) Cusp e labially shifted
(?) Unknown
NHMD 1184958 = 0

43. Cusp triangulation (cusp triangulation between the a-c crest and the a-b crest following Butler 1997; Sigogneau-Russell and Godefroite 1997; Luo and Martin 2007 character 28):
(0) Absent
(1) Present
(?) Unknown
NHMD 1184958 = 1

44. Degree of triangulation of cusps g-a-c:
(0) Broad triangle (>80 degrees)
(1) Sharp-triangled (≤80 degrees)
(?) Unknown or Not Applicable
NHMD 1184958 = 0

45. Gibbousness of crown base overhanging the roots at crown-root junction (scored at the middle molar[s] if multiple molars are known):
(0) Absent
(1) Present
(?) Unknown
NHMD 1184958 = 1

46. Number of upper molariform roots:
(0) Two
(1) Three
(?) Unknown
NHMD 1184958 = ? (not preserved)

47. Number of lower canine roots:
(0) One
(1) Two
(?) Unknown
NHMD 1184958 = ? (not preserved)

48. Lower canine size:
(0) Lower canine trenchant, and taller (>125% in crown height) than adjacent incisors, and the first premolar (if present)
(1) Lower canine forming a gradient with incisors and premolars, not taller than adjacent teeth
(?) Unknown

NHMD 1184958 = ? (not preserved)

49. Count of premolar or premolar positions:
(0) 3 premolars or fewer
(1) 4 premolars
(2) 5 premolars
(3) 6 premolars or premolar positions
(?) Unknown
NHMD 1184958 = ? (not preserved)

50. Two roots of ultimate lower molar:
(0) Fully divided roots
(1) Roots become confluent or single-rooted
(?) Unknown
NHMD 1184958 = ? (not preserved)

51. Protuberance on the medial ridge over postdentary trough:
(0) Absent
(1) Present
(?) Unknown
NHMD 1184958 = ? (not preserved)

52. Depth of anterior mandible (as measured in the canine region):
(0) Deep (mandibular depth/height near canine-p1 region ≥ 80% of mandibular depth under m1)
(1) Shallow (mandibular depth/height near canine-p1 region ≥ 75% of mandibular depth under m1)
(?) Unknown
NHMD 1184958 = ? (not preserved)

53. Strong prestylar lobe in cusp B or cusps E-B region:
(0) Absent
(1) Present
(?) Unknown
NHMD 1184958 = ? (not preserved)

54. Upper molar pre-stylar groove (bound by cusp A, E and anterior cingulum):
(0) Absent
(1) Present
(?) Unknown
NHMD 1184958 = ? (not preserved)

55. Cusp ee (= cusp “e” of Averianov *et al.* 2010):
(0) Absent
(1) Present
(?) Unknown
NHMD 1184958 = 0

56. Profile of lower premolars (in either lateral or medial view):
(0) Trenchant (cusp a height from cingulid ≥ premolar length)

(1) Lower profile (cusp a height from cingulid lower than premolar length)
(?) Unknown
NHMD 1184958 = ? (not preserved)

57. Cusp a profile and orientation:
(0) Erect
(1) Recurved
(?) Unknown
NHMD 1184958 = 0

Appendix IV - Cross-referencing and re-interpretation of characters in taxa from the matrix by Zhou *et al.* (2019).

All characters attributed were analyzed again, and those that presented inconsistencies were re-scored based on the available literature.

Borealestes

The re-scoring for *Borealestes* have been modified according with Panciroli *et al.* (2021), previously based on Panciroli *et al.* (2019).

