The dentary of *Wareolestes rex* (Megazostrodontidae): a new specimen from Scotland and implications for morganucodontan tooth replacement

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Abstract: The Middle Jurassic morganucodontan, *Wareolestes rex*, was previously known from only four isolated molars from Kirtlington, England. There has been debate over the position of the holotype tooth as an upper or lower molar. We describe a new *Wareolestes* specimen from the Kilmaluag Formation of Scotland: a partial left dentary with two erupted molars, one unerupted molar, and three unerupted premolars. Empty alveoli for a canine, p1 and p3 are also present. Through detailed comparison of the morphology of the holotype and our new material, we support the original diagnosis of the holotype *Wareolestes* as a lower molar, most likely m1. The position of erupted and unerupted replacement teeth in the newly discovered specimen supports a diphyodont pattern of tooth replacement of premolariform dentition in *Wareolestes*, as suggested for other morganucodontans such as *Morganucodon*, *Megazostrodon* and *Dinnetherium*. However, damage to the dentary means questions remain regarding the sequence of replacement in *Wareolestes* along the tooth row.

Key Words: *Wareolestes rex,* Morganucodonta, Megazostrodontidae, Middle Jurassic, Scotland, molar replacement

Morganucodontans are a diverse clade of proximate stem-group mammals known from the Late Triassic until at least the Middle Jurassic, and possibly as late as the Early Cretaceous (Butler *et al.* 2012). They were among the most abundant early mammaliaforms, and became globally distributed by the Early Jurassic, with fossils known from the USA (Jenkins *et al.* 1983), India (Datta & Das 1996), South Africa (Crompton 1964), Greenland (Jenkins *et al.* 1994), China (Kermack *et al.* 1973; Young 1978; Luo & Wu, 1994), Russia (Gambaryan & Averianov 2001), and across Europe (UK: Kermack *et al.* 1973; Freeman 1979; Clemens 2011; Switzerland: Clemens 1980; France: Sigogneau-Russell 1983; Evans & Milner 1994; Debuysschere *et al.* 2015).

Morganucodontans provide important information on the evolutionary assembly of mammalian anatomy as they possess derived mammalian characters, including diphyodont replacement of the antemolar teeth (incisors, canines, premolars) (Crompton 1974; Luo *et al.* 2004). Diphyodont replacement was argued for the second molar of *Megazostrodon* (Gow 1986), but this has subsequently been debated (Luo *et al.* 2004). As in crown-group mammals, morganucodontans also exhibited precise molar occlusion. However, full occlusion was achieved through enamel wear rather than precise occlusion upon tooth eruption (Mills 1971; Crompton 1974; Crompton & Luo 1993; Luo *et al.* 2004). Alongside these mammalian synapomorphies, morganucodontans also retained plesiomorphic character states, such as the linear, mesiodistal alignment of the main cusps of postcanine teeth, retention of a post-dentary trough, and an anteriorly positioned angular process of the dentary (Kielan-Jaworowska *et al.* 2004).

Morganucodonta (Kermack *et al.* 1973) includes two families: Morganucodontidae and Megazostrodontidae (Stucky & McKenna 1993; Kielan-Jaworowska *et al.* 2004). Megazostrodontidae (Gow 1986), was erected to include *Megazostrodon* and *Dinnetherium*, and is diagnosed by the reduction of the angular process, flaring of the ridge of the dentary condyle, and the well-developed labial cingulum on the upper molars, with the labial cingulum tends to differentiate into a posterior and anterior lobe (Gow 1986; Kielan-Jaworowska *et al.* 2004). Following the initial description of Megazostrodontidae, *Brachyzostrodon* (Late Triassic, France and Greenland; Sigogneau-Russell 1983), *Indozostrodon* (Early Jurassic, India; Datta & Das 1996, 2001) and

Wareolestes (Middle Jurassic, England; Freeman 1979) were referred to Megazostrodontidae by these subsequent authors. It should be noted that *Indozostrodon* may be a junior synonym of *Indotherium* (Prasad *et al.* 2006), which was assigned to Morganucodontidae by Prasad and Manhas (2002), and more complete material is required to resolve this.

Wareolestes rex was erected as a new genus and species by Freeman (1979) for a single well preserved molar tooth discovered at Kirtlington cement quarry, an exposure of the Middle Jurassic Forest Marble Formation in Oxfordshire, UK, which has yielded multiple representatives of early mammaliaform groups (Freeman 1976, 1979; Kermack *et al.* 1998; Sigogneau-Russell 1998, 2003; Butler & Hooker 2005). Until now, *Wareolestes* has been known only from the type molar, NHMUK PV M36525, and some referred molar fragments (see below) (Freeman 1979; Butler & Sigogneau-Russell 2016).

In 2015, field work in the Middle Jurassic Kilmaluag Formation of the Isle of Skye, Scotland recovered a dentary with multiple erupted and non-erupted teeth that we attribute to *Wareolestes rex.* This is the first occurrence of this genus in Scotland. The specimen was found at a coastal locality, with the buccal side of the jaw exposed and therefore slightly abraded. Nevertheless, it retains evidence of at least three replacement teeth and three permanent molars. The new specimen therefore provides crucial evidence for the mode of dental replacement in megazostrodontids. It also adds to our knowledge of the anatomy of

Wareolestes: it clarifies the previously disputed position of the holotype for this genus (Hahn *et al.* 1991; Butler & Sigogneau-Russell 2016), and adds a new feature that we consider to be an autapomorphy: the presence of a labial cingulid. Finally, it adds to a growing list of mammaliaforms known from the Bathonian (Middle Jurassic) Kilmaluag Formation of Scotland (Waldman & Savage 1972; Savage 1984; Clemens 1986; Evans & Milner 1994; Close *et al.* 2015), allowing comparisons with the well-sampled Middle Jurassic mammaliaform assemblage of England.

MATERIALS AND METHODS

The new specimen NMS G.2016.34.1 was scanned at 95kV and 225μa using a Nikon XT H 225 ST micro-CT scanner at the University of Cambridge Biotomography Centre (http://www.cbc.zoo.cam.ac.uk/) with an isotropic voxel size of 13.4μm, 1998 slices at export. The density of the metamorphosed limestone matrix limited the resolution of the scan. The fossil was segmented from the matrix using Mimics 19.0 (Materialise, Leuven, Belgium). The specimen was also examined directly using a Meiji Techno RZ3361 microscope. The holotype was scanned on the same equipment at 75kV and 80μa, with an isotropic voxel size of 3μm, 866 slices at export. It was also digitally reconstructed using Mimics 19.0.

TERMINOLOGY

We follow the dental cusp terminology of Crompton (1974) (Figure 1). Morganucodontans possess three main cusps, *a/A*, *b/B* and *c/C*, aligned anteroposteriorly in a triconodont pattern. There is also a distal cingulid cusp *d/D*, aligned with the three main cusps, and a series of cingulid cusps which can include mesial cusp *e/E* and midline cusp *g/G* (= the kühnecone; Parrington 1967), not aligned with the main *a* – *d* cusp row. Cusps are referred to in lower case for lower molars, and upper case for the upper molars. The terms labial and buccal are used synonymously.

Institutional abbreviations. NMS, National Museum of Scotland, Edinburgh, UK; NHMUK, Natural History Museum, London, UK.

SYSTEMATIC PALAEONTOLOGY

MORGANUCODONTA Kermack, Musset and Rigney, 1973

MEGAZOSTRODONTIDAE Gow, 1986

Wareolestes Freeman, 1979

Type and only species. Wareolestes rex Freeman, 1979

Wareolestes rex Freeman, 1979

Holotype. NHMUK PV M36525; right or left, lower or upper molar from Kirtlington Mammal Bed, Forest Marble Formation (Bathonian, Middle Jurassic), Kirtlington Cement Works Quarry, Oxfordshire, England. A 3D digital model of this specimen in .stl format, and our CT tomographs, are available in the Panciroli *et al.* 2017.

