

New partial dentaries of amphitheriid mammal *Palaeoxonodon ooliticus* from Scotland, and posterior dentary morphology in early cladotherians

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We describe two partial dentaries of mammals from the Middle Jurassic of Scotland. They belong to the early cladotherian *Palaeoxonodon ooliticus*. These dentaries comprise the first specimen of *P. ooliticus* ever found—although its significance was initially unrecognised so it remained undescribed until now—and the most recently discovered specimen, found during fieldwork in 2017. The new specimen preserves part of the coronoid process of the dentary, previously unknown for *P. ooliticus*, demonstrating the presence of a deep masseteric fossa, with a prominent crest enclosing the fossa anteriorly, and a masseteric foramen, located in the masseteric fossa on the buccal surface of the dentary. On the lingual surface, the mandibular foramen is offset from the Meckel's sulcus, and positioned below the alveolar plane. These morphologies allow an updated analysis of the phylogenetic position of *P. ooliticus*, confirming a sister-taxa relationship between *Palaeoxonodon* and *Amphitherium*. The position of the mandibular foramen, and the slight extension of the masseteric fossa into the body of the dentary are new autapomorphies for *Palaeoxonodon*.

Key words: Mammalia, Cladotheria, *Palaeoxonodon ooliticus*, Jurassic, Bathonian, Kilmaluag Formation, UK, Scotland.

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Introduction

The Middle Jurassic was a key period in the evolutionary history of mammals. Recent research suggests a global radiation of early mammals beginning in the Early Jurassic, and entailing large increases in diversity and phenotypic disparity (Luo 2007; Close et al. 2016). This gave rise to docodontans, shuotheriids, australosphenidans, multituberculates, and cladotherians in the Early to Middle Jurassic (Luo et al. 2002; Kielan-Jaworowska et al. 2004). Continued fossil discoveries are critical to understanding this radiation. Furthermore, Cladotheria includes Theria, the clade comprising living marsupials and placentals and their stem lineages. Therefore, early cladotherian fossils provide information on the ancestral morphologies of the group, from which the more derived structures of extant therians evolved.

The early cladotherian *Palaeoxonodon* was originally reported based on isolated teeth from the Middle Jurassic of England (Freeman 1976a, b, 1979; Sigogneau-Russell 2003), and its detailed phylogenetic affinities remained uncertain. An almost complete dentary from the Isle of Skye, Scotland (NMS G. 2015.17.1), described by Close et al. (2016), revealed that the lower tooth row of *Palaeoxonodon* shows a gradient of variation in several dental characters that were used to delimit species in previous taxonomy. Based on these new observations, a previously erected *Palaeoxonodon* species, *Palaeoxonodon freemani*, and the genus *Kennetheridium* (Sigogneau-Russell 2003), were both synonymised with the type species of *Palaeoxonodon*, *Palaeoxonodon ooliticus*. This dentary also provided additional characters for a more informative phylogenetic analysis, supporting previous work that suggested *Palaeoxonodon* is the sister taxon to

Amphitherium (Close et al. 2016; but see also Averianov et al. 2015 for an alternative hypothesis).

Here, we report two further specimens of *Palaeoxonodon* from the Isle of Skye. A newly discovered specimen, NMS G.2017.37.1, was found during fieldwork in 2017. Although it is not as complete as that found by Close et al. (2016), it preserves the base of the coronoid process and adjacent regions of the dentary. These features were missing from previous specimens and allow additional characters to be scored for phylogenetic analysis. Another specimen, NMS G.1992.47.123, was recovered during fieldwork by Michael Waldman and Robert J.G. Savage in 1973. It had previously been mentioned as an undescribed pantotherian by Clemens (1986) and Evans et al. (2006). The discovery of this specimen pre-dates all other known specimens of *Palaeoxonodon*, including the holotype of *P. ooliticus* (Freeman 1976a). However, for reasons unknown, it was never described. After being transferred posthumously from the late RJG Savage of the University of Bristol to the National Museum of Scotland, it was rediscovered by EP in the collections at NMS in 2016.

Institutional abbreviations.—NHMUK PV, Natural History Museum, London, UK; NMS, National Museums Scotland, Edinburgh, UK.

Other abbreviations.—MPTs, most parsimonious trees; TBR, tree bisection and re-connection.

Material and methods

The two specimens described here are both in the collections at the NMS: NMS G.1992.47.123 and NMS G.2017.37.1. Both were collected from the Kilmaluag Formation of the Great Estuarine Group (Bathonian, Middle Jurassic) of the Strathaird Peninsula, north of Elgol, Isle of Skye, Scotland. NMS G.2017.37.1 was collected at Cladach a' Ghlinne, whereas NMS G.1992.47.123 was collected approximately 0.8 km south of Cladach a' Ghlinne along the coastline. The Kilmaluag Formation comprises dolomitised blue-grey limestone, interbedded with calcareous siltstone and shale. The presence of freshwater gastropods and bivalves (*Viviparus*, *Neomidon*, and *Unio*), and abundant freshwater ostracods, such as *Darwinula* and *Theriosynoecum*, support the environmental interpretation that this was a freshwater lagoon environment (Andrews 1985; British Geological Survey 2011). The strata yielding the new specimens are frequently referred to as “the vertebrate beds”. Also known from this formation are fossil crocodylomorphs, squamates, choristoderes, salamanders, fishes, mammals, and tritylodontids, as well as rare archosaur remains (Waldman and Savage 1972; Evans et al. 2006; Close et al. 2016; Panciroli et al. 2017a, b).

