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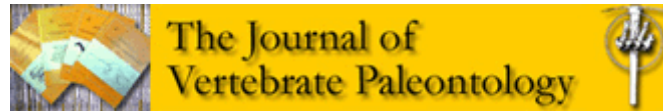
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The mandible and dentition of *Borealestes serendipitus* (Docodonta) from the Middle Jurassic of Skye, Scotland

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3 The mandible and dentition of *Borealestes serendipitus* (Docodontia) from the
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5 Middle Jurassic of Skye, Scotland
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35 RH: PANCIROLI ET AL. —MANDIBLE AND DENTITION OF *BOREALESTES*
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6 **ABSTRACT**—The Middle Jurassic docodont *Borealestes serendipitus* was the
7 first Mesozoic mammal found in Scotland over forty years ago. Its affinities and
8 morphology remain poorly understood. Although multiple dentary fragments and
9 isolated teeth have been recovered from Scotland and England, they have not
10 yet been described in sufficient detail. We report new, more complete specimens
11 collected during recent field work on Skye, Scotland, combined with previously
12 collected material. This includes upper and lower dentition and an almost
13 complete right dentary. We present an updated description and diagnosis of the
14 genus *Borealestes*, based on high resolution micro-CT and synchrotron scans.
15 We identify seven key features that distinguish *Borealestes* from other
16 docodonts, including a pronounced a–c crest, absence of the a–g crest on cusp
17 a, an anterior fovea at the buccolingual midpoint of the upper molar, and the
18 convergence of the Meckel’s groove with the ventral margin of the mandible. We
19 also present a revised diagnosis for the second species, *B. mussettae*. Our
20 phylogenetic analysis supports a clade formed by *Borealestes*, *Haldanodon*,
21 *Docofossor* and *Docodon*. Ontogenetic variation in the mandibular morphology of
22 *Borealestes* is similar to that seen in *Docodon* and *Haldanodon*, with the delayed
23 emergence of the ultimate lower molar, the shift of the last molar to the front of
24 the coronoid process, and a posterior shift of the Meckel’s sulcus in successively
25 older individuals. This supports a distinctive growth pattern in the clade including
26 *Borealestes* and *Docodon*, one that may be present in Docodonta as a whole.
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INTRODUCTION

Docodonta are an extinct clade of mammaliaforms that fall outside the mammalian crown group, and are therefore important for understanding the morphological evolution of mammals as a whole (Simpson, 1929; Lillegraven and Krusat, 1991). Docodonts were previously thought to be closely related to Morganucodonta due to some shared features (Hopson and Crompton, 1969; Kermack et al., 1973), or as the basal-most clade of stem mammals (= Mammaliaformes) (Lillegraven and Krusat, 1991). However, in recent decades more complete cranial and skeletal material has led to the consensus that the Docodonta clade is closer to crown group mammals than to *Sinoconodon* and Morganucodonta (Wible and Hopson, 1993; Luo, 1994; Luo et al., 2002; Martin, 2005). In some recent phylogenetic assessments of stem mammaliaforms, docodonts are more basal than Kuehneotheria (Gill, 2004) and haramiyidans (e.g., Luo et al., 2015a; 2017). It has been suggested that docodonts are more closely related to Late Triassic mammaliaforms such as *Tikitherium*, *Woutersia*, and *Delsatia*, but these hypothesized relationships are currently based on the isolated molars of these taxa, and are tentative at the best (Sigogneau-Russell and Hahn, 1995; Datta, 2005; Luo and Martin, 2007; Averianov et al., 2010).

All docodonts share a highly distinctive dental morphology, and they were one of the first mammaliaform clades to emerge across Eurasia in the Middle Jurassic (Lopatin and Averianov, 2005; Waldman and Savage, 1972; Luo and Martin, 2007). They are particularly abundant in fossil deposits of the Middle–

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3 Late Jurassic (Hu et al., 2006; Luo, 2007; Averianov et al., 2010; Martin et al.,
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5 2010; Meng et al., 2015; Rougier et al., 2015).
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8 The postdentary elements—homologs to mammalian middle ear—remain
9
10 attached to the dentary in docodonts, a plesiomorphic characteristic in stem
11
12 mammaliaforms (Lillegraven and Krusat, 1991; Ji et al., 2006; Luo, 2011; Meng
13
14 et al., 2015). Nevertheless, docodonts are unique among Mesozoic clades in
15
16 possessing distinctively complex molar cusps and crests. It is generally accepted
17
18 that docodont molars are capable of versatile shearing and crushing functions
19
20 not seen in other stem group mammaliaforms (Jenkins, 1969; Gingerich, 1973;
21
22 Butler, 1997; Schultz et al., 2017). This may have contributed to their unusually
23
24 diverse ecological specialisations. Docodonts are now known to have had very
25
26 divergent locomotor morphologies, including semi-aquatic, fossorial, and arboreal
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28 specialisations, as revealed by well-preserved postcranial skeletons (Ji et
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30 al., 2006; Luo et al., 2015b; Meng et al., 2015).
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35 *Borealestes* from the UK (Waldman and Savage, 1972; Sigogneau-Russell,
36
37 2003) is among the geologically oldest docodonts, being Bathonian in age.
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39 *Castorocauda* and *Agilodocodon* from China are also possibly from the latest
40
41 Bathonian (Meng et al., 2015; Xu et al., 2017). The youngest record for
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43 Docodonta is *Sibirotherium* from the Early Cretaceous of Russia (Maschenko et
44
45 al., 2002). Docodonta were most diverse in the Middle Jurassic, and had a
46
47 Laurasian distribution—this is with the possible exception of *Gondtherium* from
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49 Toarcian sediments in India (Prasad and Manhas, 2001, 2007). However, due to
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51 a paucity of material and poor preservation, the docodont affinities of
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3 *Gondtherium* are currently unresolved (Kielan-Jawarowska et al., 2004;
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5 Averianov et al., 2010).

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8 The holotype of *Borealestes serendipitus* was discovered in the Kilmaluag
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10 Formation (Bathonian) of the Isle of Skye in the 1970s, and was the first
11
12 Mesozoic mammal to be found in Scotland (Waldman and Savage, 1972). The
13
14 holotype comprises a fragment of dentary, and three other dentary fragments
15
16 were reported at the same time and referred to *B. serendipitus* by preliminary
17
18 identification. These additional specimens are described here for the first time. A
19
20 partial mammal skeleton of uncertain affinity was also collected from Kilmaluag
21
22 Formation in early 1970s. We can now confirm the identity of this specimen as
23
24 *Borealestes serendipitus* herein, on the basis of its almost complete dentary,
25
26 along with associated upper molars, and incisors. The characteristics of these
27
28 parts of the fossil are described here (the rest of the skeleton is currently under
29
30 study by EP; Panciroli et al., 2018).

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33 Isolated molars of *B. serendipitus* were later recovered from the Forest
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35 Marble Formation in Kirtlington (Sigogneau-Russell, 2003) and Watton Cliff
36
37 (Evans, 1992) in England, all Bathonian (Middle Jurassic) in age. A second
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39 species, *B. mussettae*, was later erected based on molars from Kirtlington
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41 (Sigogneau-Russell, 2003). Multiple specimens from Kirtlington have been
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43 referred to *B. serendipitus* and *B. mussettae*, but not all specimens have been
44
45 fully described.

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48 Additional specimens of *Borealestes serendipitus* have been recovered
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50 during recent field work on the Isle of Skye, along with several other Mesozoic
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3 mammaliaforms including the cladotherian mammal *Palaeoxondon ooliticus*, and
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5 the morganucodontan *Wareolestes rex* (Close et al., 2016; Panciroli et al.,
6
7 2017a, 2018b). Material found during field work in 2016 includes another dentary
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9 of *Borealestes* (NMS G.2018.27.1, found by EP).

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12 We re-examine previously collected material and combine it with newly
13
14 collected specimens. We provide a full description of the dental and mandibular
15
16 morphology of *Borealestes serendipitus*. This includes: the complete lower
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18 dentition and dental formula; postdentary trough and its related structures;
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20 Meckel's groove; efflected angular process; dentary peduncle; and nerve and
21
22 blood vessel channels within the dentary. Based on this body of new information
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24 we provide a revised and expanded diagnosis for the genus *Borealestes*, and
25
26 distinguishing features of *B. serendipitus* and *B. mussettae*. We have also
27
28 reviewed the material for *Borealestes* in light of this diagnosis, and updated the
29
30 referred specimen lists accordingly. We find evidence for ontogenetic changes in
31
32 mandibular structures, as recently described in *Docodon* (Schultz et al., 2017).
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34 The more complete documentation of the dental and mandibular morphology of
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36 *Borealestes* provides new characters for an updated phylogenetic analysis of all
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38 docodonts including *Borealestes*.
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47 GEOLOGICAL BACKGROUND