Referred material. NHMUK PV M46240, NHMUK PV M46248, NHMUK PV M46775 (Freeman 1979; Butler and Sigogneau-Russell 2016), all isolated molars from the Late Bathonian of Kirtlington, Oxfordshire, UK; plus NMS G.2016.34.1 from the Bathonian Kilmaluag Formation of the Isle of Skye, Scotland. The presence of an unerupted molar m3 indicates that NMS G.2016.34.1 represents a sub-adult. A 3D digital model of NMS G.2016.34.1 in .stl format, and our CT tomographs, are available in Panciroli *et al* (2017). Re-identified specimens previously referred to *Wareolestes* include NHMUK PV M46563 (re-identified as *Gobiconodon* sp. indet (Butler & Sigogneau-Russell 2016)) and NHMUK PV M46811 (now the holotype of *Cherwellia leei* (Butler & Sigogneau-Russell 2016)), both from the Late Bathonian of Kirtlington, Oxfordshire, UK.

Previous diagnosis. *Wareolestes rex* is a megazonstrodontid morganucodontan (s*ensu* Kielan-Jaworowska *et al.* 2004) with dental morphology that is congruent with other members of Morganucodonta: three principle cusps arranged anteroposteriorly along the tooth row (cusps *a/A*, *b/B*, and *c/C*). Megazostrodontidae is diagnosed by a reduced angular process, flared ridge of the dentary peduncle, the division of the upper labial cingulum into anterior and posterior lobes and the presence of well-developed labial cingular cusps in the upper molars. *Wareolestes* shares with some morganucodontans a central cusp *a/A* larger than the other cusps (as in *Morganucodon*), and a wrinkled enamel surface (as in *Brachyzostrodon*) (Kielan-Jaworowska *et al.* 2004). Autapomorphies of *Wareolestes* are the placement of cusp *g* bucco-lingually in line with cusp *a*, and a poorly defined labial cingulum.

Revised diagnosis. In addition to the above, a new autapomorphy of *Wareolestes rex* is the presence of a labial cingulid in the lower molars, with cusp *g* bucco-lingually in line with cusp *a*, and a poorly defined lingual cingulid. The dental formula is ?.1.5.3/?.1.5.3.

Locality and horizon of NMS G.2016.34.1. The specimen comes from the Straithaird Peninsula north of Elgol and approximately 1 km south of Cladach a'Ghlinne (see Close *et al*. 2016). It was found in a fallen boulder, below the tide line. Although not *in situ*, it can be identified as having come from the Kilmaluag Formation. The Kilmaluag Formation is part of the Middle Jurassic Great Estuarine Group of the Hebrides Basin. This Group comprises a complex series of sediments of mostly non-marine origin with minor marine horizons that indicate basin subsidence and marine transgression (Barron *et al.* 2012). The Kilmaluag

Formation itself comprises argillaceous limestones and calcareous mudstones, with desiccation cracks, formed by ephemeral lagoonal environments that periodically dried out to form mudflats (Hudson 1980; Andrews 1985). The Kilmaluag Formation is Bathonian, as are similar deposits in England, although exact biostratigraphical correlations between the English sites and exposures of the Kilmaluag Formation have proven difficult (Barron *et al.* 2012). The specimen reported here was found in an argillaceous micritic limestone.

Description

NMS G.2016.34.1 is a partial left dentary, missing its anterior portion from c/p1 anteriorly (Figures 2-3). The dentary condyle and coronoid process are also missing posteriorly. Portions of several erupted and unerupted teeth are present, and are described below. The specimen is partially embedded in matrix, so description of the lingual surface is based on digital reconstructions from µCT scans.

The dentary, as preserved, measures 22.3 mm anteroposteriorly, with a maximum buccolingual width of 1.82 mm, measured at the level where m2 abuts m3. However, the dentary is crushed just posterior to this, and it is possible that it was slightly wider ventral to m3. It is 3.23 mm in dorsoventral depth from the ventral surface of the dentary to the alveolar margin at m2.

We identify the preserved tooth portions as being a partial, unerupted p2 and roots of dp2, unerupted p4 and m3, an erupted m1 (damaged), and an erupted m2 (damaged lingually). There is also a fragment of an unerupted p5. Empty alveoli for c, p1 and p3 are present. Based on this information, we estimate a dental formula of ?.1.5.3/?.1.5.3. Both *Megazostrodon* and *Dinnetherium* have five molars (Gow 1986; Kielan-Jaworowska *et al.* 2004), but there is no indication of a fourth or fifth molar in NMS G.2016.34.1 (Figure 3), nor is there space in the dentary for further molars to form posterior to m3. We assume there was one canine in NMS G.2016.34.1, and a partial alveolus remains at the preserved anterior end of the dentary, however we are unable to determine incisor count because the anteriormost portion of the specimen is missing.

Identification of premolars and molars in NMS G.2016.34.1 was based on the replacement pattern evidenced by the position of replacement teeth within the dentary (see below). A distinct change in morphology between the posteriormost premolar and anteriormost molar has been observed in other morganucodontans (Kielan-Jaworowska *et al.* 2004). Compared to m1, the posteriormost premolar (p5) of *Megazostrodon rudnerae* has a taller cusp *a* (dorso-ventrally) and less well developed cusps *b* and *c*, and m1 has a more prominent cingulid and taller cingular cusps than p5 (Crompton 1974). Only a small portion of p5 is preserved in NMS G.2016.34.1, however, this preserved portion appears to be the anterior projection of a cingulid, indicating a molarised morphology for p5 in *Wareolestes rex* (Figure 4B). The morphology of the preserved portion of p5 is not congruent with a remnant of root, as it is not hollow along its length (unlike a root), nor does it resemble the sharp anterior portion of the p4 crown. Therefore, we identify it as the anterior projection of the cingulid, and suggest p5 in *Wareolestes* is somewhat molarised.

The morphology of p4 is distinctly different from the molars, having a proportionally taller cusp *a* compared to cusps *b* and *c*. Although its roots are absent, the preserved ventral portion of p4 and the morphology of its alveolus indicate that it was double-rooted.

The premolar we identify as dp2/p2 in NMS G.2016.34.1 is double rooted, while the alveoli anterior to dp2/p2 are single rooted (Figure 4A). In *Megazostrodon rudnerae* the first two premolars are single rooted, and the posterior three double rooted (Gow 1986). If this was the pattern in *Wareolestes*, it would suggest a premolar count of six – more than any other morganucodontan. Although it is possible that the premolar count may be higher than any other genus, it is more likely that *Wareolestes* has a different root pattern than *Megazostrodon.* We therefore suggest the anterior most alveoli to be c and p1, and identify the anteriormost double rooted premolar present in NMS G.2016.34.1 as dp2/p2.

The remnants of dp2 include the lingual half of its double roots, and a small portion of the crown where it meets the roots. Ventral to this, between the root remnants, is the cusp *a* tip of a replacement tooth p2 (Figure 3). This forms a hollow cone, and the rest of p2 has either not formed or has been lost.

The dentary is fractured just anterior to the inferred position of the angular process. Although the angular process itself is not preserved, the mandibular body ventral margin anterior to the angular process is preserved. This surface is uniformly convex anteroposteriorly, albeit slightly, as in the intact dentaries of *Megazostrodon* and *Dinnetherium* (Jenkins *et al.* 1983; Gow 1986; Kielan-Jaworowska *et al.* 2004). There is no sign of the sigmoidal curvature typically associated with the ventral projection of an angular process, as seen in *Morganucodon*, *Hadrocodium*, and in other taxa with well-developed angular processes (Kermack et al 1973; Crompton & Luo 1993; Luo *et al.* 2001). We suggest that *Wareolestes* possessed a reduced angular process, termed a 'pseudangular' by Jenkins *et al.* (1983). Due to lack of preservation it is not possible to assess if the angle of *Wareolestes* would have been slightly inflected, as in *Hadrocodium* (Luo *et al*. 2001).