1. Angular region is 90 degrees or smaller (?) modified to (0)

2. Angular process on mandible with effected ventral crest present, (?) modified to (1)

3. Posteriorly facing groove for ectotympanic, (?) modified to (1)

4. Meckel’s groove convergent with ventral margin, (?) modified to (0)

5. No replacement dental lamina, (?) modified to (1)

18. Cusp c to cusp g size ratio: → (1) modified to (0)

20. Raised a-g crest: → (2) modified to (0)

21. Crest b-g: → (0) modified to (1)

22. The c-d crest in the posterior basin – presence/absence and alignment: → (2) modified to (1)
27. Connecting structure of cusps a and d: → (2) modified to (1)

32. Antero-lingual line-like cingulid extending from cuspule e or an equivalent position: → (1) modified to (2)

38. The anterior basin is a pseudotalonid as much as the other taxa scored for this character, (1) modified to (2)

48. Lower canine is taller than adjacent teeth, (?) modified to (1)

49. There are 5 premolars, (?) to (2)

51. There is a protruberance, (?) to (1)

52. The mandible depth below c-p1 is less than 80% of the depth at m1, (?) to (1)

53. There is a strong prestylar lobe in the upper teeth, (?) to (1) (seen in *B. cuillinensis* Panciroli *et al.* 2021: fig 5B1)

54. There is a pre-stylar groove, (?) to (1)

Haldanodon

44. Degree of triangulation of cusps g-a-c: → (2) modified to (1) (based on article by Martin and Schultz (2023); figure 10.a, left lower molars (m1 and m2) in occlusal view)

Docodon

44. Degree of triangulation of cusps g-a-c: → (2) modified to (1) (based on article by Schultz *et al.* (2019); figure 11h, right lower m3-4 in occlusal view)

Docofossor

44. Degree of triangulation of cusps g-a-c: → (2) modified to (?) (based on article by Luo *et al.* (2015); figure 2, lower right teeth in occlusal view. It has some identical characteristics to the genera *Haldanodon* and *Docodon*, however, the data presented in the available literature are not sufficient to make inferences about this character)

Appendix V - Final data matrix used on the Phylogenetic Analysis.

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xread

57 26

Sinoconodon 00010000000000?00?0????0000??0020000000?00000000000000000

Morganucodon 0000000000000000100000??0000?00000000000?10000000100000000

Megazostrodon 2000000000000000100000??0000?00000001000?20000000200000000

Dinnetherium 2000000000000000100000??0000?00000000000?10000000100000000

Hadrocodium 00001000000000000?0????0000??00?00000000000?0010010100000

Kuehneotherium20000000000000?00?0????0000??0020001000?20100000310100000

Delsatia ??????????????1021000??0000?00000001000?20100???????00???

Woutersia ?????100?010101021000??0000?00000001000?201000??????00???

Tikitherium ?????110?00020???????????0???????????????????1??????00???

Gondtherium ?????110?00020???????????0???????????????????????????????

Tashkumyrodon??????????????103?2211101020?0110110121111111?????????0??

Castorocauda 111?1?????????1041221010102011020100121010111?1020?0??001

Microdocodon 110111111101111041221011002000010120221031111 1?1301111110

Tegotherium ???11111110111104122101110200001012022103111111????????1??