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51 The Kilmaluag Formation on the Isle of Skye crops out on the Scottish Inner
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53 Hebridean Islands of Eigg, Skye and Muck. It was formerly known as the
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3 Ostracod Limestone, as the base of the formation is defined by the occurrence of
4 ostracod-bearing calcareous and fissile mudstones (Barron et al., 2012).
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7 Although exact biostratigraphical correlations with Jurassic sites in England have
8 proven difficult, the Kilmaluag Formation is now considered to be late Bathonian
9
10 in age, and to correlate with the Forest Marble Formation at Kirtlington Cement
11 Quarry in Oxfordshire (Barron et al., 2012). The similarities in vertebrate faunal
12 composition with Kirtlington Cement Quarry also supports a late Bathonian age
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14 for these localities.
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21 Unlike other formations within the Great Estuarine Group, the Kilmaluag
22 Formation includes predominantly freshwater facies, and there are abundant
23 freshwater ostracods such as *Darwinula* (Wakefield, 1995), shallow freshwater to
24 oligohaline conchostracans (Chen and Hudson, 1991) and freshwater gastropods
25 (Andrews, 1985; Morton and Hudson, 1995; Barron et al., 2012).
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33 Paleoenvironmental reconstructions suggest a low-salinity environment of closed
34 off lagoons with freshwater input, occasionally drying out to form mudcracks
35 (Andrews, 1985). Highly fossiliferous vertebrate-bearing beds of the Kilmaluag
36 Formation are located on the Strathaird Peninsula and comprise micritic grey
37 limestones with detrital quartz and clay in varying fractions. Vertebrate remains
38 include fish and sharks, turtles, crocodylomorphs, pterosaurs, lepidosaurs,
39 choristoderes, mammaliaforms and tritylodontids, as well as some dinosaur
40 fossils (Waldman and Savage, 1972; Evans et al., 2005; Barrett, 2006; Anquetin
41 et al., 2009, 2010; Wills et al., 2014; Close et al., 2016; Panciroli et al., 2017a,
42 2017b, 2018).
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3 Most of the micro-computed tomographic data (microCT) were obtained at
4 the University of Bristol using a Nikon XTH225ST scanner with a 225kV rotating
5 target with a peak energy of 140 kV. Resolution varies between specimens:
6 BRSUG 20570, BRSUG20571, BRSUG29007 and NMS G.1992.47.121.4 are
7 6.77 μm ; and NMS G.1992.47.121.3 is 12.77 μm . Synchrotron data for NMS
8 G.2018.27.1 and NMS G.1992.47.121.1 were obtained at the European
9 Synchrotron Radiation facility (ESRF), Grenoble, France. The resolution for NMS
10 G.2018.27.1 is 6.35 μm . For NMS G.1992.47.121.1 the scan resolution was 6.15
11 μm , which was subsequently resampled to 12.3 μm . All microCT and synchrotron
12 scans were digitally reconstructed and image processed using Mimics 19.0 at the
13 National Museum of Scotland, Edinburgh. Specimens were also observed using
14 conventional microscopy. All digital reconstructions can be found in the online
15 depository: www.morphosource.org

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33 Measurements were taken from digitally reconstructed microCT scans in
34 Mimics 19.0. It is unclear in previous studies how molar measurements were
35 taken, so in order to standardise our measurements, we measured as follows
36 (Fig. 1): for lower molar length we measured across the length of the tooth
37 anteroposteriorly from cusps d to b, and cusps df to e; for upper molar length we
38 measured the longest length on the labial part of the molar, and the longest on
39 the lingual wing of the molar. For lower molar width we measured mediolaterally
40 across cusp c, and across cusp g at right angles (in occlusal view) to the length
41 measurement from cusp d to cusp b. For width of upper molars we measured
42 across cusp X to midway anteroposteriorly along the buccal edge of the molar.
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3 Premolar and canine tooth measurements were taken anteroposteriorly from
4 most anterior to most posterior edge of the crown, and mediolateral width was
5 taken across the cusp of the tooth at the base of the crown. Although the latter
6 width was not always the widest due to slight bulging of the cingulid in the
7 premolars, measuring in this way provides a more consistent measurement and
8 the difference was usually ≤ 0.1 mm.
9

10
11 We analysed the character matrix used by Meng et al. (2015) including
12 updated and rescored character states for *Borealestes serendipitus* and
13 *Borealestes mussettae*. This data matrix has 23 taxa (24 with *B. mussettae*)
14 scored for 48 characters of the dentary (47 in the original matrix, with one
15 additional character), and upper and lower dentition. Of these taxa, fourteen are
16 docodonts and nine are other mammaliaforms, including *Gondtherium*, a
17 disputed docodont (Averianov et al., 2010), which is now found to fall outside of
18 Docodonta (Meng et al., 2015).
19

20
21 Some character states for the other taxa in the matrices provided in Meng
22 et al. (2015) differed between the character listing, NEXUS and PAUP sections of
23 their supplementary materials. Therefore, we re-assessed all of these character
24 states for this analysis (see Supplementary material for complete character list,
25 character matrix, and details of updated and rescored characters).
26

27
28 We analysed these data as for Meng et al. (2015), using PAUP* 4.0. A
29 branch and bound tree search was conducted using parsimony with characters
30 unordered and equally-weighted. One tree of 117 steps was retained. Our time-
31 scaled phylogeny was created in R using the strap package. First and last
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3 MAMMALIAFORMES Rowe, 1988 (emended)

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5 DOCODONTA Kretzoi, 1946

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7 DOCODONTIDAE Simpson, 1929

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10 *BOREALESTES* Waldman and Savage, 1972

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12 **Revised Diagnosis**—Dental formula 4.1.?.5.4/ 4.1.5.6. Upper molars of
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14 *Borealestes*: buccolingually wide and mesiodistally short; upper molars ‘figure 8’
15 shape, with anteroposteriorly constricted waist; two main buccal cusps, A and C,
16 plus a small cusp B in the buccomesial corner; lingual half of the upper molar has
17 main anterior lingual cusp X; cusp X larger and more prominent than smaller
18 posterior lingual cusp Y; labial cusps connected by a ridge/ridges
19 anteroposteriorly; transverse ridge extends between the main anterior labial cusp
20 A and the main lingual cusp X. Lower molars: elongated anteroposteriorly, with
21 labial row of higher cusps arranged in anterioposterior alignment with largest
22 cusp a, and lingual row of smaller cusps with distinctive anterior cusp g and
23 larger posterior cusp c; lower molars have cusps b–a–c in a triangular
24 arrangement. Docodonts differs from other mammaliaforms but similar to
25 pseudotribosphenids in possessing an anterior ‘pseudotalonid basin’—anterior to
26 the ‘trigonid’—formed by cusps a, b and g. Docodonts possess the plesiomorphic
27 mammaliaform trait of attachment of postdentary elements to the dentary.
28
29 *Borealestes* has an efflected angular process (sensu Simpson, 1929) and an
30 enlarged medial ridge protuberance (sensu Schultz et al., 2017), both are
31 docodont autapomorphies. *Borealestes* possesses enlarged and pointed upper
32 and lower canines that are two-rooted, as in other docodonts.
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3 Among docodonts, *Borealestes* most closely resembles *Krusatodon*,
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5 *Castorocauda* and *Haldanodon* in lower molar morphology. These taxa share the
6
7 derived feature of a larger cusp c than cusp g. It resembles *Castorocauda* and
8
9 possibly also *Itatodon* in having a slightly recurved cusp c. *Borealestes*
10
11 possesses an anterior 'cingulid' on the lower molars incorporating cusp e, similar
12
13 to *Castorocauda* and *Docodon*. Cusp e is anteriorly projecting and forms part of
14
15 the d–df–e interlock with the neighbouring molar, as in *Krusatodon* and
16
17 *Simpsonodon*. On the premolars *Borealestes* has a distinct lingual cingulid and a
18
19 posterior labial cingulid, as seen in most other docodontans. Unlike
20
21 *Simpsonodon*, *Agilodocodon*, and *Docodon*, but like most other docodonts,
22
23 *Borealestes* does not have dense creases and pits or other ornamentation on
24
25 molar enamel surfaces. *Borealestes* species have a very distinctive a–c crest.

26
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28 In upper molar morphology, *Borealestes* differs from all other docodonts
29
30 except *Docodon* in having an anterior fovea: a concave area anterior to the
31
32 anterolingual crest. *Borealestes* differs from *Docodon* in having the anterior fovea
33
34 positioned at the anteroposteriorly constricted waist of the upper molars.
35
36 *Borealestes* differs from *Krusatodon*, *Agilodocodon*, *Simpsonodon*, *Docodon* and
37
38 *Haldanodon*, in having transversely expanded and anteroposteriorly slightly
39
40 compressed lingual wing of the upper molar, which is similar to *Docofossor* and
41
42 *Dsungarodon*. The posterior upper molars are similar to *Haldanodon*,
43
44 *Docofossor*, to some extent also to *Docodon*. *Borealestes* resembles *Docofossor*
45
46 and *Dsungarodon* in having more reduced cusps Y and Z on the upper molars,
47
48 and a larger cusp X.

BOREALESTES SERENDIPITUS Waldman and Savage, 1972

Holotype—BRSUG 20570, fragment of left dentary from the Kilmaluag Formation, Isle of Skye.