Micro-CT scan data were obtained for NMSG.1992.47.123 using the PCT scanner built in-house at the University of Edinburgh, School of Geosciences Experimental Geoscience Facility. The scanner comprises a Feinfocus 10-

160kV dual transmission/reflection source, Perkin Elmer XRD0822 amorphous silicon x-ray flat panel detection, and terbium doped gadolinium oxy-sulfide scintillator. Data acquisition software was written in-house, and scans were reconstructed using Octopus 8.7 software. The scan resolution for this scan is 20 µm. NMS G.2017.37.1 micro-CT scan data were obtained at Cambridge Biotomography Centre (<http://www.cbc.zoo.cam.ac.uk/>) using a Nikon Metrology XT H 225 ST micro-CT scanner. The scan resolution for this scan is 7.64 µm. All microCT scans were digitally reconstructed, image processed, and measured using Mimics 19.0 at the National Museum of Scotland. Digital reconstructions are available in SOM (Supplementary Online Material available at http://app.pan.pl/SOM/app63-Panciroli_etal_SOM.pdf).

Lower molar terminology follows that by Sigogneau-Russell (2003) with the following amendments: the talonid cusp is renamed the hypoconid, and the crest running from the hypoconid to the metaconid is the cristid obliqua (as in Davis 2011); the paraconal sulcus is renamed the hypoflexid (as in Close et al. 2016); cusp e is not present in *Palaeoxonodon*.

Phylogenetic analysis was carried out using TNT 1.5, with settings as in Close et al. (2016): all analyses were carried out by first using the new technology search with default command settings, and stipulating that the shortest tree was to be found 10 times. This was followed by TBR branch swapping on the recovered most parsimonious trees (MPTs), and then calculating a strict consensus. Jackknife resampling statistics were calculated using 1000 replicates, and values are displayed as absolute frequencies. Bremer support values were obtained by TBR branch swapping on the MPTs, incrementally increasing suboptimal trees from one to eight steps (see SOM for TNT script and amended data matrix).

Systematic palaeontology

Mammalia Linnaeus, 1758

Cladotheria McKenna, 1975

Amphitheriidae Owen, 1846

Genus *Palaeoxonodon* Freeman, 1976b

Type species: *Palaeoxonodon ooliticus* Freeman, 1976b; Forest Marble Formation, Bathonian, Kirtlington, Oxfordshire, England, UK.

Palaeoxonodon ooliticus Freeman, 1976b

Fig. 1.

Holotype: NHMUK PV M36508, right lower molar (Freeman 1976b: pl. 17: 1–4).

Type locality: Kirtlington, Oxfordshire, England, UK.

Type horizon: Forest Marble Formation, Bathonian (Mammal Bed).

Material.—NMS G. 2015.17.10, partial left dentary referred to this species by Close et al. (2016); NMS G.1992.47.123 and NMS G.2017.37.1, two partial left dentaries, described here; from the Kilmaluag Formation (Bathonian), Isle of Skye, Scotland, UK.

Specimens originally referred to *Palaeoxonodon freemani*, *Palaeoxonodon* sp., *Kennetheridium leesi*, and *Kennetheridium* sp. (Close et al. 2016). Right lower molars: NHMUK PV MJ.59, MJ.196, ?MJ.242, M36507 (Freeman 1979: pl. 17: 1–4, but now lost), MJ.197, MJ.213, MJ.388, MJ.530, MJ.569, MJ.593, MJ.715, ?M44303, MJ.702, MJ.290, MJ.117, MJ.379, ?MJ.430, MJ.514, MJ.428, MJ.515, MJ.532, MJ.801; left lower molars: NHMUK PV ?MJ.200, MJ.236, MJ.619, MJ.639, MJ.849, ?MJ.220, ?MJ.350, ?MJ.618, MJ.626, MJ.628, MJ.657, MJ.701, MJ.727, MJ.825, MJ.827, MJ.837, ?M51823, MJ.802, MJ.53, MJ.746, MJ.289, ?MJ.518, MJ.824, MJ.214, MJ.846); right upper molars: NHMUK PV MJ.146, MJ.524, MJ.749, MJ.754, MJ.792, M36512, MJ.99, MJ.238, MJ.241, MJ.458, MJ.817, M36532. More questionably, Sigogneau-Russell (2003), also referred right upper molars: NHMUK PV MJ.44, MJ.231, MJ.669, M34994, MJ.32, MJ.506, MJ.508, MJ.512bis, MJ.742, MJ.743, MJ.788; and left upper molars NHMUK PV MJ.137, MJ.392, MJ.436, MJ.636, M36504, M36530, M36526, MJ.25, MJ.294, MJ.627. All from the Forest Marble Formation (Bathonian), Kirtlington, Oxfordshire, England, UK.

Emended diagnosis (modified from Close et al. 2016).—Tribo-sphenic cladotherian mammal differing from dryolestoids in possessing an elongate lower molar talonid with hypoconid placed buccal to the midline of the crown, well-developed upper molar metacone, and winglike parastylar region. Differs from all other non-zatherian cladotherians in possession of a mesiolingual lower molar cingulid. Differs from *Amphitherium* in possession of five molars instead of six or seven, the more lingual position of the hypoconid, and presence of an entocristid partially enclosing an incipiently basined talonid (sensu Sigogneau-Russell 2003). Differs from *Nanolestes* in possessing less cuspidate upper molars with weaker development of cusp B, and relatively taller and less procumbent lower molar paraconid. Differs from *Arguimus* in the presence of a more fully triangulated trigonid of m1 with a larger paraconid, more spirelike lower molar cusps, absence of a distinct cusp e, and larger metaconid on ultimate molar. Resembles *Amphitherium* and *Nanolestes* but differs from zatherians in the absence of a distinct cusp e on lower molars, absence of hypoconulid, and buccally positioned metacone. Relatively slender dentary unlike dryolestids, with a deep masseteric fossa and coronoid scar as in other amphitheriids. The masseteric fossa intrudes slightly into the body of the dentary below the ultimate molar, unlike all other early cladotherians. The posterior opening of the mandibular

canal, the mandibular foramen, is offset from the Meckel’s sulcus, unlike *Amphitherium* or *Peramus*. The posteriormost mental foramen is positioned in the canine/incisor region of the dentary.