The ventral margin of the masseteric fossa is visible buccally on the posteroventral portion of the dentary, and there is some buccolingual crushing and abrasion of this feature (Figure 3). The dentary is crushed ventral to m3, but the preserved morphology suggests it was bucco-lingually widest at this point of the jaw, as in *Megazostrodon* (Gow 1986). The Meckel's sulcus is present on the ventrolingual surface of the dentary. The sulcus extends from the crushed section of dentary ventral to m3, to the base of p5. Examination of the X-ray CT data indicates that the Meckel's sulcus is crushed transversely, causing the lingual surface of the dentary to collapse buccally towards the mandibular canal, an internal neurovascular canal inside the mandibular body.

The ventral surface of the dentary is more strongly convex anteroposteriorly than in either *Megazostrodon* or *Dinnetherium*, but is closest in curvature to the latter (Figure 2) (Gow 1986; Kielan-Jaworowska *et al.* 2004). This curvature is consistent with the presence of a reduced angular process (as in *Dinnetherium*), and is accentuated by the dorsal curvature of the anterior portion of the dentary, particularly anterior to p5. This curvature is unlike the straighter morphology seen in most other morganucodontans, or in closely related groups such as Docodonta, but resembles some eutricodontans such as *Phascolotherium*, and later eutherians such as *Kennalestes* (Kielan-Jaworowska *et al.* 2004). This similarity is probably functional, resulting from convergent evolution; we do not infer a close relationship between these taxa and *Wareolestes*.

The coronoid crest rises posterodorsally from just posterior to the unerupted m3. The dentary is broken posteriorly, so the coronoid process is missing. It is likely that *Megazostrodon* possessed a coronoid facet that articulated with the coronoid bone just posterior to the ultimate molar. However, this facet is not evident in NMS G.2016.34.1 due to crushing on the lingual surface of the dentary. Despite crushing, the postdentary trough is clearly visible, as in other morganucodontans, and other stem mammals with the primitive character of retaining post-dentary bones (Kielan-Jaworowska *et al.* 2004; Luo 2011; Meng *et al*. 2015). It is smaller than in *Morganucodon*, closer in morphology to *Dinnetherium* (Kielan-Jaworowska *et al.* 2004). Ventral to m3, just ventral to mid-height on the buccal surface of the dentary, abrasion has revealed two small windows into the mandibular canal for the nerves and vessels in the interior of the dentary. This has been digitally reconstructed along some of the length of the dentary (Figure 4) – although crushing and abrasion prevent full reconstruction of this feature.

Anterior to p5 the dentary flares lingually, forming the mandibular symphysis. However, because the dentary is broken anterior to the remnants of the alveoli of c/p1, few morphological details of the symphysis are evident. Foramina are visible anteriorly on the ventrolingual surface of the symphysis, immediately posterior to its broken anterior portion, around the level of dp2/p2. There are at least two foramina, positioned approximately below c and pm1.

The most completely preserved molar tooth is m2. As in the holotype molar, NHMUK PV M36525, the central cusp *a* of m2 in NMS G.2016.34.1 is higher dorso-ventrally than cusps *b* and *c*. Cusp *a* also has distinct dorsoventral ridges on the posterior and anterior surfaces, with corresponding troughs, and there is an expanded labial cingulid that curves around the posterior edge of the tooth. The cingulid bears a prominent cusp *d,* and the cingulid continues onto the labial and lingual surfaces of the tooth. Damage to the buccal side of m2 in NMS

G.2016.34.1 means the highest cingular cusp *g* is not preserved. In the holotype (NHMUK PV M36525), cusp *g* is directly lingual to cusp *a*, unlike in *Morganucodon, Megazostrodon,* and upper molars of *Brachyzostrodon* (Freeman 1979; Hahn *et al*. 1991)). The double roots of m2 are deep in NMS G.2016.34.1, extending close to the ventral surface of the dentary, and are not clubbed at their ventralmost point.

The other molar teeth of NMS G.2016.34.1 are less complete, and show morphologies that are congruent with that of m3. Cusps *c* and *d* are still present on m1, but *a* and *b* are missing, as is the lingual cingulid. The ridge extending from cusp *d* forms the posterior cingulid, which curves onto the lingual side of the tooth. The roots of m1 do not diverge as they extend ventrally, unlike in m3. Instead, they converge at their ventral ends, and they are slightly longer than in m2. Also, the lingual surface of m1 appears slightly flatter than that of m3.

Cusps *a*, *b*, *c* and *d* are visible in m3, despite the tooth being somewhat fractured. This tooth is longer anteroposteriorly than either m1 or m2 (Table 1). The distinct dorsoventral ridges and embayments seen in m2 and the holotype of *Wareolestes rex* are also visible in m3. There is no root present in m3.

DISCUSSION

Referral of NMS G.2016.34.1 to Wareolestes rex

NMS G.2016.34.1 is undoubtedly a morganucodontan: it retains the anteroposterior linear arrangement of the molar cusps that distinguishes morganucodontans from kuehneotheriids. Furthermore, like all other morganucodontans, it retains the postdentary trough and has diphyodont tooth replacement in the preserved premolar positions. This can clearly be seen by the presence or inferred presence of replacement teeth (Crompton & Luo 1993; Luo *et al.* 2004; Kielan-Jaworowska *et al.* 2004) (see below).

Wareolestes was placed in Megazostrodontidae by Hahn *et al.* (1991) and subsequently by Kielan-Jaworowska *et al.* (2004). We refer NMS G.2016.34.1 to Megazonstrodontidae because we infer that it had an apomorphic reduced angular process (the ‘pseudangular’) as seen in *Megazostrodon* (Crompton 1974) and *Dinnetherium* (Jenkins *et al.* 1983). We cannot state whether it also shares the flaring of the dentary peduncle, as this is not preserved in NMS G.2016.34.1, nor the lobed upper molars and well developed cingular cusps, as no upper molars were recovered with NMS G.2016.34.1. However, as we consider this specimen to be referable to *Wareolestes* (see below), these features may be inferred as having been present based on their presence in other megazostrodontids.

We refer NMS G.2016.34.1 to *Wareolestes* based on the following apomorphies shared with the holotype: a substantial cusp *d* positioned directly distal to cusp *c* on a labial cingulid that curves around the posterior of the tooth and continues onto the lingual surface. Like the holotype, it also has wrinkled enamel on cusp *a*, a feature shared with *Brachyzostrodon* and *Helvetiodon*, but that distinguishes it from *Megazostrodon.* We also consider the overall structure and appearance of the tooth to be highly consistent with the holotype of *Wareolestes* (see above and Figure 5). As in the holotype molar, cusp *a* is proportionally longer anteroposteriorly than in *Morganucodon,* and has distinct dorsoventral ridges on its posterior and anterior surfaces, with corresponding troughs, producing shallow 'embayments' (Freeman 1979; p. 160). Kielan-Jaworowska *et al.* (2004; p. 182) noted that the holotype tooth of *Wareolestes rex* is 'one-and-a-half times [the size of] most morganucodont teeth.' The m2 of NMS G.2016.34.1 is larger than the holotype (see Table 1 and Figure 6) and close in size to *Brachyzostrodon maior* and *Helvetiodon schutzi* (Table 1; Figure 6; it is slightly anteroposteriorly shorter and bucco-lingually wider than the m3 teeth of those taxa). The m1 and m3 are also large (though smaller than the holotype). The largest morganucodontid currently known is *Paceyodon davidi* (Clemens 2011), the known molar of which is approximately 20% larger than m3 in NMS G.2016.34.1.

The holotype of *Wareolestes rex* has an enlarged cusp *g* and subequal cusps *b* and *c*, distinguishing it from the megazostrodontid *Dinnetherium,* in which cusp *g* is not enlarged, and cusps *b* and *c* are approximately equal in height. While cusp *g* is missing in NMS G.2016.34.1, it shares the slight elevation of cusp *b* compared to cusp *c*. Finally, it differs from *Indozostrodon* in having a larger cusp *a* – this cusp is smaller, positioned more posteriorly and twinned with cusp *c* in *Indozostrodon*.