Referred Specimens—BRSUG 20571 fragment of left dentary; BRSUG 29007 fragment of right dentary; BRSUG 29008 three fragmentary molars in matrix – all from the Kilmaluag Formation, Isle of Skye. NMS G.1992.47.121.1, partial skeleton that includes upper molar rows and some incisors; NMS G.1992.47.121.3, almost complete right dentary detached from NMS G.1992.47.121.1; NMS G.2018.27.1, fragment of right dentary in matrix; NMS G.1992.47.121.4 (previously BRSUG 29006) anterior upper incisors, premaxilla and nasal fragment – all from the Kilmaluag Formation, Isle of Skye.; OUMNH J.79474, OUMNH J.79475, and OUMNH 79498, all isolated lower molars - all from the Forest Marble Formation of Kirtlington, Oxfordshire. Lower molars NHMUK PV M46039, NHMUK PV M46521, NHMUK PV M46549, NHMUK PV M46610, NHMUK PV M46632, NHMUK PV M46728, NHMUK PV M46791, NHMUK PV M46841, NHMUK PV M46842, NHMUK PV M46845, NHMUK PV M46869, NHMUK PV M46389, NHMUK PV M46399, NHMUK PV M46401, NHMUK PV M46588, and upper molars NHMUK PV M46316, NHMUK PV M46396, and possibly NHMUK PV M46607 (uncertain) - all from the Forest Marble Formation of Kirtlington, Oxfordshire. NHMUK PV M46058, NHMUK PV M44301 and probably NHMUK PV M46116, all lower molars from the Forest Marble Formation of Watton Cliff, Dorset. (The following specimens were referred

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3 to *B. serendipitus*, but were re-identified during this study: OUMNH J.79446 re-
4 identified as *Krusatodon* or *Simpsonodon*, OUMNH 79497 re-identified as
5 *Simpsonodon*; OUMNH J.79514 re-identified as *Krusatodon*; NHMUK PV
6 M46580 re-identified as *B. mussettae*; NHMUK PV M46445 possibly *Krusatodon*;
7 NHMUK PV M46066 not *B. serendipitus*, but identification uncertain. See
8 Supplementary Material for details).

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17 **Revised Diagnosis**—*B. serendipitus* differs from all other docodonts and
18 from *B. mussetti* in that the primary cusp a has a rounded surface and as result an
19 absence of the a–g crest on cusp a (present to variable extent on cusp g) and the
20 absence of an a–d crest on cusp a (but a labially oriented a–d crest is present on
21 cusp d). *B. serendipitus* has a stronger and more elevated b–g crest and c–d
22 crest, than *B. mussettae*. Cusp e in *B. serendipitus* is positioned more lingually
23 than in *B. mussettae*. *B. serendipitus* differs from *B. mussettae* in having a
24 distinct anterolabial and anterolingual crest between cusps A and X in the upper
25 molars, and in that cusp Z is reduced. The anterior fovea is more distinct than in
26 *B. mussettae*.

DESCRIPTION

Upper Tooth Row

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49 NMS G.1992.47.121.4 is a rostral skull fragment consisting of the
50 premaxillae and a part of one nasal of *Borealestes serendipitus*. This component
51 belongs to the same partial skeleton as the upper molars (below), NMS
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3 G.1992.47.121.1 (currently under study by EP). This skull component became
4
5 separated from the rest of the skeleton in the 1980s, after collection of this fossil
6
7 in the field in the early 1970s. It was accessioned to the University of Bristol (as
8
9 BRSUG 29006), but was subsequently relocated to National Museums Scotland
10
11 where the rest of the skeleton is held.
12
13

14
15 The premaxilla of NMS G.1992.47.121.4 has the right I1 and I2 and a partial
16
17 root of I3, the left I2 root, and the complete left I3 and I4 (Fig. 2). Combining the
18
19 information from the right and the left incisors, we determine that *B. serendipitus*
20
21 possesses four upper incisors. It has a single-rooted I1 with a leaf shaped crown,
22
23 which has a convex external (buccal) surface and a concave internal (lingual)
24
25 surface with a lingual cingulum (Fig. 2A1, C1–2). The roots of I2 to I4 are deeply
26
27 bifurcated, diverging at their tips. This bifurcation is similar to that seen in
28
29 *Agilodocodon* (Meng et al., 2015: fig. s2) and *Haldanodon* (Krusat, 1980). The
30
31 crowns of I2 to I4 are caniniform in lateral outline: they are recurved, and the
32
33 anterior edge of the tooth is convex and smooth. The buccal aspect of I2–I4 is
34
35 gently convex and the lingual aspect is broadly concave with a ridge running from
36
37 the apex of the crown to the base. There is a weak lingual cingulum with a small
38
39 cuspsule on the posteriormost edge, which connects to the incisor apex via a
40
41 curved low ridge. This overall morphology of upper incisors of *Borealestes* is
42
43 similar to *Agilodocodon*.
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50 The upper molars and premolars preserved with the partial skeleton of
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52 *Borealestes serendipitus* NMS G.1992.47.121.1 include: roots of right P4 and P5,
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54 and almost complete M1 to M4 (Fig. 2A1); and the partial roots of left P5, and
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3 almost complete M1 to M4 (Fig. 2A2) (for tooth measurements see Table 1). The
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5 premolar-molar boundary in *Borealestes* (as for docodonts as a whole) can be
6
7 clearly defined as two roots for the ultimate premolars and three roots for the first
8
9 molar, which we also observe here.
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12 The molars are transversely wide and have a figure-of-eight shaped outline
13
14 in occlusal view. This occurs due to the anteroposterior mid-point constriction of
15
16 the molar, which creates a distinct lingual wing (Fig. 2A1–2). The lingual wing
17
18 comprises a large cusp X, a smaller, more posterior cusp Y, and a much smaller
19
20 cusp Z positioned on the anterior cingular margin of the tooth. The labial portions
21
22 of the molar crown on right M1–3 and on left M1–3 are missing due to wear after
23
24 exposure in the field. The buccodistal corner of M3 on both sides is preserved,
25
26 and the M4s are well preserved. Although the left and right M3s are missing cusp
27
28 A, the broad base of this cusp indicates that it is larger than cusp C, and both are
29
30 positioned in anteroposterior alignment (Fig. 2A1–2). A transverse crest connects
31
32 cusps A and X. This crest is nearly continuous and is made up of the anterolabial
33
34 and anterolingual crests. The transverse crest leading from cusp Y is not distinct,
35
36 and only extends to the midpoint constriction of the crown. This crest does not
37
38 extend further buccally and has no connection to the rounded cusp C or the
39
40 buccodistal cingulum.
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47 M4 is reduced, especially mesiodistally, and as such it is smaller than M3.
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49 M4 has a much reduced cusp C. Cusps A and C are joined by a short A–C crest,
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51 and both cusps are more lingually positioned, than on the preceding molars.
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3 We infer that in all upper molars, there is an anterior crest running from
4 cusp A to the position of an indistinct 'cusp B', as best seen in the right M3 (Fig.
5 2A1). This feature is incomplete in some upper molars where this region is
6 broken/abraded. The upper molars have a buccal cingulum, which takes the
7 form of a thin line, rather than a fully formed crest. The buccal margin is indented
8 by an ectoflexus. The buccal cingulum is also present in what remains of both
9 M3.
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19 There is a distinct occlusal basin at the point of mid constriction, formed
20 between cusps C and Y, and posterior to A–X crest, on all upper molars. This is
21 functionally analogous to the trigon basin of the tribosphenic upper molars. This
22 is a general feature shared by most docodonts, with the exception of *Docofossor*
23 (Luo et al., 2015b). There is a distinctly concave region anterior to the
24 anterolabial and anterolingual crest (connecting cusps A–X), near the
25 buccolingual mid-point of the crown. This is formed partly because of the mid-
26 point constriction of the tooth and partly by the saddle-shape of the anterolabial
27 and anterolingual crests. We have named this area the anterior fovea of the
28 upper molars (Fig. 1B, 2, 7C–E). The anterior fovea is present in *Borealestes* and
29 *Docodon*, but in *Docodon* the fovea is positioned more lingually on the anterior
30 face of cusp X. We interpret the buccolingual midpoint position of the anterior
31 fovea as a diagnostic feature of *Borealestes*.
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49 A minor difference between M4 and more anterior molars is that the
50 posterior half of M4 is more reduced such that the A–X crest almost becomes the
51 transverse midline across the tooth crown (Fig. 2A1–2). The M4 crown bears
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3 strong resemblance to the upper molars of *Haldanodon* by this placement of this
4 crest, and by the mid-point constriction.
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8 The molar crowns bulge outwards from the roots at their bases where they
9 meet the alveolar margin (Fig. 2B1, C1). There are three roots per molar, and
10 they are straight except for M4. The roots of M4 curve anteriorly, suggesting that
11 during the eruption of this tooth, the tooth rotated, causing the bending of the
12 roots. M4 roots are slightly shorter than the other molar roots. All of the upper
13 molar roots widen towards their base in the maxillary alveolar margin. Roots of
14 upper molars, especially the lingual root and posterior root, tend to have slightly
15 inflated root-tips, indicating ontogenetic cessation of root growth.
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28 **Lower Tooth Row**