Description.—NMS G.1992.47.123 is a fragment of left dentary containing m2, m3, and m4 in position, with roots, and the anterior part of the alveolus for m5 (Fig. 1). The molar crowns were broken and detached from their roots, and the latter remained inside the dentary fragment. The crowns have been restored to their original positions digitally to facilitate description and comparison. The dentary fragment measures 2.5 mm in anteroposterior length, 0.62 mm in width at the widest point, and the dentary dorsoventral depth below m3 is 1.3 mm (for tooth measurements see Table 1).

All three crowns of NMS G.1992.47.123 are well preserved, except for the following damage: the protoconid, metaconid, and paraconid cusp tips of m4 are missing; the hypoconid tip and tip of cusp f of m3 are missing; and the hypoconid and buccal apical portion of the protoconid are missing from m2 (Fig. 1). The surface of the paraconid of m3 is damaged, missing enamel on the lingual surface of the paraconid, metaconid, and cingulid, and some of the anterobuccal enamel surface is also missing apically on the protoconid. The cristid obliqua of m3 is well preserved, revealing a distinct incipient talonid basin in occlusal view (Fig. 1C), defined lingually by the entocristid. The incipient talonid basin of m4 is well preserved, with a clear entocristid on the lingual edge.

NMS G.2017.37.1 is a fragment of left dentary 7.2 mm long with an approximate dorsoventral depth of 1.6 mm below m3 (Fig. 2) (for tooth measurements see Table 1). The teeth m3 and m4 are preserved in position. Most of m2 is also preserved in position, but was fragmented prior to discovery. A fragment of the m1 root is also present. The alveolus for m5 is present but empty (Fig. 2B₁). The cusp tips are missing from both m3 and m4, but the protoconid, paraconid, and metaconid positions are clear on both molars, as are the hypoflexid, hypoconid, and incipient talonid basin, defined lingually by the entocristid. None of these features are easily identified in m2, in which the hypoconid and hypoflexid are missing, and only the base of the anterior half of the crown is present.

Multiple fractures are present on the dentary, but the general osteology is evident. The Meckel’s sulcus is preserved on the lingual surface of the dentary, extending an-

Table 1. Dental measurements (in mm) for *Palaeoxonodon ooliticus* Freeman, 1976b, NMS G.1992.47.123 and NMS G.2017.37.1. Measurements follow Sigogneau-Russell (2003) and Close et al. (2016).

Specimen	Tooth	Total length	Total width	Total crown height	Trigonid		Talonid		Protoconid height
					length	angle	length	cuspid to metacristid	
NMS G.1992.47.123	m2	0.88	0.62	0.91	0.63	60°	0.25	0.19	0.21
	m3	0.88	0.60	0.98	0.61	49°	0.27	0.11	0.31
	m4	0.89	0.64		0.61	50°	0.27	0.12	
NMS G.2017.37.1	m3	1.00	0.78		0.75	47°	0.25	0.15	
	m4	0.89	0.84		0.60	58°	0.40	0.15	