A previously cited difference between *Morganucodon* and *Megazostodon* is the manner of occlusion of the molar cusps. In *Morganucodon* it was thought that cusp *a* occludes between cusps *A* and *B* on the opposing upper molar, known as offset shearing (Crompton & Jenkins, 1968; Mills 1971). In *Megazostrodon* cusp *a* was stated to occlude between cusp *B* of the opposing upper molar, and cusp *C* of the preceding upper molar, called embrasure shearing (Crompton 1974). However, recent preliminary work suggests that in *Morganucodon* at least, shearing patterns may be more variable along the tooth row than previously understood (Jäger *et al.* 2016).

Positions of isolated Wareolestes *teeth within the tooth row*

NMS G.2016.34.1 provides information about the positions of previously reported, isolated teeth of *Wareolestes* within the tooth row, and their taxonomic identifications. Since the initial description of *Wareolestes*, there has been disagreement about whether the holotype is an upper or lower molar (Hahn *et al.* 1991; Kielan-Jaworowska *et al.* 2004). The holotype of *Wareolestes rex* NHMUK PV M36525 was described as a lower molar by Freeman (1979), but Hahn *et al.* (1991) and Butler and Sigogneau-Russell (2016) suggested that it may be an upper molar, due to the presence of what appears to be a labial cingulum with ‘well developed labial cingular cusps’ (Kielan-Jaworowska *et al.* 2004; p. 179). Both of these features have been considered diagnostic for megazostrodontid upper molars, alongside partitioning of the labial cingulum into anterior and posterior lobes (Kielan-Jaworowska *et al.* 2004). If NHMUK PV M36525 represents an upper molar, then the surface considered to be the buccal side by Freeman (1979) would be the lingual side (Butler & Sigogneau-Russell 2016) (Figure 1).

Thanks to the *in situ* placement of molars within the dentary in NMS G.2016.34.1, we can clarify the absence of a continuous lingual cingulid in the lower molars of *Wareolestes rex*. Unfortunately, the labial portion of the cingulid is not preserved in any of the molars of NMS G.2016.34.1. The specimen therefore provides no information on the morphology of the labial cingulid in *Wareolestes*. We cannot therefore, compare these cingular structures with those of the holotype to evaluate the status of the holotype (NHMUK PV M36525) as an upper or lower molar based on the cingulum/cingulid. Nevertheless, we have re-examined the anatomy of NHMUK PV M36525 using µCT scanning (Figure 5). The resulting 3D models show that, due to the absence of enamel in the region of the “labial” cingulum/cingulid (Figure 5A) there is no conclusive evidence for a continuous labial cingulum/cingulid, nor what can be described as ‘well developed’ labial cingular/cingulid cusps in the remaining dentine. The cingular cusps appear less well developed in NHMUK PV M36525 than they are in the upper molars of

Megazostrodon (Crompton 1974) or *Brachyzostrodon* (Hahn *et al.* 1991) based on the remaining dentine, and more closely resemble the size of the lingual cusps in lower molars of *Brachyzostrodon maior* (Hahn *et al.* 1991, figure 2). Therefore, the preserved cingular morphology of NHMUK PV M36525 does not provide strong evidence of identity as an upper molar.

Butler and Sigogneau-Russell (2016) referred a megazostrodontid molar from Kirtlington, NHMUK PV M46775, to *Wareolestes* sp. indet., identifying it as an upper. They suggested that the dorsoventrally longer cusps of this specimen, compared to the holotype NHMUK PV M46775 may indicate that this represents a distinct species of *Wareolestes*. We suggest that NHMUK PV M46775 may be an upper molar of *Wareolestes rex*. We base this on the presence of a prominent cingulid both labially and lingually, more developed “labial” cusps than those in the holotype NHMUK PV M36525, and proportionally dorsoventrally longer cusps (see below) than the holotype. Consistent with this, Butler and Sigogneau-Russell (2016) suggested that *Wareolestes* upper molars were transversely wider than the lowers. The morphological difference between NHMUK PV M46775 and the holotype further supports our identification of the holotype as a lower left molar.

The m2 of NMS G.2016.34.1 strongly resembles the holotype specimen of *Wareolestes rex,* NHMUK PV M36525 (Figure 5). The m2 has similar proportions of cusps *c* and *d* and the posterior cingulid where it extends onto the lingual side of the tooth. The m2 of NMS G.2016.34.1 has a more expanded posterior cingulid than the cingulids on m1 or the holotype molar NHMUK PV M36525. The unerupted m3 crown in NMS G.2016.34.1 shows that it had an enlarged posterior portion of the cingulid, also similar to that of m3 but distinct from m1 and the holotype molar. This provides strong evidence for variation along the tooth row and suggests that the holotype molar, NHMUK PV M36525 likely represents an m1 lower molar. The lingual cingulid in both NHMUK PV M36525 and m1 and m2 in NMS G.2016.34.1 tapers out directly below cusp *a*. Gow (1986) described the lower molars in *Megazostrodon* as having dorsoventrally taller cusps than the uppers; the molar cusp heights are proportionally similar between NMS G.2016.34.1 and NHMUK PV M36525 (Figure 5), consistent with identification of NHMUK PV M36525 as a lower molar.

There are some small differences between NHMUK PV M36525 and the new specimen NMS G.2016.34.1, but most are the result of missing portions of enamel in the former, and the missing labial portion of the latter (Figure 6). For example, NMS G.2016.34.1 at first appears bucco-lingually narrower and the lingual molar surface slightly flatter. However, as we have already identified from differences between m1, m2 and m3 in NMS G.2016.34.1, there is variability in tooth morphology along the tooth row. Debuysschere *et al.* (2015) also noted variability in dental characters among Morganucodonta, such as features of the cingulum, related to position in the tooth row. They recommended such characters should therefore be treated with caution. What remains of the molars in NMS G.2016.34.1 supports this assertion. The paucity of megazostrodontid material, lack of enamel on the *Wareolestes* holotype, damage to the specimens, and intraspecific variation in cusp height and cingulum protrusion, suggests caution in treating these differences as anything other than intraspecific variation, and further supports our identification of NMS G.2016.34.1 as *Wareolestes rex*.

Brachyzostrodon lacks a distinguishable cusp *g* on the lower molars (Hahn *et al*. 1991; Crompton & Luo 1993; Kielan-Jaworowska *et al.* 2004). The distinct wrinkling of enamel in *Wareolestes* and *Brachyozostrodon* could suggest a close relationship between these genera. However we consider it unlikely that *Wareolestes* did not possess a cusp *g* on the lower molars, based on the strong morphological similarity between the holotype (above) – which possesses a cusp *g* in the apomorphic position buccal to cusp *a* – and the lower molars in NMS G.2016.34.1.

Pattern of dental replacement in Megazostrodontidae

NMS G.2016.34.1 provides information on the pattern of dental replacement in Megazostrondontidae, thanks to the presence of unerupted and partially erupted premolar and molar teeth, alongside fully developed teeth with complete roots for which no replacement tooth is present (Figure 3). Modes of dental replacement are important for understanding the origins of key aspects of mammalian oral processing. The precise occlusion between upper and lower teeth seen in morganucodontans, while still honed by wear after eruption, is closer to the more precise occlusion of the derived mammalian dentition (Kielan-Jaworowska *et al.* 2004; Luo *et al.* 2004). Critically, it is likely that such occlusion is only possible when rates of tooth replacement are reduced (i.e. diphyodont or single tooth generations).

It is considered beyond doubt that *Morganucodon* exhibited diphyodont replacement of antemolar teeth (incisors, canines, premolars) (Mills 1971; Parrington 1971; Crompton & Luo 1993; Luo *et al.* 2004). Morganucodontans are considered to be the most basal mammaliaforms possessing this pattern of dental replacement (Mills 1971; Parrington 1973; Luo *et al.* 2004; Kielan-Jaworowska *et al.* 2004). This is in contrast to the more stemward mammaliaform *Sinocondon*, which replaced its premolars once, but replaced the canine at least three times and replaced incisors in an alternating sequence, as in many non-mammalian cynodonts (Crompton & Luo, 1993; Zhang *et al.* 1998). There is evidence for the resorption of anterior postcanines in mature individuals of *Morganucodon, Eozostrodon* and *Dinnetherium,* without replacement (Mills 1971; Parrington 1971; Crompton & Luo, 1993). This is a plesiomorphic cynodont characteristic also seen in more basal taxa such as *Sinoconodon* (Crompton & Luo, 1993). There is no evidence to indicate such resorption in NMS G.2016.34.1.