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30 The morphology of five dentaries including the holotype BRSUG 20570
31 confirm the diagnosis and morphology of *Borealestes serendipitus* (see Table 1
32 for tooth measurements). The holotype comprises part of the left dentary
33 containing the posterior root of p3, intact p4 and p5, and fully erupted m1 to m4
34 (Fig. 3). Although the crown of m5 is lost, the roots are in place within the
35 dentary, and a hidden (but almost erupted) m6 is present (Fig. 3). Only a thin wall
36 of bone separates the anterior alveolus of m6 and the posterior alveolus of m5.
37
38 There is sign of bone regrowth just below the rim of the m5 alveolus (Fig. 3F),
39 suggesting possible (traumatic) pre-mortem loss of this molar. BRSUG 20571 is
40 a fractured section of left dentary (Fig. 4A–E). It is broken anteriorly at the
41 position of m1, and posteriorly behind the coronoid scar and depression that
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3 represents the entrance of the mandibular nerve (V3 notch). The roots of m1,
4 roots and base of the crown of m2, the almost complete crown of m3, most of
5 m4, and almost complete m5 remain in the dentary. The ultimate molar (m5) is
6 much reduced in crown size, and the two roots are fused along much of their
7 length, typical of the ultimate lower molars of docodonts. Only m3 has a
8 preserved cusp a, m2–5 retain cusp b, and m3–5 cusp d. Most other cusps are
9 broken or missing, but the preserved parts of these teeth show the clear
10 morphology of *B. serendipitus*, including the distinct a–c crest, and the b–g crest
11 with an absence of the a–g crest on cusp a.
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24 BRSUG 29007 is an incomplete portion of right dentary (Fig. 4F–H). It is
25 broken anteriorly at m1, and posteriorly just posterior to the coronoid scar. It has
26 been extensively worn, although it is unclear whether this occurred as a result of
27 pre-depositional transport, or during field exposure. Due to this wear, molars are
28 identified by size (see Table 1, and Supplementary Information) and remaining
29 morphological features. The posterior root of m1, the roots of m2, m3 to m4, and
30 the roots of m5 and m6, are all present. The crowns of m3–4 are heavily worn,
31 but the presence of a large cusp a lacking an a–g crest and possessing a strong
32 a–c crest can still be distinguished on m4. The presence of these features helps
33 to establish the specimen's identity as *Borealestes serendipitus*.
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47 NMS G.2018.27.1 (Fig. 5) is an almost complete right dentary, still
48 embedded in a small block of limestone matrix (Fig. 5B). The specimen has not
49 been prepared, and only the posteriormost molars protrude from the surface of
50 the block (Fig. 5A). The rest of the dentary is revealed through digital
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3 reconstruction of synchrotron CT scan data. The roots of i2 and i3 remain inside
4 the alveoli, although the incisor crowns are missing, the canine is complete and
5 double-rooted, p1, p2 and p5 are missing but their positions are represented by
6 their alveoli. The posterior root of p3 remains inside the alveolus. The crown of
7 p4 is present, although fractured in the mid-length of the tooth. Of the molars, m1
8 to m4 are present, and m5 crown is missing but its roots remain in the alveolus.
9 The m3 crown is fractured and displaced, but still identifiable, while m4 is missing
10 cusp a. The molars are otherwise intact, and possess a strong a–c crest and b–e
11 crest, with the a–g crest absent on rounded cusp a: all are diagnostic features of
12 *Borealestes serendipitus*.
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26 NMS G.1992.47.121.3 is an almost complete right mandible (Fig. 6). It
27 belongs to a partial skeleton, NMS G.1992.47.121.1 (currently under study by
28 EP). It is complete except for the apex of the coronoid process and buccal
29 surface of the incisor region. The incisors are missing, but exposed incisor alveoli
30 indicate that the specimen had four incisors, consistent with the count of incisor
31 alveoli in NMS G.2018.27.1 (above). The roots of the canine remain in their
32 alveoli, and the roots and some of the crown of p1 remain. The crowns of the
33 rest of the remaining teeth are well-preserved, except for the missing tips of cusp
34 a of m3 and m4. The molar morphology matches that of the holotype of
35 *Borealestes serendipitus*, with distinct a–c and b–g crests, and an absent a–g
36 crest on the rounded cusp a.
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54 **Dentary Morphology**

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3 The dentary of *Borealestes serendipitus* is gracile, as exemplified by NMS
4 G.2018.27.1 and NMS G.1992.47.121.3 (Fig. 5, 6), similar to *Agilodocodon*
5 (Meng et al., 2015). The most complete dentary, NMS G.1992.47.121.3,
6 measures 23.3 mm in length from the alveolus of first incisor to the dentary
7 condyle, which represents the complete length of the mandible. The body of the
8 mandible of NMS G.1992.47.121.3 is between 0.9–1.2 mm in buccolingual width,
9 and is 2.2 mm in dorsoventral depth below m3.
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19 The mandibular symphysis of *Borealestes serendipitus* is vertically shallow,
20 but anteroposteriorly long, and is indicated by a slightly rugose area on the
21 medial surface of the dentary (Fig. 5C, 6A). The symphysis begins anteriorly in
22 the incisor region, and continues posteriorly ventral to the canine and posteriorly
23 to below p4–p5. The posterior extension of symphysis is similar to that of
24 *Docodon* (Schultz et al., 2017).
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33 There are three mental foramina on the buccal surface of the dentary,
34 below i3–4, c, and p1, as seen in NMS G. 2018.27.1, NMS G.1992.47.121.3 (Fig.
35 5C, 6A). In BRSUG 20570 there are also two small nutritive foramina ventral to
36 p5 and to m1, at around midheight dorsoventrally on the buccal surface of the
37 dentary (Fig. 3C).
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45 A very small nutritive foramen is present in the masseteric fossa, as seen in
46 BRSUG 20570, BRSUG 20571, BRSUG 29007 and NMS G.1992.47.121.3 (Fig.
47 3C, 4B, G, 6B). Its position is low and it is not connected to the masseteric
48 foramen, nor is the masseteric foramen large, unlike in zatherians such as
49 *Peramus* (Davis, 2012). This appears to be a unique feature of *Borealestes*, as
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3 the same foramen is not present in the well preserved mandibles of *Docodon*
4
5 (Rougier et al., 2015) or other docodonts (Meng et al., 2015).
6

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8 The V-3 notch is located above the postdentary trough, posterior to the
9
10 coronoid scar (Fig. 4F, 6A). The postdentary trough is dorsoventrally deep and
11
12 clearly defined. Within the postdentary trough, there is a well-defined diagonal
13
14 ridge (sensu Kermack et al., 1973) as in *Morganucodon* (Fig. 6A). The diagonal
15
16 ridge is much better developed in *Borealestes* here than in *Docodon* (Schultz et
17
18 al., 2017). There is an angular concavity or notch, for receiving the hook-like
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20 reflected lamina of the angular bone, or the ectoympanic ‘hook’ as in
21
22 *Castorocauda* and *Agilodocodon* (Ji et al., 2006; Meng et al., 2015).
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26 The dorsal half of the trough is connected anteriorly to the mandibular
27
28 canal. The mandibular canal is located ventral to the coronoid scar (Fig. 3A, 4A,
29
30 F, 6A). The canal opening is connected to the postdentary trough in a deep
31
32 groove defined by the diagonal ridge, best seen in NMS G.1992.47.121.3 (Fig.
33
34 6A). In well-preserved specimens, the mandibular canal can be traced inside the
35
36 dentary, extending along the length of the mandibular body at the base of the
37
38 tooth roots, on the buccal side of the root tips (Fig. 3G, 4D–E). In BRSUG 20571,
39
40 a fine vascular network can also be traced posterior to and around the base of
41
42 m5. This vascular network is near the position of the crypt for m6 in the (likely
43
44 older) holotype of *Borealestes serendipitus*, BRSUG 20570. We hypothesise this
45
46 may represent vascularization of the bone prior to the initial formation of the m6
47
48 tooth bud.
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3 In BRSUG 29007, the alveolus of m6 is positioned anterior to the anterior
4 margin of the coronoid process. In the growth series of *Docodon* (Schultz et al.,
5 2017:fig 2), the ultimate molar in the juvenile mandible erupts medial to the
6 coronoid process; but in successively older mandibles, the last molar shifts in
7 relative position so that it is anterior to the coronoid process. Based on the
8 shifting placement of the ultimate lower molar(s) in *Docodon*, the placement of
9 the ultimate lower molar directly anterior to the coronoid process of the mandible
10 in BRSUG29007 indicates that this individual of *B. serendipitus* was a fully grown
11 adult.
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24 The Meckel's sulcus is connected to the anterior end of the postdentary
25 trough, and the sulcus starts from below the diagonal ridge and extends
26 anteriorly to below the m4. Further anteriorly, it extends only a millimetre into the
27 medial surface of the dentary. A faint line continues beyond this to the ventral
28 surface of the dentary below m2
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35 The entrance to the mandibular canal is located dorsal to the Meckel's
36 sulcus. The anteriormost extent of Meckel's sulcus varies between specimens,
37 representing ontogenetic change in morphology (see Discussion). In
38 BRSUG20570 the Meckel's sulcus extends from a point ventral to the mandibular
39 canal opening and ends ventral to m3, stopping short of the ventral surface of the
40 dentary. In BRSUG 29007 the Meckel's sulcus extends to a point ventral to m4,
41 where it is reduced to a faint external groove. In NMS G.2018.27.1 the sulcus is
42 open and reaches anteriorly until a point ventral to m4. In all cases, the sulcus
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3 does not continue internally beyond the anteriormost point on the surface of the
4
5 dentary.
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8 Fragments of Meckel's element remain in the sulcus of all specimens
9
10 except BRSUG 29007 (Fig. 3A, 4A, 5C, 6A). This is equivalent to the ossified
11
12 Meckel's cartilage as identified for several extinct clades of crown group
13
14 mammals (Luo, 2011; Meng et al., 2011). This element was identified as the
15
16 prearticular in older literature (Kermack et al., 1973; Allin, 1975). As both the
17
18 prearticular and the Meckel's element are anterior extensions of the articular (=
19
20 malleus), these are synonymous terms for the homologous structure (Luo et al.,
21
22 2017). The Meckel's sulcus ends anteriorly below m3, but continues as a faint
23
24 external groove to meet the ventral surface of the dentary below m1 (Fig. 3A). A
25
26 fragment of the postdentary complex remains in the post dentary trough in
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28 BRSUG 20571.
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33 The anterior margin of the masseteric fossa along the coronoid process is
34
35 distinct. There is an efflected angle of the angular process. The dentary condyle
36
37 is a mediolaterally broad, projecting posteriorly on the dentary peduncle. In
38
39 posterior view, the dentary condyle has a spindle shaped outline (see
40
41 Supplementary Material). In lateral view, there is a low ridge extending from the
42
43 dentary condyle along the dentary peduncle anteroventrally into the masseteric
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45 fossa (Fig. 6B). This is the lateral ridge, which is interpreted as the demarcation
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47 of the superficial masseter below and the deep masseter above (sensu Schultz
48
49 et al., 2017). The peduncle sits above the line of the toothrow. What remains of
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51 the coronoid process is gracile, as is the whole dentary.
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3 There is a strongly projecting medial ridge that overhangs the postdentary
4 trough on the lingual side of the mandible (Fig. 6A). The ridge has a large
5 protuberance, which appears to be curved dorsally, but close examination of the
6 CT scan data shows this to be the result of a fracture along the flat shelf of the
7 medial ridge, which has subsequently been glued into the incorrect anatomical
8 position (EP, pers. obs) (Fig. 6A and Supplementary Material). Therefore we
9 interpret the apparent dorsally curved morphology is an artefact of post-mortem
10 distortion.