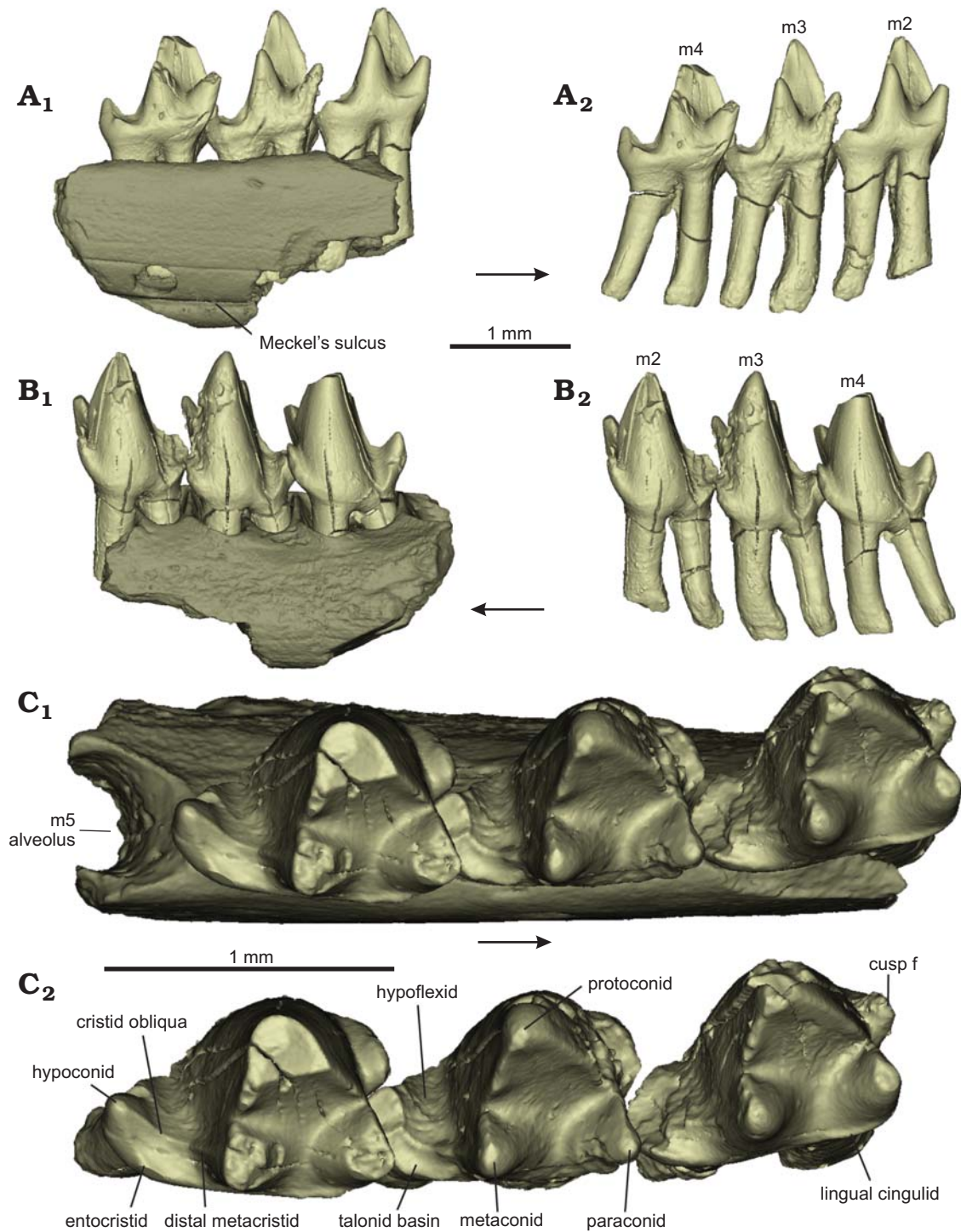


Fig. 1. Amphitheriid mammalian *Palaeoxonodon ooliticus* Freeman, 1976b (NMS G.1992.47.123) from the Kilmaluag Formation, Bathonian, in lingual (A), buccal (B), and occlusal (C) views; partial left dentary (A₁–C₁); dentition only (A₂–C₂). Arrows indicate anterior direction.

teriorly from a point just ventral to the mandibular foramen, up to the fractured region ventral to m2 (Fig. 2C₁). The mandibular foramen is present posteriorly on the lingual surface of the dentary, posteroventral to the empty alveolus for m5 and offset from the Meckel's sulcus. The pterygoid shelf is unclear from the preserved morphology.

The masseteric fossa, located posteriorly on the buccal surface of the dentary, is deep and is defined by ridges an-

terodorsally and ventrally. A masseteric foramen is located anteroventrally within the masseteric fossa. The anterior margin of the masseteric fossa is well-developed and extends anteriorly, ventral to the alveolus for m5. It extends just slightly into the body of the mandible ventral to m5 (Fig. 2A₁, B₁).

Stratigraphic and geographic range.—Middle to Late Bathonian, England and Scotland.

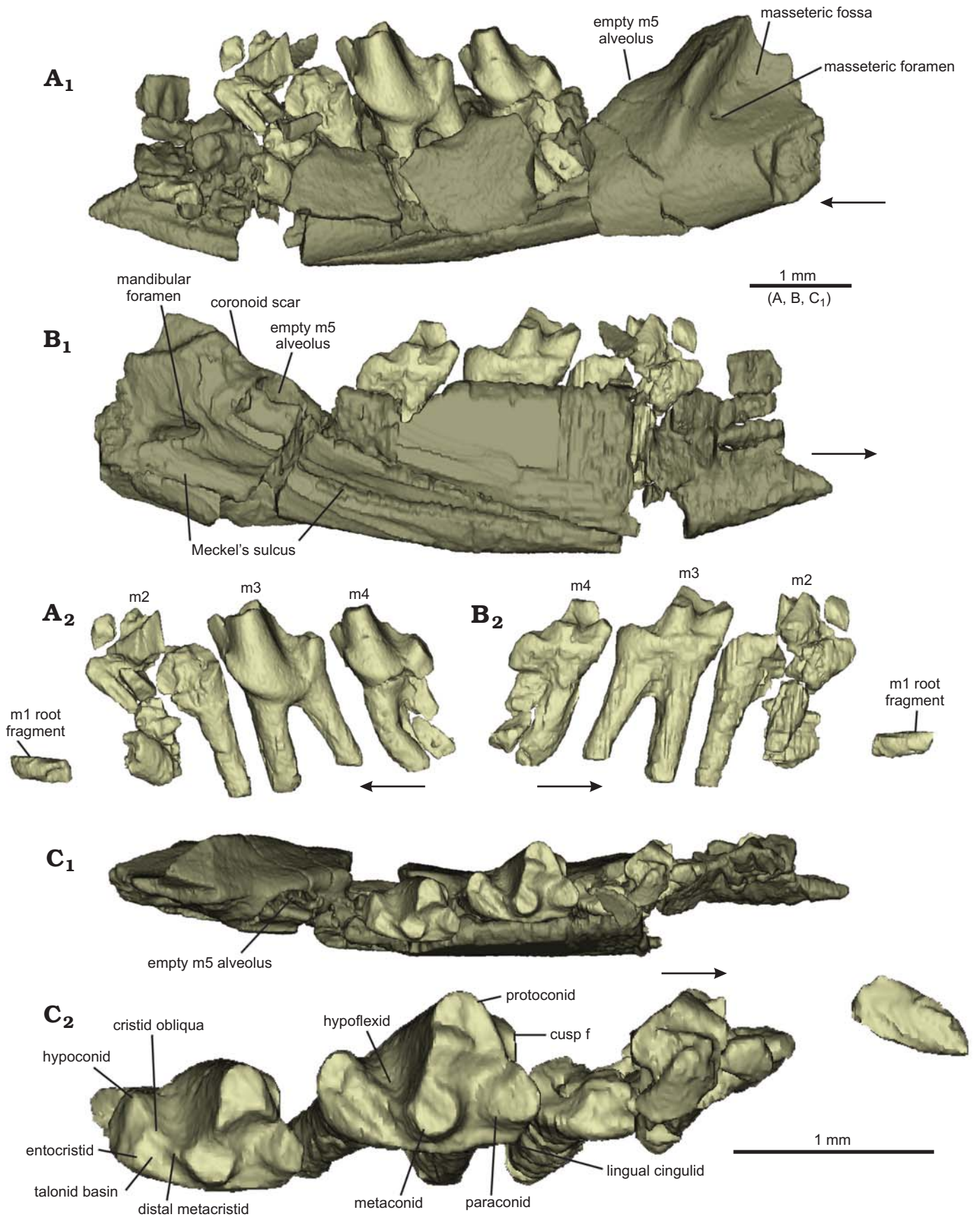


Fig. 2. Amphitheriid mammalian *Palaeoxonodon ooliticus* Freeman, 1976b (NMS G.2017.37.1) from the Kilmaluag Formation, Bathonian, in lingual (A), buccal (B), and occlusal (C) views; partial left dentary (A₁–C₁), dentition only (A₂–C₂). Arrows indicate anterior direction.