Hutegotherium ???11111110111104122101110200001012022103111111???0??111??
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Sibirotherium   ???111111101111031221011102000010110221031111111?????110??
Dsungarodon     1????11111012110411210011010211101001210111111 1???1???011
Borealestes     011011111101211030101100101011121110121031111111201111010
Haldanodon      111111111211211031311100111021111110111140110110111000000
Docodon         111111111211211131311110111021021110111140110110101010000
Itatodon        ???11?????????10412201?0102011010110121030111?1???????010
Krusatodon      ?????11?0101111041221211102110010110121030111 1??????100??
Simpsonodon     ????11111101101041221210112011010110121030111 1???0??00?10
Agilodocodon    111111110101111041221211112110010110121030111111301111010
Docofossor      1111111112112111313111001010211 21110?111401?0110111010000
NHMD1184958??????????????1031121100101110120110011020101?????????0?0
;
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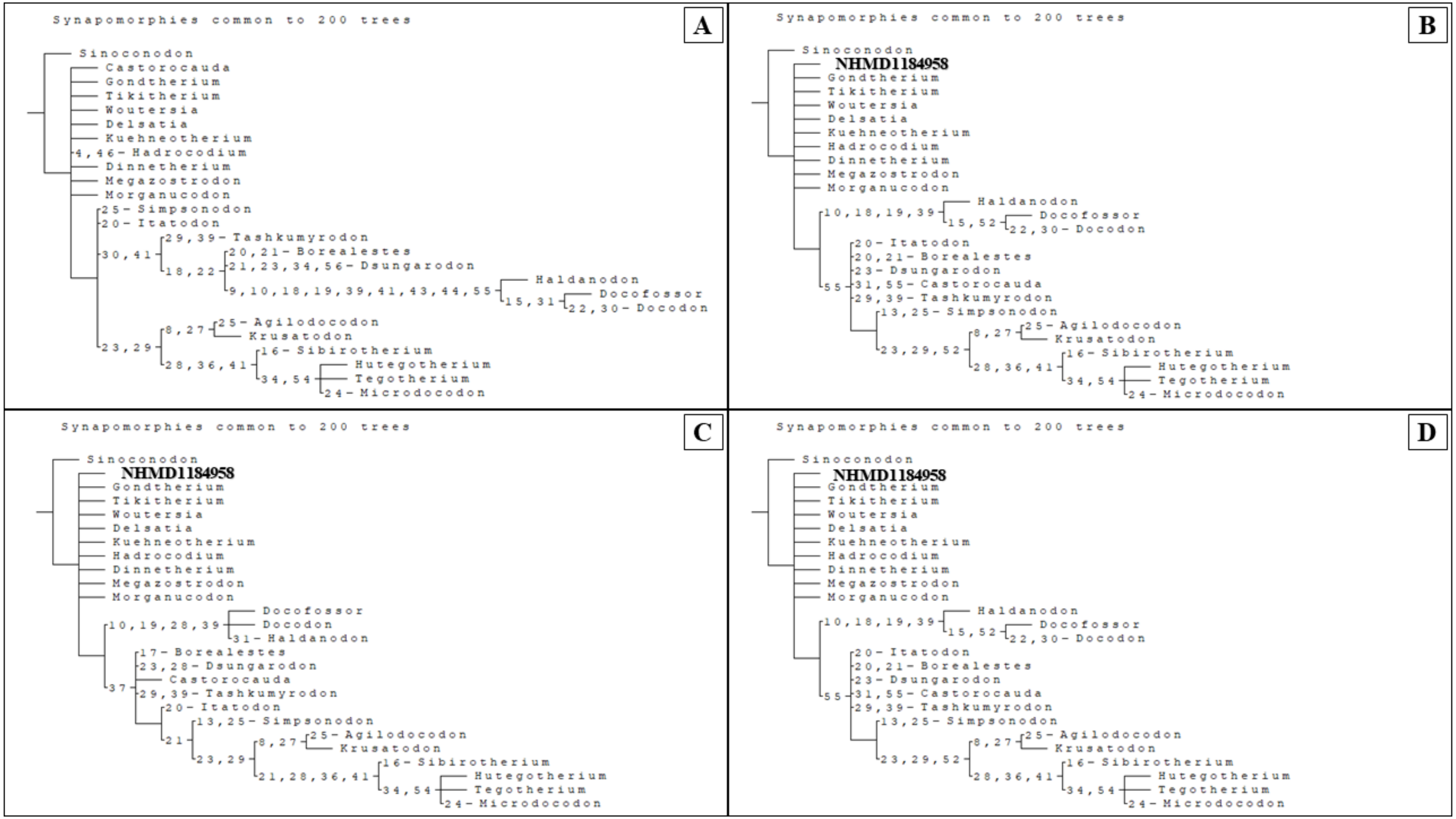
Appendix VI – Common Synapomorphies of (A) Zhou *et al.*’s (2019) original matrix; (B) Zhou *et al.*’s original matrix with NHMD 1184958 added; (C) Zhou *et al.*’s matrix with NHMD 1184958 added, but amending character scores (see Appendix IV); and (D) Zhou *et al.*’s matrix with NHMD 1184958 and amended scores, but using different parameters.