11
12 The medial ridge ends at the protuberance, and there is a distinct and broad
13 notch between the protuberance and the dentary peduncle, which is termed the
14 medial ridge notch (Fig. 6A). This notch is present in *Docodon* (Schultz et al.,
15 2017), but it appears to be more pronounced in *Borealestes*. The medial ridge
16 lessens at the V3 notch, just posterior to the coronoid scar (Fig. 6A).

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35 *BOREALESTES MUSSETTAE* Sigogneau-Russell, 2003

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37 *Borealestes mussetti* Sigogneau-Russell, 2003; Averianov, 2004:3 (emended
38 gender)

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42 **Holotype**—NHMUK PV M46495 right lower molar from the Forest Marble
43 Formation at Kirtlington, Oxfordshire.

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47 **Referred Specimens**— NHMUK PV M46224, NHMUK PV M46239;
48 NHMUK PV M46001; NHMUK PV M46066, NHMUK PV M46836, NHMUK PV
49 M46319, NHMUK PV M46809, NHMUK PV M46835, all lower molars, and
50 NHMUK PV M46394, NHMUK PV M46448, NHMUK PV M46580, NHMUK PV
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3 M46871 all upper molars from the Forest Marble Formation at Kirtlington,
4 Oxfordshire. NHMUK PV M46001 lower molar from Watton Cliff, Dorset.
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6 (NHMUK PV M46401, NHMUK PV M46389, NHMUK PV M46588 were
7
8 previously referred to *B. mussettae*, but were re-identified as *B. serendipitus*
9
10 during present study). NHMUK PV M46404, NHMUK PV M46204 were referred
11
12 to *B. mussettae*, but lack clear diagnostic features above order-level. Previously
13
14 assigned to *B. mussettae*, but unavailable for confirmation NHMUK PV M46796.
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19 **Revised Diagnosis**—Diagnosis for the genus *Borealestes* as for *B.*
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21 *serendipitus* (above). *B. mussettae* (Fig. 7B, D, E) differs from *B. serendipitus* in
22
23 lower molar morphology in that the a–g crest is present on both cusp g and cusp
24
25 a, and in having a strong a–d crest on cusp a—both features are absent on cusp
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27 a in *B. serendipitus*. Cusp g is slightly more developed in *B. mussettae*, and
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29 cusps g and c are placed further apart mesiodistally than in *B. serendipitus*. *B.*
30
31 *mussettae* has an anterior lingual cingulid that passes below cusp g to the
32
33 midway along the molar mesiodistally. The df cusp is more developed in *B.*
34
35 *mussettae* than in *B. serendipitus*, and is distinct from the d cusp. Cusp e is
36
37 positioned in alignment with the anteroposterior axis of the molar, whereas cusp
38
39 e is lingual of the anteroposterior axis on molars of *B. serendipitus* (Fig. 7).
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45 Although *B. mussettae* resembles *B. serendipitus* in most features of upper
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47 molars, *B. mussettae* is distinctive in having a more rounded cusp A so that there
48
49 is no anterior crest and no anterolabial crest on cusp A. *B. mussettae* is also
50
51 distinguishable from *B. serendipitus* in having a short anterolingual crest on cusp
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53 X, with a cuspule on the crest. Cusp Z is reduced to absent relative to *B.*
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3 *mussettae*. The anterior fovea is less distinct in *B. mussettae* than in *B.*
4
5 *serendipitus* (Fig. 7D-E).
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10 DESCRIPTION

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14 The holotype of *B. mussettae*, NHMUK PV M46495, is a lower right molar.
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16 Its crown is fractured between cusps a and c on the original specimen, as
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18 illustrated by Sigogneau-Russell (2003:fig 2). Here this fracture is digitally
19
20 restored after segmentation of CT scans (Fig. 7B). Cusp b is missing, but the
21
22 crown is otherwise intact. The overall morphology of the tooth is more
23
24 mesiodistally elongate and buccolingually compressed, than in *B. serendipitus*.
25
26 For molar measurements see Table 1, and Supplementary Material.
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31 Because cusp b is missing, it is not clear how strong the b–g crest is in this
32
33 specimen. However it is clear that the b–g crest is notched in the depression
34
35 between these cusps. There is a strong c–d crest on cusp c, although it is less
36
37 distinctive on cusp d. The c–d crest is posteriorly oriented as in *B. serendipitus*.
38
39 The a–c crest and the a–d crest are both distinctive, and there is a less distinct
40
41 a–g crest. The a–g and a–c crests create a mesiodistally flat lingual surface on
42
43 cusp a, with a faint ridge running from the tip of cusp a to the base dorsoventrally
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45 (Fig. 8B1).
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49 Cusp g and cusp c are placed further apart in the holotype of *B. mussettae*
50
51 than in *B. serendipitus*, leaving a small gap at the base of cusp a that is less
52
53 distinct to absent in *B. serendipitus*, especially in more posterior molars (Fig. 2
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3 and 7). However, if we are correct that the holotype represents an m1, this gap
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5 may not be a feature of the whole tooth row, as we observe a similar larger gap
6
7 in the m1 of *B. serendipitus* (Fig. 3). Further material is required to resolve this.
8
9
10 The anterior lingual cingulid extends posteriorly from cusp e around the base of
11
12 cusp g to the midpoint of tooth, and terminates ventral to cusp a. Unlike *B.*
13
14 *serendipitus*, cusp df is very distinct in *B. mussettae*, projecting further posteriorly
15
16 and dorsally. The divergent cusps c and g, and the buccolingually compressed
17
18 crown, are key features of *B. mussettae* distinguishing it from *B. serendipitus*.
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24 RESULTS OF PHYLOGENETIC ANALYSIS