Gow (1986) argued that *Megazostrodon,* a morganucodontan, also replaced its anteriormost molars. There is clear evidence that among morganucodontans the molars in more posterior positions are never replaced, erupting as the individual reaches maturity as in most modern mammals (Parrington 1971; Crompton & Parker, 1978; Luo *et al.* 2004; O'Meara and Asher 2016). The wear facet patterns on many hundreds fragmentary mandibles of *Morganucodon watsoni* show no evidence of replacement in the posterior molars (Parrington 1971; Young 1982; Crompton & Luo 1993); with molars frequently heavily worn in larger and older individuals, suggesting they had not been replaced (Parrington 1971). A similar observation has been made in four dentaries of *Megazostrodon* (Crompton 1974; Gow 1986) and eight dentaries of *Dinnetherium* (Jenkins *et al.* 1983). Gow (1986) suggested that *Megazostrodon* may have replaced its m2 due to this molar being less worn than m1 or m3 in two specimens from the Early Jurassic Elliot Formation, South Africa. However, Luo *et al*. (2004) considered the sample size too small to be definitive.

Our observations are consistent with the proposition that *Wareolestes*, a megazostrodontid morganucodontan, did not replace its molar teeth. We find no evidence for replacement for m1, m2 or m3 in NMS G.2016.34.1, despite the presence of replacement teeth more anteriorly along the tooth row. The m1 and m2 of this specimen have deep and well-developed roots that have not been even partially resorbed, and no portions of any replacement teeth are present at these loci. In contrast, the alveolus of p5 does not contain well developed roots or fragments thereof, suggesting that the preserved portion of p5 was an unerupted replacement tooth (Figure 3). In support of this hypothesis, we note that the preserved portion of p5 is located within the body of the jaw, roughly level with the emerging p4, indicating that this tooth was developing and erupting from the dentary at approximately the same time as p4.

NMS G.2016.34.1 provides evidence for specifically diphyodont replacement of the premolar teeth in *Wareolestes*, consistent with observations of *Morganucodon* (Young 1982; Crompton & Luo, 1993). Premolar dp2/p2 comprises the roots of an erupted ‘milk tooth’ with the replacement premolar forming beneath. The alveoli for the deciduous premolars are clearly visible in the dentary, and the p4 remains within the dentary just ventral to the alveolar border.

Nevertheless, the pattern of dental replacement seen in *Wareolestes* is not identical to that described for *Morganucodon*. In both *Morganucodon*, and the more stemward mammaliaform *Sinoconodon*, premolar replacement occurs in a sequence from anterior to posterior (‘antero-posterior replacement’; Crompton & Luo, 1993; Zhang *et al.* 1998). However, in NMS G.2016.34.1 both preserved replacement premolars (p2, p4), and the preserved portion of p5, are located at approximately equal height within the dentary, indicating that antero-posterior replacement did not occur, or was only weakly manifested. Interestingly, p3 is represented only by an empty alveolus, and it is possible that the absence of a replacement p3 within the body of the dentary indicates a different timing of replacement at this locus. If correct, then this suggests possible alternate replacement of premolars in *Wareolestes*. Antero-posterior replacement of premolars is considered a derived character for Mammaliaformes (Rowe 1998; McKenna & Bell 1997). However, some stem therians and eutherian mammals developed alternating premolar replacement (Luo *et al.* 2004). Due to damage to the buccal side of the dentary, we do not consider there to be conclusive evidence for the sequence of premolar replacement in *Wareolestes*. As the anterior portion of the dentary is missing, NMS G.2016.34.1 also does not provide evidence on the replacement patterns of incisors or canines in *Wareolestes*.

CONCLUSIONS

The megazostrodontan morganucodontid *Wareolestes rex* was erected for a single molar tooth from Kirtlington in England (Freeman 1979), and until now only four isolated molariform teeth we referred to *W. rex*. Our new specimen NMS G.2016.34.1, a left dentary, extends the known distribution of this genus to the Kilmaluag Formation of the Isle of Skye, Scotland, and adds to the faunal list for this locality.

Through morphological comparison, the molars remaining in the dentary provide strong evidence supporting the original identification of holotype specimen of *W. rex* as a lower left m1. NMS G.2016.34.1 indicates an apomorphic labial cingulid in *Wareolestes rex*, previously incorrectly identified as lingual cingulid.

Replacement teeth within the dentary indicate a diphyodont replacement of the premolariform dentition. This supports previous evidence for such tooth replacement patterns in other morganucodontans, including *Morganucodon, Megazostrodon* and *Dinnetherium*. We find no evidence for replacement in m2, as suggested for *Megazostrodon* (Gow 1986).

Due to abrasion on the buccal portion of the dentary and loss of p1 and p3, we cannot clearly identify the sequence of dental replacement along the tooth row of NMS G.2016.34.1. However, the absence of a replacement p3 within the body of the dentary suggests possible alternating premolar replacement in *Wareolestes*, a character seen in some stem therians and eutherian mammals. We hope that further finds may clarify this. We emphasize the importance of ongoing field work and collection in the Kilmaluag Formation, and the wealth of data it adds to our understanding of Middle Jurassic mammaliaform diversity and the assembly of mammalian characters.

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DATA ARCHIVING STATEMENT

Data for this study are available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.5n36j

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Figure 1: *Megazostrodontidae* cusp terminology. A, holotype *Wareolestes rex* NHMUK PV M36525 as an upper molar, lingual view. B, holotype *Wareolestes* NHMUK PV M36525 as an upper molar, labial view. C, holotype NHMUK PV M36525 as a lower molar as originally described, lingual view. D, segmented tooth from new specimen NMS G.2016.34.1 in labial view. Light shading indicates loss of enamel, dark shading missing portion of tooth. Arrow indicates anterior direction. Scale bar equals 1 mm.

Figure 2: New specimen of *Wareolestes rex*, NMS G.2016.34.1 with comparative material. A, buccal view of *Wareolestes rex*, NMS G.2016.34. B, line drawing of *Wareolestes rex*, NMS G.2016.34, reduced in size for comparison with corresponding portions of C and D. C, line drawing of buccal view of *Dinnetherium nezorum*. D, line drawing of buccal view of *Megazostrodon rudnerae*. Sources: C, composite drawing from Gow (1986) and Keilan-

Jaworowska *et al*. (2004); D, composite drawing from Jenkins *et al*. (1983) and Keilan-Jaworowska et al. (2004). Scale bar equals 1 mm.

Figure 3: Segmentation and digital reconstruction of the new specimen of *Wareolestes rex* G.2016.34.1 from µCT scan data. A, lingual view of dentition. B, lingual view of dentary. C, occlusal view of dentition. D, occlusal view of dentary. E, buccal view of dentition. F, buccal view of dentary with replacement pattern in *Wareolestes* underneath. G, dp2/p2 enlarged, showing deciduous premolar outlined in dotted line (blue), replacement premolar cusp *a* in solid line (red). p = premolar, dp = deciduous premolar, m = molar. Arrows indicate anterior direction. Scale bar equals 1 mm.