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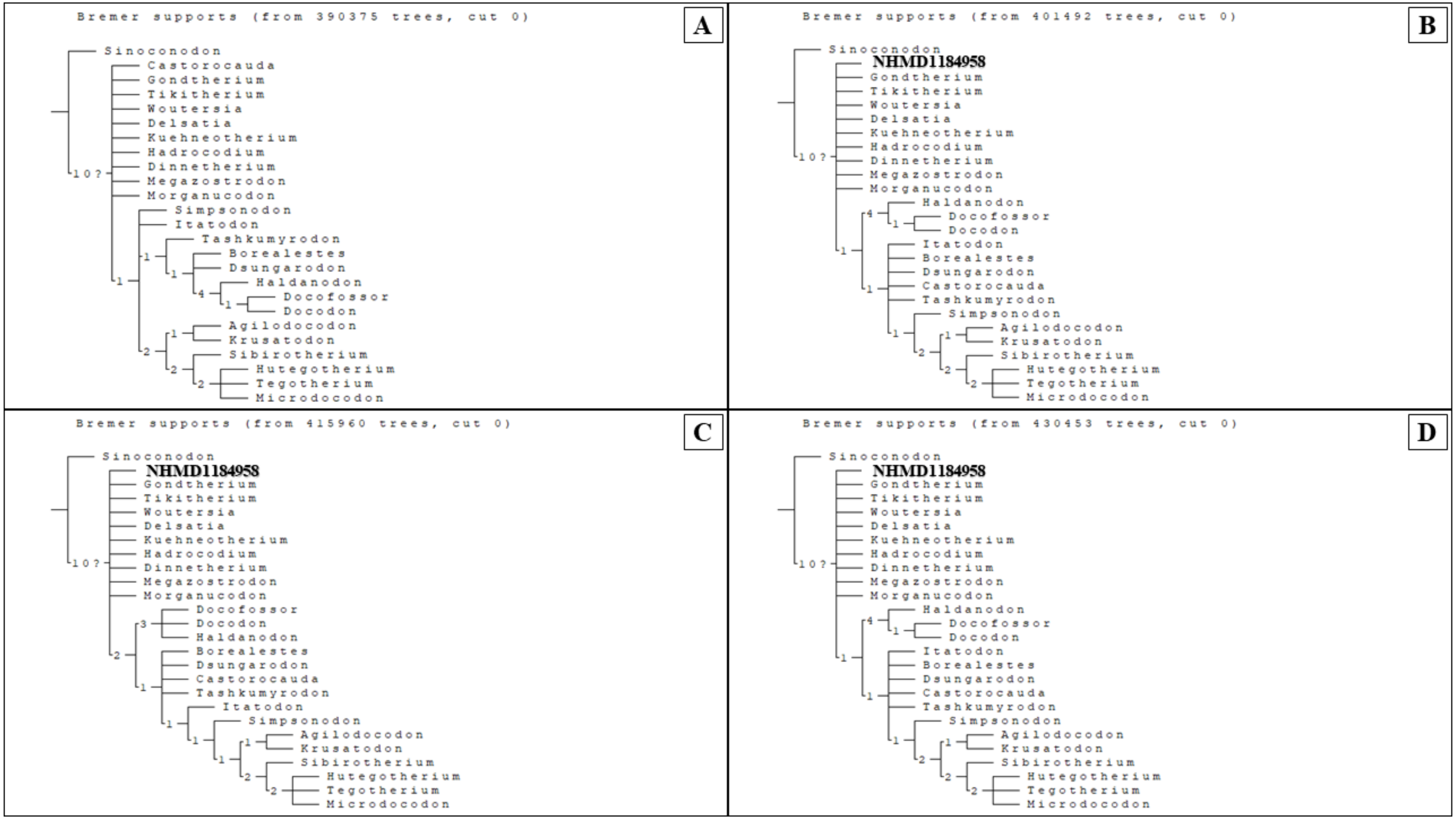
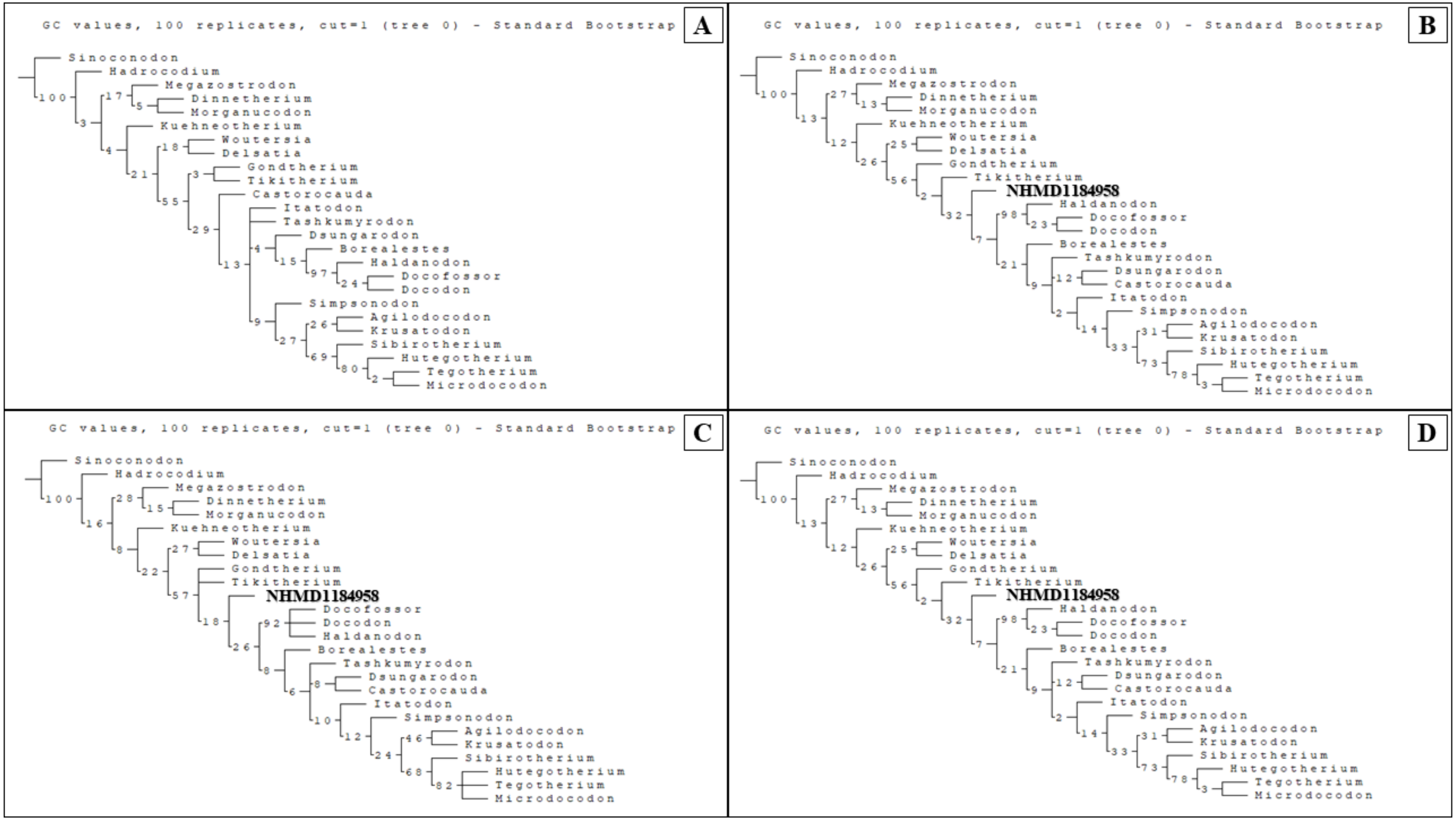
Appendix VII – Bremer Supports trees of (A) Zhou *et al.*’s (2019) original matrix; (B) Zhou *et al.*’s original matrix with NHMD 1184958 added; (C) Zhou *et al.*’s matrix with NHMD 1184958 added, but amending character scores (see Appendix IV); and (D) Zhou *et al.*’s matrix with NHMD 1184958 and amended scores, but using different parameters.