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28 Our analysis includes updated scores for previously missing characters for
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30 *Borealestes serendipitus*, described here for the first time. This phylogenetic
31
32 analysis recovered a single most parsimonious tree of 117 steps (Fig. 8). The
33
34 topology is almost the same as for Meng et al. (2015), with the following
35
36 differences: *Morganucodon*, *Megazostrodon* and *Dinnetherium* no longer form a
37
38 clade, but instead form successive outgroups to the rest of the taxa in the
39
40 analysis; *Simpsonodon* has become an outgroup to the clade comprising
41
42 (*Tashkumyrodon* + (*Dsungarodon* + *Castorocauda*), (*Borealestes* + (*Haldanodon*
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44 + (*Docodon* + *Docofossor*)). *Itatodon* has become an outgroup to the clade
45
46 comprising (*Krusatodon* + *Agilodocodon*), *Simpsonodon*, (*Tashkumyrodon* +
47
48 (*Dsungarodon* + *Castorocauda*), (*Borealestes* + (*Haldanodon* + (*Docodon* +
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50 *Docofossor*)) (Fig. 8). Including *B. mussettae* in the analysis did not alter the tree
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3 topology. *B. serendipitus* and *B. mussettae* are united in the genus *Borealestes*,
4
5 and *Borealestes* is found as the sister taxon of the clade comprising *Haldanodon*,
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7 *Docofossor* and *Docodon*.
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10 Characters recovered as apomorphies of *Borealestes* in this analysis are:
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12 character 1, the obtuse angle of the angular process; character 4, the
13
14 convergence of the Meckel's groove with the ventral margin of the mandible;
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16 character 18, cusp c is much larger than cingular cusp g in the lower molars; and
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18 48, the presence of an anterior fovea in the buccolingual midpoint of the upper
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20 molar (also present in *Docodon*; Schultz et al., 2017).
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24 Characters recovered as apomorphies of *Borealestes serendipitus* are:
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26 character 22, the c–d crest is present and angled; and character 32, the cusp e
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28 cingulid being limited to the mesial part of the tooth; character. Characters
29
30 recovered as apomorphies of *Borealestes mussettae* (lower molar characters
31
32 only) are: Character 8, the absence of the anterolabial connecting crest on the
33
34 upper molars; character 19, the pseudo-talonid being bound by the b–e crest;
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36 character 20, the presence of an a–g crest with a v-notch; character 21, the
37
38 weakly developed b–g crest; character 27, presence of an a–d crest connected
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40 with a v-notch; character 42, a labially shifted cusp e; and character 44, the
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42 broad angle formed by cusps g–a–c (> 80 degrees).
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49 DISCUSSION

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54 **Diagnostid Features of *Borealestes***

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3 The new specimens collected from the Kilmaluag Formation on the Isle of
4
5 Skye, combined with the specimens collected previously, allow us to clarify the
6
7 diagnoses for *Borealestes serendipitus* and *B. mussettae*. We can confirm that
8
9 the dental formula for *Borealestes serendipitus* is 4.1.?⁵4/ 4.1.5.6. The
10
11 estimated number of upper premolars will hopefully be clarified by better
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13 preserved fossils in the future. Previously referred specimens have been
14
15 preserved fossils in the future. Previously referred specimens have been
16
17 checked in light of this new diagnosis, and the specimen lists herein are up to
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19 date.

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21 *Borealestes* resembles *Krusatodon*, *Castorocauda* and *Haldanodon* in
22
23 possessing a very large cusp a, and larger cusp c than cusp g. Like most
24
25 docodonts—except *Simpsonodon*, *Krusatodon*, *Agilodocodon*, and *Docodon*—
26
27 *Borealestes* does not have pits or ornamentation in molar tooth enamel. The key
28
29 features that distinguish *Borealestes* from other docodonts include: (1) a
30
31 distinctly pronounced a–c crest; (2) the obtuse angle of the angular process; (3)
32
33 the convergence of the Meckel's groove with the ventral margin of the mandible;
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35 (4) cusp c being much larger than cusp g; (5) and the c–d crest being present
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37 and angled; (6) the presence of an anterior fovea in the buccolingual midpoint of
38
39 the upper molars. However, it should be noted that the angular process and
40
41 Meckel's groove are not known for *B. mussettae*, and so although these are
42
43 returned as apomorphies in this analysis, further material is necessary to confirm
44
45 features (2) and (3) for both taxa.

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47 The differences between *B. serendipitus* and *B. mussettae* are summarised
48
49 in Figure 8. The species *B. serendipitus* differs from *B. mussettae* in: (1) the
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3 pseudo-talonid being bound by the b–g crest; (2) the better developed b–g crest;
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5 (3) the angle formed by cusps g–a–c being < 80 degrees; (4) the presence of the
6
7 anterolabial and anterolingual crest (the A–X crest) on the upper molars; (5) the
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9 reduction/absence of cusp Z; (6) absence of a–g crest on cusp a. The a–d crest
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11 and df cusp are better developed, and cusps c and g placed anteroposteriorly
12
13 further apart in *B. mussettae* than in *B. serendipitus*. Our re-examination of
14
15 *Borealestes mussettae* shows that it is valid species, and sufficiently different
16
17 from *B. serendipitus* (further details in Discussion).
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24 **Toothrow Size Gradient**

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26 The molars of *B. serendipitus* increase in size along the tooth row from m1–
27
28 m3, then decrease from m3 posteriorly (Table 1, Supplementary). In all
29
30 docodonts for which the relatively complete tooth rows are known the ultimate
31
32 molar is smaller than the penultimate molars and the ultimate upper molar is also
33
34 less symmetrical than preceding molars. The decreasing size from m2–3 through
35
36 to m5–6 documented in *Borealestes* is similar to the tooth size gradient known
37
38 for *Haldanodon* (Krusat, 1980; Luo and Martin, 2007), *Docodon* (Jenkins, 1969;
39
40 Schultz et al., 2017), *Castorocauda* (Ji et al., 2006) and *Agilodocodon* (Meng et
41
42 al., 2015). However, *Borealestes* shows the steepest gradient for decreasing size
43
44 toward the posterior molars, of all docodonts. For example, both *Borealestes* and
45
46 *Docodon* have six molars, but the decreasing trend of m3 to m6 is more
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48 pronounced in *Borealestes* (Table 1, Supplementary).
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3 The large sample of specimens of *Borealestes serendipitus* allows a
4
5 quantitative comparison of *B. serendipitus* to *B. mussettae*. The initial diagnosis
6
7 and description of *B. mussettae* suggested that *B. mussettae* was larger than *B.*
8
9 *serendipitus* (Sigogneau-Russell, 2003:358). Our measurements do not support
10
11 this, and show instead that specimens of *B. mussettae* are of similar size to *B.*
12
13 *serendipitus* (Table 1, Supplementary). The width/length ratio of the type
14
15 specimen of *B. mussettae* NHMUK PV M46495—a lower molar—is similar to p5
16
17 in *B. serendipitus*, but we suggest from the morphology that this specimen
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19 represents an m1, suggesting that *B. mussettae* has a buccolingually narrower
20
21 molar row than *B. serendipitus*.
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26 An alternative hypothesis is that NHMUK PV M46495 could represent a
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28 deciduous p5 in *B. serendipitus*. The sharply cusped crown, divergent orientation
29
30 of cusps c and g (Fig. 7), and the lack of roots in the preserved tooth of *B.*
31
32 *mussettae* type specimen could be consistent with the hypothesis that the type
33
34 specimen is a deciduous dp5. However, the assessment of isolated deciduous
35
36 premolars without the context of contiguous toothrow can be a complex issue
37
38 (Averianov, 2004), which can only be resolved reliably when well preserved tooth
39
40 row is available (Schultz et al., 2017). Much of the material currently referred to
41
42 *B. mussettae* is fragmentary. More complete specimens of *B. mussettae*, or more
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44 juvenile material from *B. serendipitus*, would help resolve this.
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51 **Ontogenetic Changes in *Borealestes***

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3 Most of the specimens of *B. serendipitus* found so far have not developed
4 m6 (the ultimate molar) except for the holotype BRSUG 20570 (Fig. 3). A recent
5 detailed analysis of *Docodon victor* shows that its ultimate molar did not erupt
6 until late in adulthood, only in very mature individuals (Schultz et al., 2017). Our
7 observations that *B. serendipitus* also shows a late eruption of m6 suggest this
8 condition of delayed eruption of the ultimate molar may be widespread among
9 docodonts. A corollary of this observation is that the holotype of *Borealestes*
10 *serendipitus* BRSUG 20570 is the most mature individual of the species currently
11 known.
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24 Other changes in mandibular morphology of *D. victor*, as seen in
25 successively older adult specimens, include a posterior shift in the Meckel's
26 sulcus, a posterior shift in the anterior border of the coronoid process, and a
27 medial-to-anterior shift of the ultimate molar placement relative to the coronoid
28 process (Schultz et al., 2017). The morphology of BRSUG 20570 also conforms
29 to this, further supporting our interpretation that there is some ontogenetic
30 variation in the sample of mandibles of *B. serendipitus* from the Isle of Skye, and
31 that the type specimen BRSUG 20570, and possibly also BRSUG 29007, are the
32 most mature individuals.
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44 Of the other specimens described here, BRSUG 20571 is likely to represent
45 the ontogenetically youngest individual, with the Meckel's sulcus meeting the
46 ventral edge of the mandible below m1 (Fig. 4A–E). In NMS G.2018.27.1 (Fig. 5)
47 and NMS G.1992.47.121.3 (Fig. 6) the anterior end of the Meckel's sulcus has
48 become shorter and ends below m3 and m4, becoming a faint line on the exterior
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3 of mandible anterior to this. Although this posteriorly receding Meckel's sulcus is
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5 best documented in *Docodon* (Schultz et al., 2017) it was also previously shown
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7 for *Haldanodon* (Nowotny et al., 2001; Martin et al., 2010). This supports the
8
9 hypothesis that a similar pattern of ontogenetic variation in mandibular
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11 morphology may be widespread throughout Docodonta.
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17 **Phylogeny of *Borealestes* and Docodonts**