Phylogenetic analysis

We reran the phylogenetic analysis of Close et al. (2016), which was based on the matrix of Zhou et al. (2013), updating scores for characters of the posterior portion of the dentary present in NMS G.2017.37.1. These included the position of the mandibular foramen, the morphology of the anterior margin of the masseteric fossa, the presence of the masseteric foramen, and the presence of a coronoid scar (see Appendix 1 for newly scored characters and SOM for full matrix and TNT script). We also re-evaluated and amended six characters present in NMS G. 2015.17.1 that were either not scored by, or that we interpreted differently from, Close et al. (2016). These include confirming the absence of Crompton's groove, the absence of a premolar or precanine diastema, confirming the presence of the hypoconid, and the morphology of the postcanine roots. Additionally, we re-evaluated and re-scored six characters present in *Amphitherium*, *Peramus*, and *Arguimus* (see Appendix 1 for justification for rescoring, and Zhou et al. 2013 for full character list).

The phylogenetic analysis recovered 5376 most parsimonious trees. Despite the additional character scores, we found no change in the relationships between *Palaeoxonodon*, *Amphitherium*, and *Peramus* from previous analyses, with *Palaeoxonodon* and *Amphitherium* placed in a sister-group relationship. These relationships have weak Bremer support values of 1, and this clade (Amphitheriidae) forms an unresolved polytomy with *Nanolestes*, *Arguimus*, and the clade including *Kielantherium* + *Aegialodon* + Theria, as in Close et al. (2016).

Five autapomorphies were recovered for *Palaeoxonodon* by our phylogenetic analysis, the first three of which were already identified by Close et al. (2016), and the last two of which are identified for the first time here: (i) the posterior-most mental foramen being positioned in the canine/incisor region of the dentary (more anteriorly than in *Amphitherium* or *Peramus*); (ii) the absence of a mesio-lingual cingular cuspule e; and (iii) an absent/weak ectoflexus in the second upper molar; (iv) the slight extension of the masseteric fossa onto the body of the mandible; and (v) the position of the mandibular foramen offset from the Meckel's sulcus. *Palaeoxonodon* and *Amphitherium* share synapomorphic characters in the presence of a narrow labial styler shelf of the penultimate upper molar, and the more labial position of the metacone relative to the paracone. *Palaeoxonodon*, *Amphitherium*, and *Peramus* share the following synapomorphies: the convergence of the Meckel's sulcus with the ventral border of the mandible; and possessing open rooted postcanines.

Discussion

Most previous cladistic analyses support a sister group relationship between *Palaeoxonodon* and *Amphitherium* (Prothero 1981; Close et al. 2016; but see Averianov et al. 2015 for an alternative view). In these previous analyses this

was based on (i) the large talonid (accounting for one-third of molar length), (ii) possessing a buccally positioned principal hypoconid, (iii) roots that are mostly equal in diameter along their length except for a slight narrowing distally, and (iv) the possession of five premolars with (v) moderately well-developed lingual cingulids.

Close et al. (2016) identified the variably present cuspule on the cristid obliqua (mesoconid) in their specimen NMS G. 2015.17.1 as a feature shared with the holotype NHMUK PV M36508 (and two other specimens according to Sigogneau-Russell 2003: NHMUK PV MJ530 and NHMUK PV MJ618) from the Forest Marble Formation. The mesoconid is not present in either of our specimens, NMS G.1992.47.123 or NMS G.2017.37.1. Therefore we support the interpretation of this character as variable among specimens of *Palaeoxonodon*.

Close et al. (2016) also suggested that the different dental characters used to erect the species *P. freemani* and *Kennetheridium leesi* on the basis of isolated teeth (Sigogneau-Russell 2003) are the morphological differences between tooth positions in the same tooth row of their specimen, relegating the latter two taxa to junior subjective synonyms of *P. ooliticus*. This character variation includes differences in talonid length, prominence of the cingulid, size of the paraconid, and height and cusp sharpness of the trigonid, among different molars in the same individual. Similarly, we see some of this variation in NMS G.1992.47.123: for example the paraconid is much smaller in m3 and m4 than in m2, and slopes at a shallower angle in m2; and the cingulid is more prominent in m2 than m3 or m4. We can add that the entocristid is more prominent in m2, and that the protoconid is broader both anteroposteriorly and buccolingually in m4. This adds to the evidence for variation along the tooth row, and emphasises the need for caution in erecting new species based on isolated teeth.

A posterior portion of the dentary including the base of the coronoid process, masseteric fossa, and mandibular foramen are preserved in NMS G.2017.37.1 and have not previously been preserved in any other specimen of *Palaeoxonodon*. The preserved morphology suggests a sloping coronoid process, as in other early cladotherians. Strong masseteric ridges and a deep masseteric fossa are also present, as in other early cladotherians including other amphitheriids such as *Amphitherium* (Butler and Clemens 2001), other peramurids, dryolestids, and paurodontids (Martin 1999; Kielan-Jaworowska et al. 2004; Davis 2012). Unlike paurodontids, the dentary is relatively slender. The preserved morphology of NMS G.2017.37.1 suggests that a pterygoid shelf may have been present on the lingual surface of the dentary; however, its extent is not clear from this specimen. The pterygoid shelf is strongly protruding in many other early cladotherians (Martin 1999; Kielan-Jaworowska et al. 2004). The anterior position of the posteriormost mental foramen, in the canine/incisor region of the dentary, is recovered here as an autapomorphy of *Palaeoxonodon*. While there is a possibility that a more posterior foramen may have been present in the frac-