Appendix VIII –Standard Bootstrap trees of (A) Zhou *et al.*’s (2019) original matrix; (B) Zhou *et al.*’s original matrix with NHMD 1184958 added; (C) Zhou *et al.*’s matrix with NHMD 1184958 added, but amending character scores (see Appendix IV); and (D) Zhou *et al.*’s matrix with NHMD 1184958 and amended scores, but using different parameters.



Appendix IX - Matrix of first and last chronological appearances of mammaliaform taxa - R (FAD: First appearance datum; LAD: Last appearance datum).

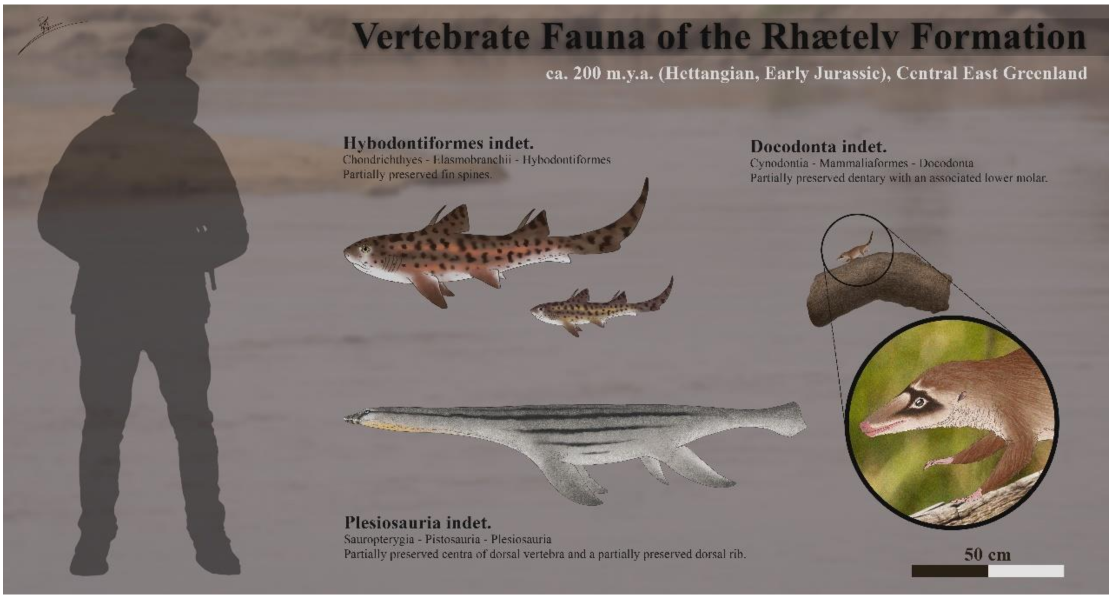
Taxa	**FAD**	**LAD**
Sinoconodon	205.6	189.6
Morganucodon	201.6	164.7
Megazostrodon	201.6	189.6
Dinnetherium	196.5	183
Hadrocodium	199.3	190.8
Kuehneotherium	201.6	189.6
Delsatia	208.5	201.3
Woutersia	205.6	201.6
Tikitherium	235	221.5
Gondtherium	183	171.6
Tashkumyrodon	164.7	161.2
Castorocauda	166	148
Microdocodon	161.5	145
Tegotherium	161.2	130
Hutegotherium	167.7	164.7
Sibirotherium	130	112.6
Dsungarodon	157.3	136.5
Borealestes	167.7	166.1
Haldanodon	155.7	150.8
Docodon	150.8	145.5
Itatodon	167.7	164.7
Krusatodon	167.7	145.5
Simpsonodon	164.7	161.2
Agilodocodon	166	148
Docofossor	166	148
NHMD1184958	201.3	199.3

Appendix X – Comparison between percentage (%) of characters scored by taxon.