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19 Our phylogenetic analysis with updated characters for the upper and lower
20
21 dentition and dentary of *B. serendipitus* and *B. mussettae* returned similar results
22
23 to previous analyses of Docodonta (Fig. 8; see Meng et al., 2015). Our analysis
24
25 continues to support Docodonta as a clade, with *Tikitherium*, *Woutersia* and
26
27 *Delsatia* as their putative near relatives (Sigogneau-Russell and Hahn, 1995; Ji
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29 et al., 2006; Luo and Martin, 2007). *Borealestes* was found to form a clade with
30
31 *Haldanodon*, *Docodon* and *Docofossor*, as recovered by previous authors (Martin
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33 and Averianov, 2004; Pfretzschner et al., 2005; Ji et al., 2006; Luo and Martin,
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35 2007; Averianov et al., 2010; Meng et al., 2015). As noted in the description of
36
37 molars, the posterior upper molar(s) of *Borealestes* bears strong resemblance to
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39 the molars of *Haldanodon*, also somewhat similar to those of *Docodon* (although
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41 to a lesser extent). These taxa share a relatively strong A–X crest, in
42
43 perpendicular arrangement to the A–C crest on the upper molars.
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49 The broad agreement of many studies is that there is strong support for the
50
51 close relationship of *Borealestes* to *Haldanodon*, *Docodon* and *Docofossor*.
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53 However, Sigogneau-Russell (2003) suggested a sister-group relationship
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3 between *Borealestes* + (*Simpsonodon* and *Krusatodon*), based on the
4 morphology of the lower molars. This was an older study, prior to the discoveries
5 of many more docodont taxa. Inclusion of additional taxa has changed the
6 phylogeny. Also the earlier analysis was a manual and ad hoc cladistic
7 phylogeny, not a parsimony analysis with comprehensive coverage of taxa and
8 characters.
9

10
11 Another analysis that returned an alternative placement for *Borealestes*
12 species was Hu et al. (2006). Their analysis of 24 lower molar characters
13 included 13 docodont genera with *Morganucodon* as an outgroup. They found
14 both *Borealestes* species at the base of the docodont tree. Their closest
15 relationship to *Borealestes* was with *Docodon*—and as the outgroup to a clade
16 formed by all other docodonts. Several taxa in this phylogeny are in an
17 unresolved polytomy (Hu et al., 2006:fig 5). The small size of their character list
18 may have contributed to this result, and this earlier study is before our addition of
19 many more characters of *Borealestes* from the new specimens.
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37 Some authors have proposed Docodonta be split into two families:
38 Tegothereiidae (*Tegothereium*, *Sibirothereium*, *Hutegothereium* and *Krusatodon*) and
39 Simpsonodontidae (*Simpsonodon* and *Dsungarodon*), with basal docodonts
40 represented by *Borealestes*, *Haldanodon* and *Docodon* (Maschenko et al., 2002;
41 Martin and Averianov 2004; Averianov et al., 2010). This was based on an
42 analysis of 37 molar and dentary characters scored for 18 taxa, 13 of them
43 docodonts. In the resulting tree, *Borealestes*, plus *Haldanodon* and *Docodon*
44 were placed in an unresolved polytomy with *Castorocauda*, *Tashkumyrodon*, and
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3 a clade formed by the rest of Docodonta except *Itatodon*, which formed the
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5 outgroup to all other docodonts (Averianov et al., 2010:fig 6). They considered
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7 *Castorocauda*, *Tashkumyrodon* and *Acuoduolodon* to be Docodonta incertae
8
9 sedis (*Acuoduolodon sunae* has since been suggested to be a junior synonym of
10
11 *Dsungarodon zoui* [Martin et al., 2010]).
12
13

14 Our analysis does not fully support the dichotomous relationships of families
15
16 Tegotheriidae and Simpsonodontidae as hypothesized by Averianov et al.
17
18 (2010). Although there is support for Tegotheriidae comprising *Tegotherium*,
19
20 *Sibirotherium* and *Hutegotherium*, we find *Krusatodon* as the sister taxon to
21
22 *Agilodocodon* outside of this clade (Fig. 8). We also find *Simpsonodon* as an
23
24 outgroup to two clades formed by *Tashkumyrodon* + (*Dsungarodon* and
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26 *Castorocauda*), and the clade of *Borealestes* + (*Haldanodon* + (*Docodon* and
27
28 *Docofossor*)), which has been corroborated by multiple previous analyses.
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33 'Simpsonodontidae' has therefore become paraphyletic in our analysis.
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35 All of these studies are based on molar, or molar plus dentary,
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37 morphological characters, without postcrania. This is due to the lack of
38
39 postcranial material for many docodontans. The addition of postcrania to a
40
41 phylogenetic analysis would undoubtedly help further resolve and stabilize
42
43 docodont relationships.
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49 FIGURE 1. Terminology of molar and mandibular morphologies of *Borealestes*.
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51 **A**, lower molar cusp terminology (left molar): **A1**, occlusal; **A2**, occlusal
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53 diagrammatic; **A3**, lingual view. Lower molar crest terminology: **A4**, occlusal; **A5**,
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3 occlusal diagrammatic; **A6**, lingual view. **B**, upper molar cusp terminology (right
4 molar): **B1**, occlusal; **B2**, occlusal diagrammatic. Upper molar crest terminology:
5 **B3**, occlusal; **B4**, occlusal diagrammatic. **C**, molar measurements
6 (measurements listed in Table 1): **C1**, lower molar measurements; **C2**, upper
7 molar measurements. Figures based on lower m3 of holotype BRSUG 20570,
8 and upper M3 of NMS G.1992.47.121.1. **D**, restoration of complete mandible in
9 medial view; **E**, restoration of mandible in buccal view. **D** and **E** based on
10 composite of specimens herein, incisors in dash-outline based on *Agilodocodon*.
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26 FIGURE 2. *Borealestes serendipitus* upper dentition. Composite upper tooth row
27 from NMS G.1992.47.121.1 (molars and premolars), and from NMS
28 G.1992.47.121.4 (incisors). **A1**, right tooth row occlusal view; **A2**, left tooth row
29 occlusal view; **B1**, left tooth row lingual view; **B2**, left tooth row buccal view; **C1**,
30 right tooth row lingual view; **C2**, right tooth row buccal view. Digital
31 reconstructions from micro CT scans. Letters in grey color indicate tooth
32 positions represented by empty alveoli of lost teeth. Arrows in bold indicate
33 anterior direction. All scale bars equal 1 mm. [Intended for page width 183 mm]
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44 FIGURE 3. *Borealestes serendipitus* BRSUG 20570 (holotype), partial left
45 dentary. **A**, lingual; **B**, anterolingual; **C**, buccal; **D**, occlusal views of the dentary
46 and dentition; **E**, posterolingual view showing the opening for mandibular canal
47 and relationship to postdentary trough; **F**, micro CT scan slice showing the
48 possible overgrowth of m5 roots suggesting pre-mortem tooth loss; **G**, buccal
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3 view of dentary semi-transparent with segmented mandibular nerve and vessel
4 pathway inside the dentary. Digital reconstructions from micro CT scans. Arrows
5 in bold indicate anterior direction. Scale bar same for **A–D** and **G**. All scale bars
6 equal 1 mm. [Intended for page width 183 mm]
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15 FIGURE 4. *Borealestes serendipitus* BRSUG 20571 (partial left dentary), and
16 BRSUG 29007 (partial right dentary). **A**, lingual; **B**, buccal; **C**, occlusal views of
17 the dentary and dentition of BRSUG 20571. **D**, lingual; and **E**, buccal views of the
18 dentary semi-transparent with segmented mandibular nerve and vessel pathway
19 inside the dentary of BRSUG 20571. **F**, lingual; **G**, buccal; and **H**, occlusal views
20 of the dentary and dentition BRSUG 29007. Digital reconstructions from micro
21 CT scans. Arrows in bold indicate anterior direction. Same scale throughout. All
22 scale bars equal 1 mm. [Intended for page width 183 mm]
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35 FIGURE 5. *Borealestes serendipitus* NMS G.2018.27.1, partial right dentary. **A**,
36 the jaw of NMS G.2018.27.1 as found in situ; **B**, digital reconstruction of dentary
37 in matrix, showing original breakage at p4. Dentary reconstructed from micro CT
38 scans and anterior and posterior portions re-aligned: **C**, lingual; **D**, occlusal; and
39 **E**, buccal view of the dentary and dentition. Letters in grey color indicate tooth
40 positions represented by empty alveoli of lost teeth. Arrows in bold indicate
41 anterior direction. Same scale for **C–E**. All scale bars equal 1 mm. [Intended for
42 page width 183 mm]
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3 FIGURE 6. *Borealestes serendipitus* NMS G.1992.47.121.3, almost complete
4 right dentary. **A**, lingual; **B**, buccal; **C**, occlusal views of dentary and dentition.
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6 Digital reconstructions from micro CT scans. Arrows in bold indicate anterior
7 direction. Scale same throughout. All scale bars equal 1 mm. [Intended for page
8 width 183 mm]
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17 FIGURE 7. Distinguishing characters of *Borealestes serendipitus* and *B.*
18 *mussettae*. **A**, and **B**, lower molar characters. **A**, *Borealestes serendipitus* based
19 on m1 of holotype BRSUG 20570: **A1**, lingual; **A2**, occlusal; **A3**, buccal; **A4**,
20 anterior; and **A5**, posterior views of molar. All **B**, *B. mussettae* based on holotype
21 NHMUK PV M46495, but crack through cusp a is repaired, and molar mirrored to
22 facilitate comparison: **B1**, lingual; **B2**, occlusal; **B3**, buccal; **B4**, anterior; and **B5**,
23 posterior views of molar. **C**, **D** and **E**, distinctive upper molar characters for each
24 species of *Borealestes*: **C**, M3 of *B. serendipitus*, NMS G.1992.47.121.1; **D**, *B.*
25 *mussettae*, NHMUK PV M46871; **E**, *B. mussettae*, NHMUK PV M46871 anterior
26 view. **D** and **E** mirrored to facilitate comparison. Digital reconstructions from
27 micro CT scans. Dotted lines indicate missing portions of tooth. Arrows in bold
28 indicate anterior direction. Same scale for **A–B**, and same scale for **C–E**. All
29 scale bars equal 1 mm. [Intended for page width 183 mm]
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49 FIGURE 8. Phylogeny of docodonts, with tree-topology based on updated
50 phylogenetic analysis. Results of parsimony branch and bound analysis of
51 docodonts and outgroups, tree of 117 steps. First to last appearances are
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3 represented by black box for each taxon (for sources of FAD/LADs see
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5 Methods). Nodes uniting taxa do not imply divergence times. [Intended for page
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TABLE 1: Measurements of *Borealestes* lower dentition. Measurements in italics are from broken specimens. Dashes indicate missing teeth or tooth portions prevented measurement from being taken. See Figure 1 for measurement methodology.