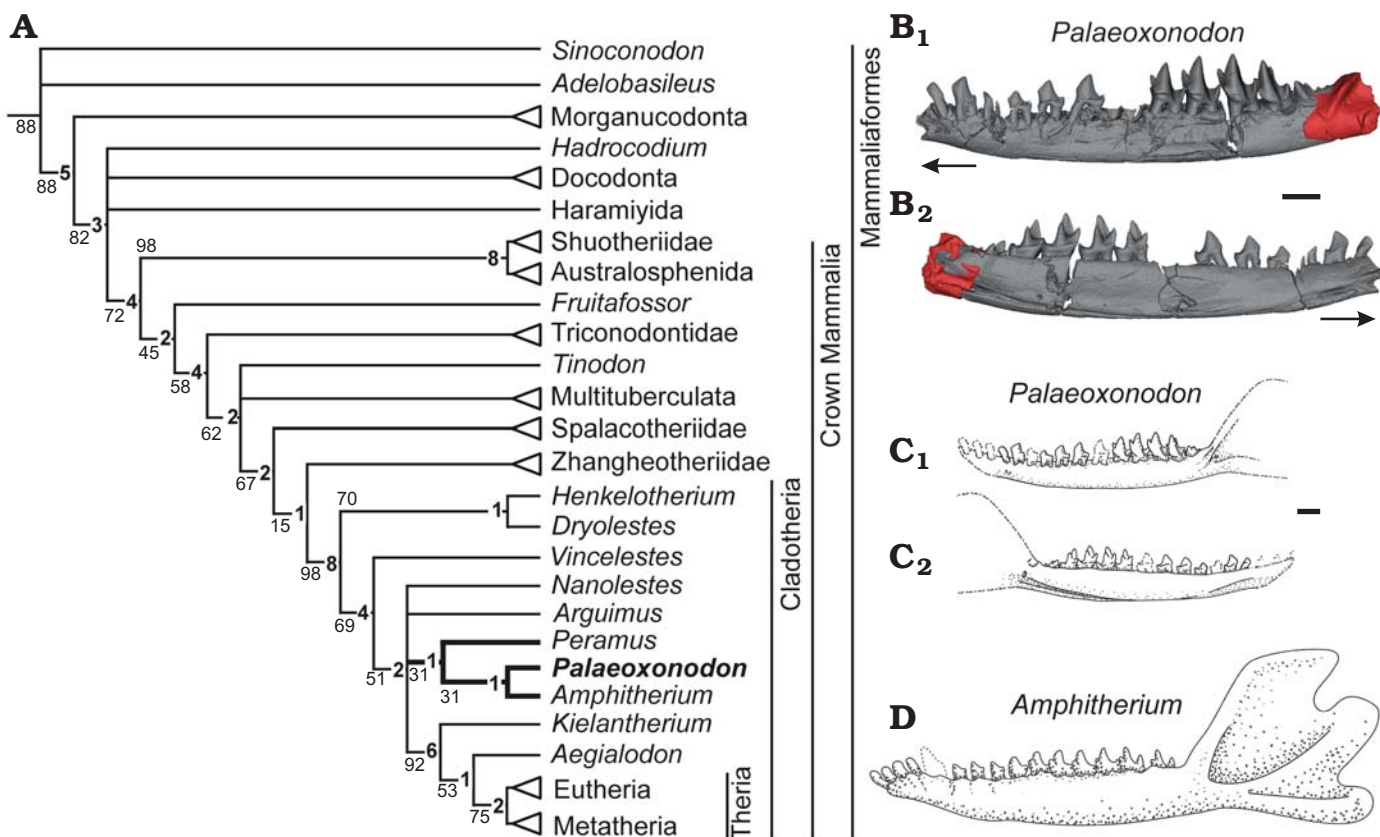


Fig. 3. Parsimony analysis and reconstructions of dentary of *Palaeoxonodon ooliticus* (B, C), with *Amphitherium* (D) for comparison. **A**. Equally weighted parsimony analysis with additional mandibular characters for the early cladotherian *Palaeoxonodon ooliticus*, and rescored and updated matrix from Close et al. 2016 (adapted from Zhou et al. 2013). Jackknife resampling statistics and Bremer values (bold) are shown adjacent to individual nodes. **B**. Composite of NMS G. 2015.17.1 (grey) and coronoid of NMS G.2017.37.1 (red) in buccal (B₁) and lingual (B₂) views (arrows indicate anterior direction). Data for NMS G. 2015.17.1 from Close et al. (2016). **C**. Reconstruction of jaw in buccal (C₁) and lingual (C₂) views. **D**. Reconstruction based on composite created by EP from NHMUK PV M.36822 and OUMNH J.20075 in buccal view. Scale bars 1 mm.

tered portion of the dentary below p1 in NMS G. 2015.17.1, we find no evidence for this at present, pending the recovery of new specimens.

Close et al. (2016) identified a possible coronoid scar in NMS G. 2015.17.1, which we can confirm in NMS G.2017.37.1. This is absent in *Peramus* according to previous analyses (Clemens and Mills 1971; Davis 2012), but was coded as present by Zhou et al. (2013). We have rescored this character as absent in *Peramus* in our analysis. The coronoid scar is present in *Amphitherium* (Butler and Clemens 2001) and many other early cladotherians, including the zatherian *Nanolestes* (Martin 2002). However, it is absent in another zatherian, *Arguimus* (Lopatin and Averianov 2006). Close et al. (2016) also inferred a lower incisor count of four based on comparison to *Amphitherium*. Although we cannot verify this feature using NMS G.1992.47.123 or NMS G.2017.37.1, we consider it likely to have been present, as this character state is common among early Cladotheria. As such, we have used it in our reconstruction (Fig. 3C).