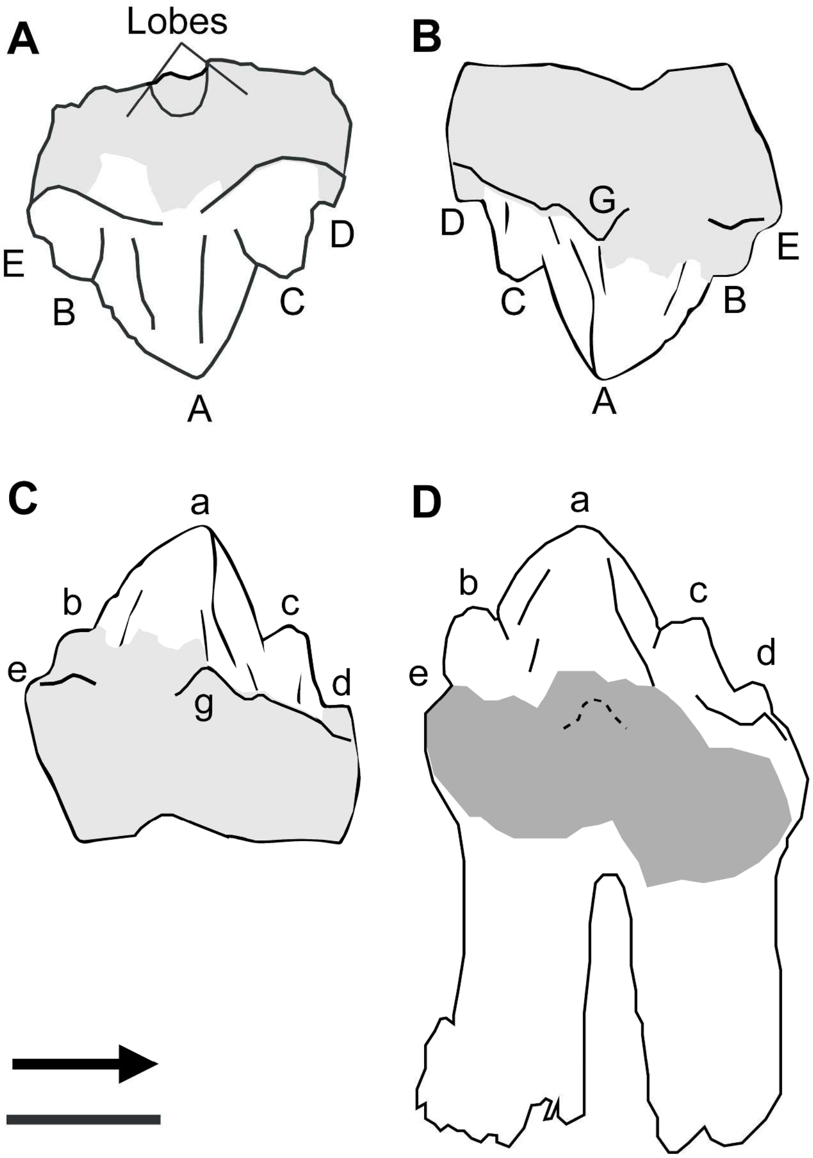
Figure 4: Detail of features of NMS G.2016.34.1. A, buccal view of the anterior of the dentary showing the single root alveoli followed by double root (see text). B, molarised morphology of the remnant of cingulid in p5. C, segmented pathway of the mandibular nerve within the dentary. Scale bars equal 1 mm.

Figure 5: Comparisons between the reconstructed µCT scan of the holotype *Wareolestes rex* NHMUK PV M36525 as a lower molar, and m1 and m2 from NMS G.2016.34.1. A, buccal view of NHMUK PV M36525. B, buccal view of m1 NMS G.2016.34.1. C, buccal view of m2 NMS G.2016.34.1. D, lingual view of NHMUK PV M36525. E, lingual view of m1 NMS G.2016.34.1. F, lingual view of m2 NMS G.2016.34.1. G, occlusal view of NHMUK PV M36525. H, occlusal view

of m1 NMS G.2016.34.1. I, occlusal view of m2 NMS G.2016.34.1. Grey areas indicate broken portions of tooth. Dotted lines indicate reconstructed features based on comparisons. Arrows indicate anterior direction. Scale bar equals 1 mm.

Figure 6: Lower molar measurements for new specimen and comparative material (see Table 1). Mean measurement from multiple specimens used for *Brachyzostrodon coupatezi*, *Bridetherium* and *Hallautherium*. Includes largest (l) and smallest (s) measurements for *Morganucodon watsoni* from Pacey (1978).

Table 1: Measurements of new specimen and comparative data from Morganucodontidae. For partial teeth of *Wareolestes rex*, estimates were made conservatively.



Megazostrodontidae cusp terminology. A, holotype *Wareolestes rex* NHMUK PV M36525 as an upper molar, lingual view. B, holotype *Wareolestes* NHMUK PV M36525 as an upper molar, labial view. C, holotype NHMUK PV M36525 as a lower molar as originally described, lingual view. D, segmented tooth from new specimen NMS G.2016.34.1 in labial view. Light shading indicates loss of enamel, dark shading missing portion of tooth. Arrow indicates anterior direction. Scale bar equals 1mm.

Figure 1

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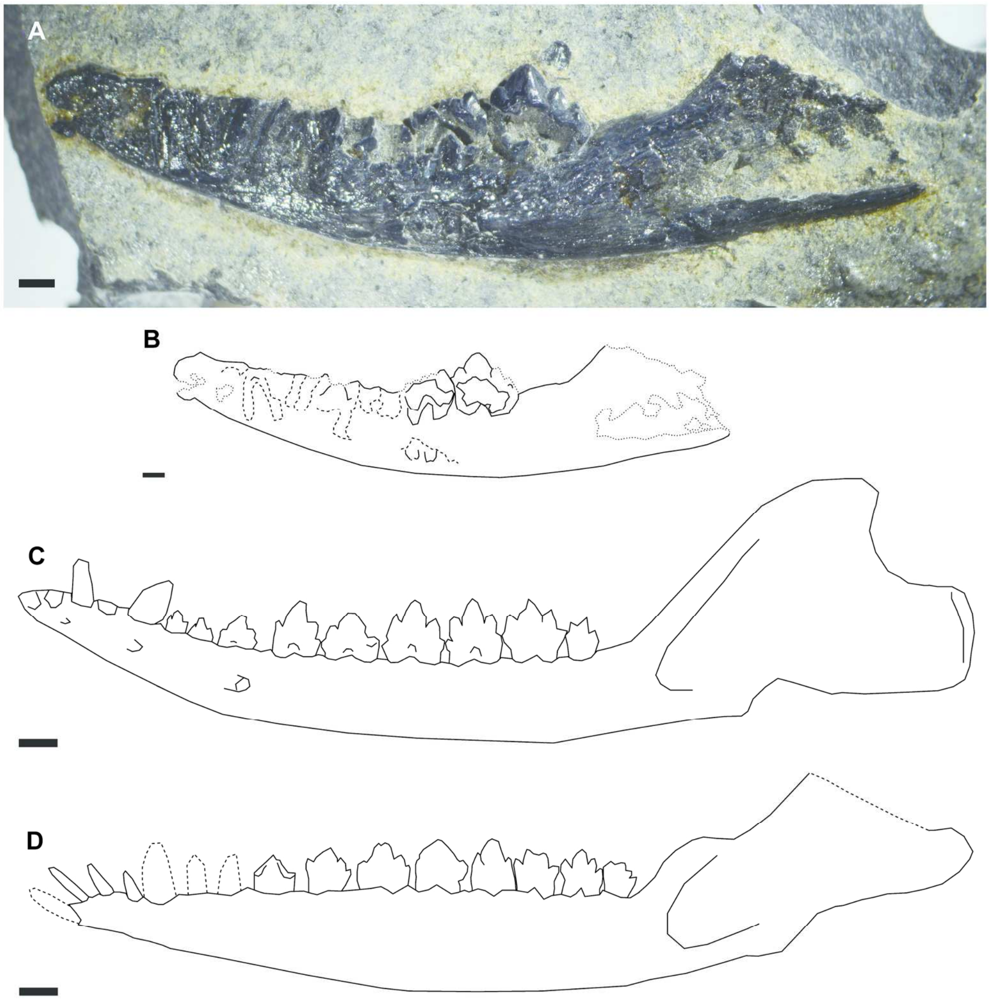
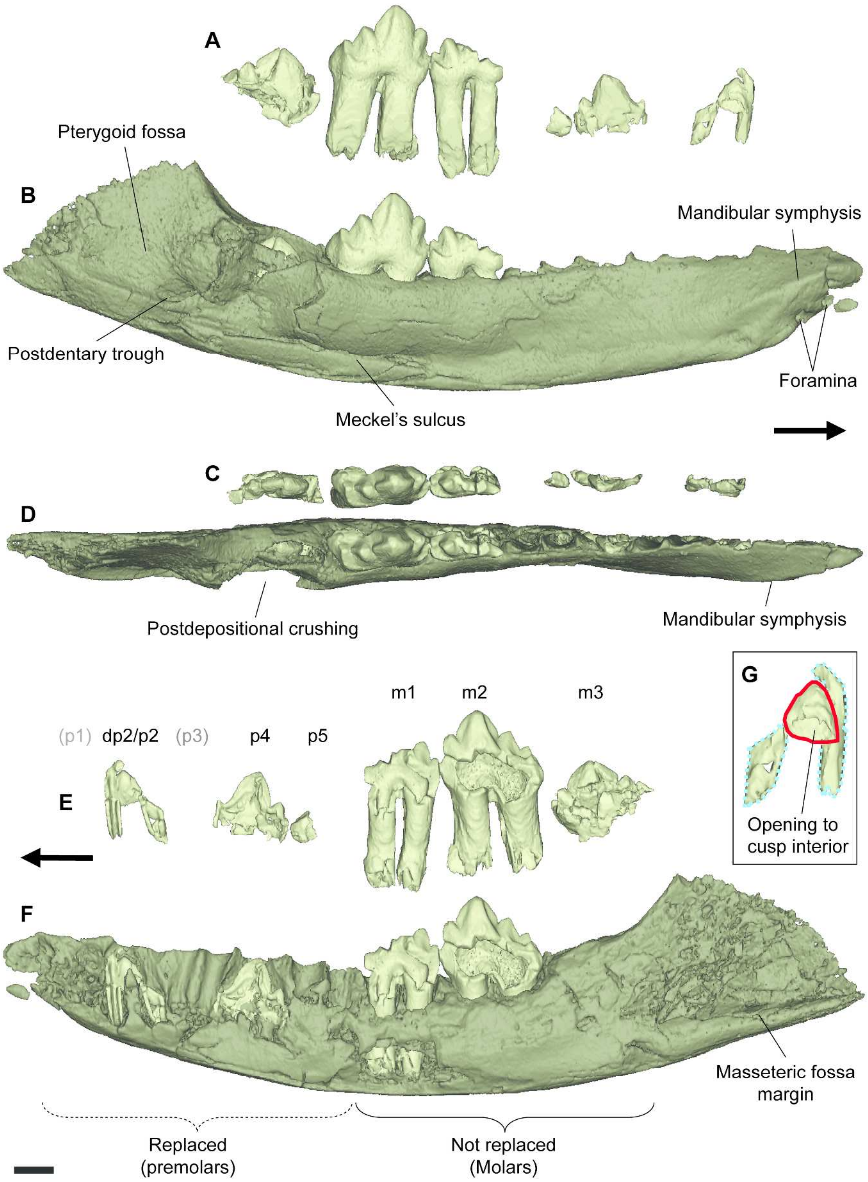