Taxa	**% Characters scored**
Gondtherium	16%
Tikitherium	21%
Delsatia	51%
Tashkumyrodon	53%
NHMD1184958	58%
Itatodon	63%
Woutersia	67%
Tegotherium	72%
Castorocauda	75%
Krusatodon	75%
Hutegotherium	83%
Sibirotherium	83%
Dsungarodon	83%
Simpsonodon	83%
Sinoconodon	84%

Hadrocodium	84%
Kuehneotherium	84%
Morganucodon	93%
Megazostrodon	93%
Dinnetherium	93%
Docofossor	97%
Microdocodon	98%
Borealestes	100%
Haldanodon	100%
Docodon	100%
Agilodocodon	100%

Appendix XI - Illustration of vertebrate fauna found in the Rhaetelv Formation, Central East Greenland (by Pedro Andrade).



Appendix XII – Bibliography of the Docodonta occurrences used in Figure 27: “Early Jurassic to early Cretaceous paleogeography, with locations of Jurassic docodonts and the Greenland specimen”.

Taxa	**Reference**
Borealestes	Waldman, M., & Savage, R. J. G. (1972). The first Jurassic mammal from Scotland. *Journal of the Geological Society*, *128*(2), 119-125.
Dobunnodon	Panciroli, E., Benson, R. B., Fernandez, V., Butler, R. J., Fraser, N. C., Luo, Z. X., & Walsh, S. (2021). New species of mammaliaform and the cranium of Borealestes (Mammaliformes: Docodonta) from the Middle Jurassic of the British Isles. *Zoological Journal of the Linnean Society*, *192*(4), 1323-1362.
Hutegotherium	Averianov, A. O., Lopatin, A. V., Krasnolutskii, S. A., & Ivantsov, S. V. (2010). New docodontans from the Middle Jurassic of Siberia and reanalysis of Docodonta interrelationships. *Proceedings of the Zoological Institute of the Russian Academy of Sciences*, *314*(2), 121-48.

Tashkumyrodon	Martin, T., & Averianov, A. O. (2004). A new docodont (Mammalia) from the Middle Jurassic of Kyrgyzstan, central Asia. *Journal of Vertebrate Paleontology*, *24*(1), 195-201.
Haldanodon	Kühne, W. G., & Krusat, G. (1972). Legalisierung des Taxon Haldanodon (Mammalia, Docodonta). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, *1972*, 300-302.
Docodon	Marsh, O. C. (1881). Notice of new Jurassic mammals. *American Journal of Science*, *3*(126), 511-513.
Tegotherium	Tatarinov, L. P. (1994). On an unusual mammalian tooth from the Mongolian Jurassic. *Paleontologicheskii Zhurnal*, (2), 97-105.
Gondtherium	Prasad, G. V. R., & Manhas, B. K. (2007). A new docodont mammal from the Jurassic Kota Formation of India. *Palaeontologia Electronica*, *10*(2), 1-11.
Peraiocynodon	Damon, R. (1884). *Geology of Weymouth, Portland, and coast of Dorsetshire, from Swanage to Bridport-on-the-sea: with natural history and archæological notes*. RF Damon.
Docodonta indet.	Ruiz-Omeñaca, J. I., Canudo, J. I., & Cuenca-Bescós, G. (1996). Dientes de dinosaurios ornitópodos en el Barremiense superior de Castellote y Mas de las Matas (Teruel). *125 Aniversario-XII Bienal de la Real Sociedad Española de Historia Natural. Tomo extraordinario*, 315-319.
Khorotherium	Tolmachof, I. P. (1904). Neue Funde zur Geologie Sibiriens [New discoveries about the geology of Siberia]. *Centralblatt für Mineralogie, Geologie und Paläontologie*, 1904(1):233-234
Sibirotherium	Maschenko, E. N., Lopatin, A. V., & Voronkevich, A. V. (2002). A new genus of the tegotheriid docodonts (Docodonta, Tegotheriidae) from the Early Cretaceous of West Siberia. *Russian Journal of Theriology*, *1*(2), 75-81.