The presence of a Meckel’s sulcus is common among stem mammals. In NMS G.2017.37.1, the mandibular foramen is preserved, indicating that *Palaeoxonodon* had a Meckel’s sulcus that was offset from the foramen, a feature

not shared with either *Amphitherium* (Butler and Clemens 2001) or *Peramus* (Clemens and Mills 1971; Davis 2012). The mandibular foramen in *Palaeoxonodon* also does not appear to be confluent with the pterygoid shelf, unlike in *Amphitherium* and *Peramus*, although damage to this part of the dentary in NMS G.2017.37.1 makes this interpretation uncertain. The position of the mandibular foramen ventral to the alveolar plane, seen in *Palaeoxonodon* and *Amphitherium*, is also shared with other early cladotherians, and the basal metatherian *Sinodelphys*. The clade comprising *Palaeoxonodon* + *Amphitherium* + *Peramus* is in a polytomy with *Nanolestes*, the clade comprising *Kielantherium* + *Aegialodon* + Theria, and *Arguimus*. *Arguimus* shares few dentary character states with *Palaeoxonodon*. *Arguimus* has no Meckel’s sulcus (the absence of Meckel’s sulcus is an autapomorphy of *Arguimus*; see Lopatin and Averianov 2006) and no coronoid scar. *Vincelestes* also has no Meckel’s sulcus or coronoid scar (Bonaparte and Rougier 1987). While other analyses have recovered the relationship of *Vincelestes* as closer to Theria than either *Peramus* or *Amphitherium* (Kielan-Jaworowska et al. 2004; Bonaparte 2008), our results, like those of Close et al. (2016) and Zhou et al. (2013) place *Vincelestes* as a sister group to the polytomy compris-

ing *Palaeoxonodon* + *Amphitherium* + *Peramus*, *Nanolestes*, *Arguimus*, and *Kielantherium* + *Aegialodon* + *Theria*.

The phylogenetic affinities of *Palaeoxonodon* have been contested due to the presence of an “incipient basin” (Sigogneau-Russell 1999, 2003) on the talonid, referred to as the incipient talonid basin herein, and the variable presence of a cuspule on the cristid obliqua. In an alternative hypothesis, Averianov et al. (2015) recovered a close relationship between *Amphibetulimus* and *Palaeoxonodon*, placing them in a clade with *Nanolestes*. This clade was found to be phylogenetically distinct from, and crownward to, *Amphitherium* (Averianov et al. 2015). Support for this relationship with *Nanolestes*, rather than with *Amphitherium* and *Peramus* was based on the absence of a “retromolar space”, the proportional size of the stylocone relative to the metacone in the upper molars, and absence of a coronoid scar. We now confirm the coronoid scar is in fact present in *Palaeoxonodon*. The analysis by Averianov et al. (2015) also included *Mozomus*, which was found to form a polytomy with *Zatheria* (including *Peramus* and *Arguimus*), and the clade comprising *Palaeoxonodon* + *Nanolestes* + *Amphibetulimus*. Neither *Mozomus* nor *Amphibetulimus* were included in our analysis and so we did not test the relationships between these taxa and other early cladotherians.

Characters of the talonid basin have previously been used to argue for a close affinity between *Palaeoxonodon* and *Peramus*, to the exclusion of *Amphitherium* (Freeman 1976b, 1979; Kielan-Jaworowska et al. 2004). However, the presence of plesiomorphies such as the principal talonid cusp (hypoconid) with no embrasure for occlusal contact with the metacone of the upper molar may suggest *Palaeoxonodon* is more stemward than *Peramus*, and indeed several authors have suggested that *Palaeoxonodon* and the morphologically similar *Amphitherium* are sister-taxa, occurring stemward of *Peramus* (Sigogneau-Russell 2003; Davis 2011, 2012). Close et al. (2016) suggested that the “incipient” talonid basin of *Palaeoxonodon* and the talonid basin of *Peramus* could either be homoplastic, or a synapomorphy of the clade *Palaeoxonodon* + *Amphitherium* + *Peramus*, and this currently cannot be resolved. We agree with Close et al. (2016) that the phylogenetic analyses carried out in their paper and herein cannot resolve this unambiguously.

Palaeoxonodon is the only taxon in our analysis in which the mandibular foramen is located in the pterygoid fossa and offset from the Meckel’s sulcus. In *Amphitherium*, the foramen is aligned with the posterior end of the Meckel’s sulcus, as it is for the most closely related taxa among early Cladotheria (Butler and Clemens 2001; Kielan-Jaworowska et al. 2004). This is a condition seen in crown Marsupialia and some basal metatherians, such as *Didelphodon* (Fox and Naylor 1986; Wilson et al. 2016), but not in more crownward Metatheria. However, there is some damage to the posterolingual portion of the dentary in NMS G.2017.37.1. More complete, undamaged specimens may shed further light on the placement of the mandibular foramen. The very slight extension of the anterior crest of the masseteric fossa into

the body of the dentary is not shared with any other taxon in this analysis, except the extant *Oryctolagus* (European rabbit). However the more extreme extension of the anterior crest of the masseteric fossa, where it extends below the ultimate pre-molar or first molar, is commonly seen in multituberculates (e.g., Gambaryan and Kielan-Jaworowska 1995). This may suggest *Palaeoxonodon* had a more extensively developed superficial masseteric muscle than other early cladotherians. Without knowing the position and morphology of the condylar process, which is crucial for determining the in-lever for the dentary (Gill et al. 2014), it is not possible to make informed inferences about the biomechanics of mastication in this genus. This would require more complete mandibles that are amenable for muscle reconstruction, as shown in other studies (Lautenschlager et al. 2017).