New specimen of *Wareolestes rex*, NMS G.2016.34.1 with comparative material. A, buccal view of *Wareolestes rex*, NMS G.2016.34. B, line drawing of *Wareolestes rex*, NMS G.2016.34, reduced in size for comparison with corresponding portions of C and D. C, line drawing of buccal view of *Dinnetherium nezorum*. D, line drawing of buccal view of *Megazostrodon rudnerae*. Source: C, composite drawing from Gow (1986) and Keilan-Jaworowska et al. (2004). D, composite drawing from Jenkins et al. (1983) and Keilan-Jaworowska et al. (2004). Scale bar equals 1 mm.

Figure 2

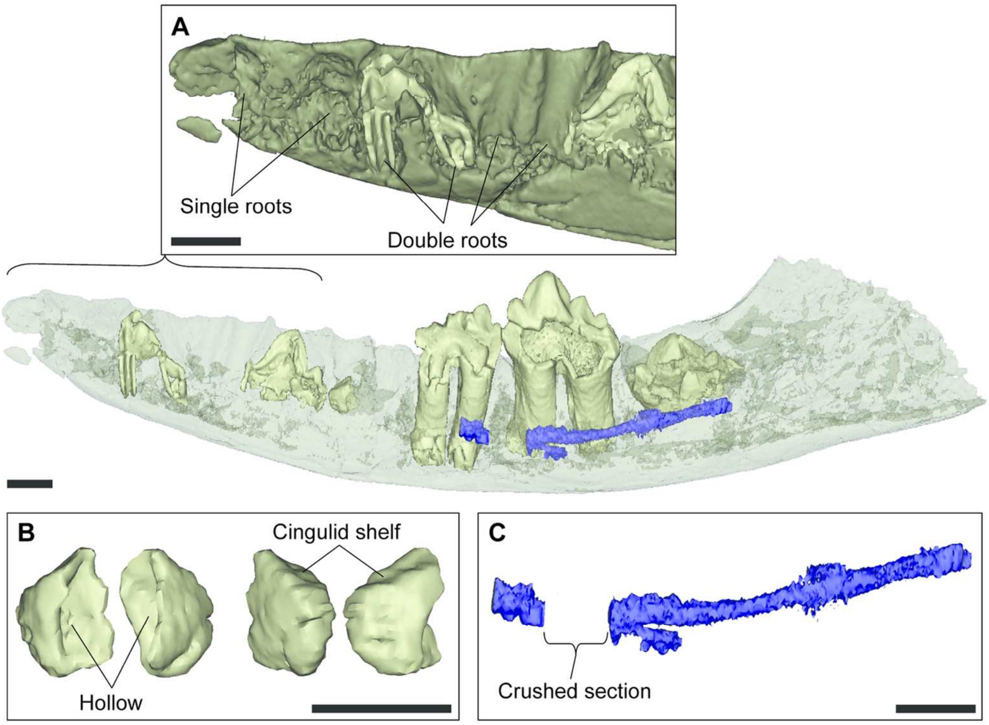
175x181mm (300 x 300 DPI)



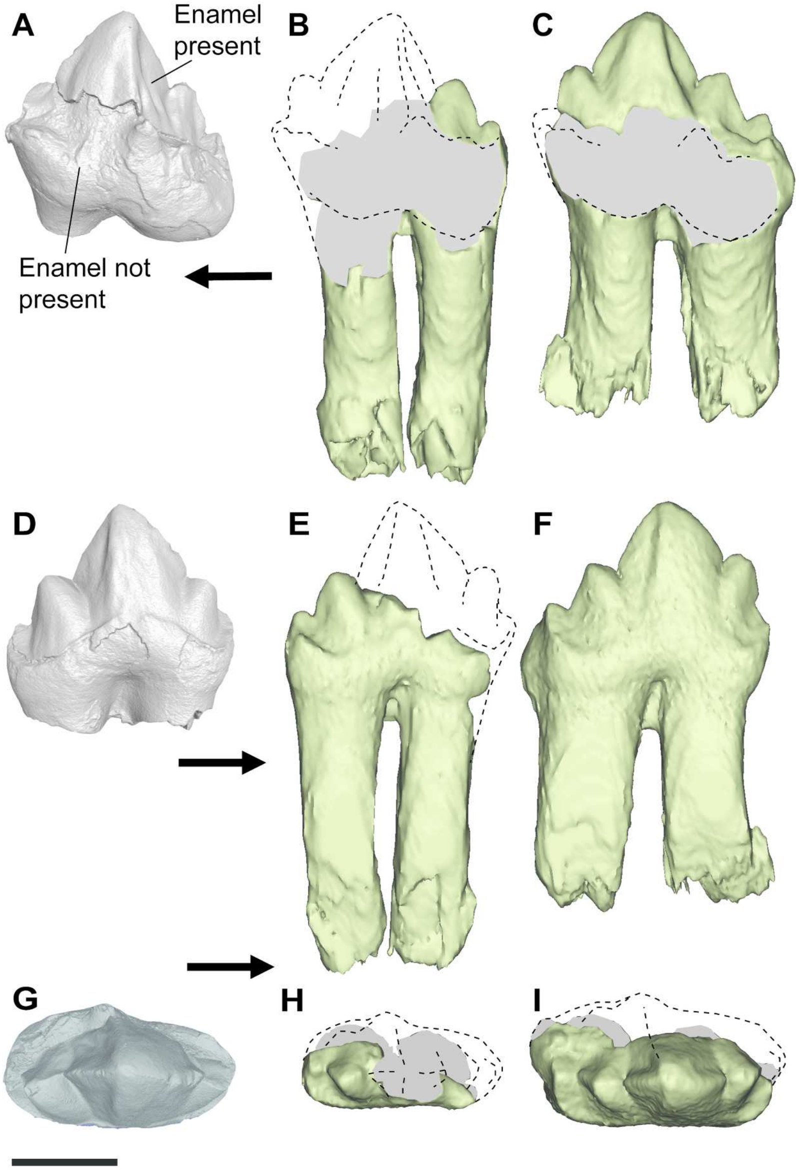
Segmentation and digital reconstruction of new *Wareolestes rex* G.2016.34.1 from µCT scan data. A, lingual view of dentition. B, lingual view of dentary. C, occlusal view of dentition. D, occlusal view of dentary. E, buccal view of dentition. F, buccal view of dentary with replacement pattern in *Wareolestes* underneath. G, dp2/p2 enlarged, showing deciduous premolar outlined in dotted line (blue), replacement premolar cusp a in solid line (red). p = premolar, dp = deciduous premolar, m = molar. Arrows indicate anterior direction. Scale bar equals 1 mm.