The presence of a masseteric foramen (also referred to as the labial mandibular foramen), located in the masseteric fossa on the buccal side of the dentary, is a newly identified feature in *Palaeoxonodon*. A deep masseteric fossa with a distinct masseteric foramen is a feature shared with peramurans, but is also present in numerous taxa across different lineages, including other zatherians, triconodontids, and basal metatherians and eutherians (Davis 2012). In *Palaeoxonodon* the foramen is not as large as in some specimens of *Peramus*, but it quickly merges with the mandibular canal inside the dentary, posteroventrally to the position of m5. The morphology of this foramen in *Palaeoxonodon* is similar to that described by Davis (2012) for the specimens of *Peramus* that lack an enlarged masseteric foramen: the mandibular canal is enlarged mesial to the masseteric fossa, and is separated by only a thin wall of bone (Davis 2012: 813–814). Davis suggests the variability in the size of the masseteric foramen in specimens of *Peramus* may be attributed to post-depositional crushing and infill. Until further specimens of *Palaeoxonodon* are found possessing the posterior portion of the dentary, it is not possible to say if the size of this feature similarly varies in this taxon.

Conclusions

Newly described specimens of *Palaeoxonodon ooliticus* from the Isle of Skye add valuable new information for morphological comparison, and new data for phylogenetic analysis. The additional features of the masseteric fossa, and the position of the mandibular foramen identified in NMS G.2017.37.1, while not altering the phylogenetic relationships between *Palaeoxonodon* and its nearest relatives among cladotherians, are new autapomorphies for this genus. They provide additional character scores for future analysis, reducing the amount of missing information for this taxon.

The “re-discovery” of NMS G.1992.47.123 provides a cautionary tale for palaeontologists who delay in the publication of specimens. By not pursuing identification and description of this specimen, an opportunity was missed to name a second Mesozoic mammal from Scotland, an

important taxon for understanding the morphology of early Cladotheria. This more complete specimen would also have provided a holotype with some variation in the tooth row, perhaps preventing the erection of taxa that are now suggested to be junior synonyms. This is an informative lesson from the palaeontological history of Mesozoic mammals. NMS G.1992.47.123 also contributes to the description of rich Scottish Mesozoic mammal specimens that have, until now, remained undescribed, and therefore unrecognised scientifically.

Although a relatively large number of upper teeth and lower dentitions from *Palaeoxonodon* are now known, they have not yet been found in association, and postcrania have yet to be identified. This provides a goal for further discoveries in the rich microvertebrate beds of the Isle of Skye in the coming years.

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Appendix 1

Newly scored characters for *Palaeoxonodon*—the following six characters (from Zhou et al. 2013) were newly scored based on morphology present in specimen NMS G.2017.37.1:

12. Coronoid bone (or its attachment scar): (1) absent to (0) present
13. Location of the mandibular foramen (posterior opening of the mandibular canal): ? to (1) in the pterygoid fossa and offset from Meckel's sulcus (the intersection of Meckel's sulcus at the pterygoid margin is ventral and posterior to the foramen).
14. Vertical position of the mandibular foramen: ? to (0) below the alveolar plane.
22. Crest of the masseteric fossa along the anterior border of the coronoid process: ? to (1) present and distinctive.
23. Anteroventral extension of the masseteric fossa: ? to (1) extending anteriorly onto the body of the mandible.
24. Labial mandibular foramen (masseteric foramen) inside the masseteric fossa: ? to (1) present.

Re-scored characters for *Palaeoxonodon*—we re-scored and added the following characters (from Zhou et al. 2013) for *Palaeoxonodon* differently from Close et al. (2016):

6. Groove for the replacement dental lamina (Crompton's groove): (1) absent. Crompton's groove for the replacement dental lamina, as seen in *Morganucodon* and some other stemward mammaliaformes, is not present on any of the specimens of *Palaeoxonodon ooliticus* so far recovered from England or Scotland. We therefore consider it justifiable to score this character as absent.
97. Hypoconid (we designate the distal cingulid cuspule d as the homolog to the hypoconid in the teeth with linear alignment of the main cusps; we assume the cusp to be the hypoconid if there is only a single cusp on the talonid in the teeth with reversed triangulation): (1) present (as distal cusp d, sensu Crompton 1971), elevated above the cingulid level, labially positioned (or tilted in the lingual direction). We score this based on the morphology of all known material so far.

174. Diastema separating the lower first and second premolars (defined as the first and second functioning premolar or premolariform postcanine): (0) absent (gap less than one tooth root for whichever is smaller of the adjacent teeth). No diastema separates the premolars pm1 and pm2, nor is there a diastema pre- or post-canine, in this taxon in any specimens known so far.
182. Enlarged diastema in the lower incisor-canine region (better developed in older individuals): (0) absent; as for 174.
195. Open root end of the postcanines: (1) present; based on NMS G. 2015.17.1.
196. Degrees of root division: (2) two or three complete divided roots. All specimens now recovered confirm that *Palaeoxonodon ooliticus* has two completely divided roots in all teeth except incisors, and that they are not connected by dentine sheets.

Re-scored characters for *Arguimus*—we re-scored and added the following characters for *Arguimus* differently from Close et al. (2016):

13. Location of the mandibular foramen (posterior opening of the mandibular canal): 4 to (?) the location of this structure cannot be confirmed in *Arguimus*.
14. Vertical position of the mandibular foramen: 1 to (0) below the alveolar plane.
24. Labial mandibular foramen inside the masseteric fossa: ? to (1) present.
26. Posterior-most mental foramen: ? to variable (1, 2, 3, 4).

Rescored characters for *Amphitherium* and *Peramus*—we re-scored and added the following characters for *Amphitherium* and *Peramus* from Zhou et al. (2013):

12. Coronoid bone (or its attachment scar): (1) absent in *Peramus*.
195. Open root end of the postcanines: (1) present (for both taxa). This character was previously scored as (2) for *Amphitherium* and *Peramus*, which is not an option for this character.