Figure 3

227x312mm (300 x 300 DPI)



Detail of features of NMS G.2016.34.1. A, buccal view of the anterior of the dentary showing the single root alveoli followed by double root (see text). B, molarised morphology of the remnant of cingulid in p5. C, segmented pathway of the mandibular nerve within the dentary. Scale bars equal 1mm.
Figure 4
122x90mm (300 x 300 DPI)



Comparisons between the reconstructed µCT scan of the holotype Wareolestes rex NHMUK PV M36525 as a lower molar, and m1 and m2 from NMS G.2016.34.1. A, buccal view of NHMUK PV M36525. B, buccal view of m1 NMS G.2016.34.1. C, buccal view of m2 NMS G.2016.34.1. D, lingual view of NHMUK PV M36525. E, lingual view of m1 NMS G.2016.34.1. F, lingual view of m2 NMS G.2016.34.1. G, occlusal view of NHMUK PV M36525. H, occlusal view of m1 NMS G.2016.34.1. I, occlusal view of m2 NMS G.2016.34.1. Grey areas indicate broken portions of tooth. Dotted lines indicate reconstructed features based on comparisons. Arrows indicate anterior direction. Scale bar equals 1mm.

Figure 5

161x238mm (300 x 300 DPI)

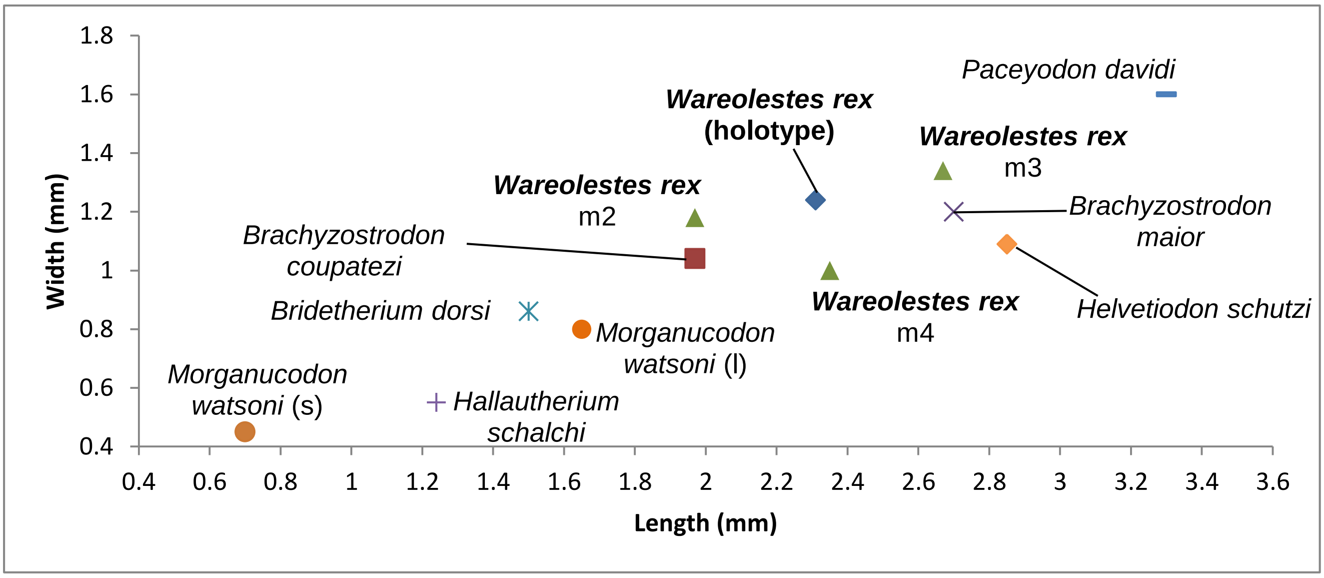

Paceyodon davidi
Wareolestes rex (holotype)
Wareolestes rex m3
Wareolestes rex m2
Brachyzostrodon coupatezi
Brachyzostrodon maior
Helvetiodon schutzi
Wareolestes rex m4
Bridetherium dorsi
Morganucodon watsoni (l)
Morganucodon watsoni (s)
Hallautherium schalchi
Width (mm)
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.4
0.6
0.8
1
1.2
1.4
1.6
1.8
2
2.2
2.4
2.6
2.8
3
3.2
3.4
3.6
Length (mm)

Table 1: Measurements of new specimen and comparative data from Morganucodontidae. For partial teeth of *Wareolestes rex,* estimates were made conservatively.

Taxon	**Dentition**	**Specimen No.**	**Max length (mm)**	**Max width (mm)**	**Reference**
Megazostrodontidae					
Wareolestes rex	Lower m2	NMS G.2016.34.1.	1.97 (estimate)	1.18 (estimate)	
Wareolestes rex	Lower m3	NMS G.2016.34.1.	2.67	1.30 (estimate)	
Wareolestes rex	Lower m4	NMS G.2016.34.1.	2.35 (estimate)	1.0 (estimate)	
Wareolestes rex	molar	NHMUK PV M36525	2.31	1.24	Freeman (1979)
Brachyzostrodon coupatezi	lower molars	Multiple	1.75-2.15	0.75-1.21	Hahn *et al.* (1991)
Brachyzostrodon maior	lower molars		2.7	1.2	Hahn *et al.* (1991)
Morganucodontidae					
Paceyodon davidi	lower molars	multiple	3.3	1.6	Clemens (2011)
Morganucodon watsoni	lower molars	multiple	0.70-1.65	0.45-0.80	Pacey (1978)
Morganucodon watsoni	upper molars	multiple	0.80-1.60	0.45-0.80	Pacey (1978)
Morganucodon oehleri	lower molars	Multiple	1.06-2.30	CUP 2320	Kermack *et al.* (1973)
Morganucodon oehleri	upper molars	Multiple	1.40-2.30	CUP 2321	Kermack *et al.* (1973)
Hallautherium schalchi	lower molars	Multiple	1.08-1.39	0.44-0.66	Clemens (1980)
Helvetiodon schutzi	upper molar		2.85	1.09	Clemens (1980)
Incertae sedis					
Bridetherium dorsi	lower molars	Multiple	0.85-1.90	0.48-1.15	Clemens (2011)
Bridetherium dorsi	upper molars	Multiple	1.02-1.70	0.55-0.96	Clemens (2011)