	All in		c	pm1	pm2	pm3	pm4	pm5	m1/ M1	m2/ M2	m3/ M3	m4/ M4	m5/ M5	m6
	mm													
BRSUG 20570	Length	d to b	-	0.97	1	1.2	0.97	1	1.2	1.32	1.32	1.2	-	0.61
		df to e	-	0.97	1	1.19	0.97	1	1.19	1.33	1.29	1.17	-	0.55
	Width	cross c	-	-	-	-	0.45	0.45	0.65	0.79	0.8	0.74	-	0.36
		cross g	-	-	-	-	0.45	0.45	0.57	0.76	0.84	0.82	-	0.37
BRSUG 20571	Length	d to b	-	-	-	-	-	-	-	1.66	1.67	1.37	0.81	-
		df to e	-	-	-	-	-	-	-	1.6	1.6	1.37	0.78	-
	Width	cross c	-	-	-	-	-	-	-	-	<i>0.94</i>	0.73	0.42	-
		cross g	-	-	-	-	-	-	-	-	0.99	0.86	0.56	-
BRSUG 29007	Length	d to b	-	-	-	-	-	-	-	-	<i>1.37</i>	<i>1.35</i>	-	-

TABLE 1. (Continued)

		df to e	-	-	-	-	-	-	-	-	1.42	1.36	-	-
	Width	cross c	-	-	-	-	-	-	-	-	0.66	0.67	-	-
		cross g	-	-	-	-	-	-	-	-	0.59	0.64	-	-
NMS	Length	d to b	-	-	0.84	1.04	1.15	1.25	1.38	1.47	1.5	1.33	0.93	-
G.1992.47.121.3		df to e	-	-	0.84	1.04	1.15	1.25	1.35	1.41	1.49	1.31	0.85	-
	Width	cross c	-	0.36	0.39	0.42	0.46	0.48	0.79	0.89	0.97	0.78	0.43	-
		cross g	-	0.36	0.39	0.42	0.46	0.48	0.69	0.83	0.92	0.83	0.57	-
NMS G.2018.27.1	Length	d to b	0.9	-	-	-	1.1	-	1.25	1.34	1.35	1.5	-	-
		df to e	0.9	-	-	-	1.1	-	1.22	1.33	1.31	-	-	-
	Width	cross c	0.41	-	-	-	0.5	-	0.63	0.83	0.87	0.86	-	-
		cross g	0.41	-	-	-	0.5	-	0.56	0.76	0.84	-	-	-
NHMUK PV M46495	Length	d to b	-	-	-	-	-	-	1.51	-	-	-	-	-
(<i>B. mussetti</i>)		df to e	-	-	-	-	-	-	1.57	-	-	-	-	-
	Width	cross c	-	-	-	-	-	-	0.67	-	-	-	-	-
		cross g	-	-	-	-	-	-	0.58	-	-	-	-	-

TABLE 1. (Continued)

NMS	Right	Length	buccal	-	-	-	-	-	-	-	1.6	1.17	-	-
G.1992.47.121.1	tooth		lingual	-	-	-	-	-	0.81	0.98	0.95	0.7	-	-
<i>(B. serendipitus)</i>	row	Width		-	-	-	-	-	1.4	1.6	1.67	1.41	-	-
	Left	Length	buccal	-	-	-	-	-	-	-	1.42	1.18	-	-
	tooth		lingual	-	-	-	-	-	0.77	0.9	0.93	0.7	-	-
	row	Width		-	-	-	-	-	1.77	1.63	1.39	1.77	-	-

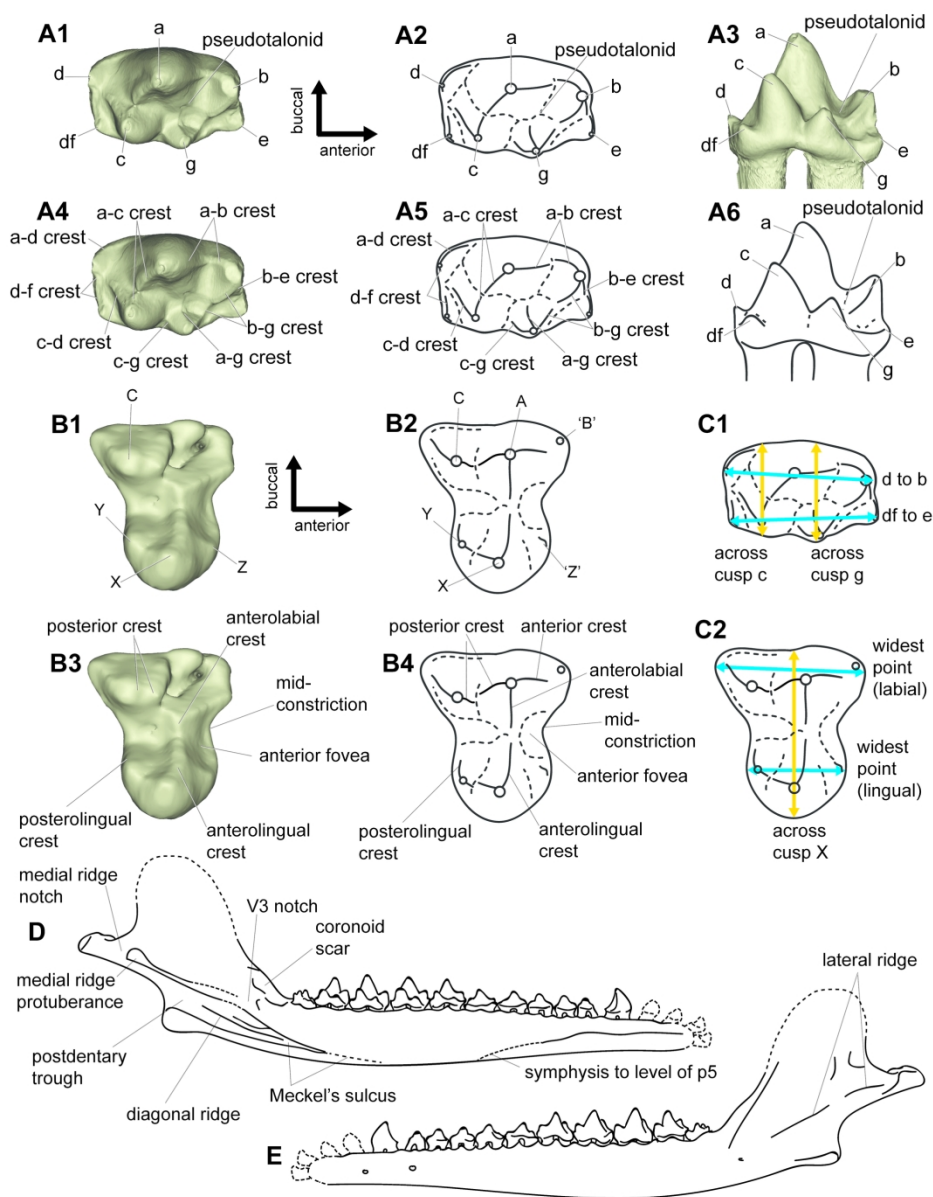


FIGURE 1. Terminology of molar and mandibular morphologies of *Borealestes*. A, lower molar cusp terminology (left molar): A1, occlusal; A2, occlusal diagrammatic; A3, lingual view. Lower molar crest terminology: A4, occlusal; A5, occlusal diagrammatic; A6, lingual view. B, upper molar cusp terminology (right molar): B1, occlusal; B2, occlusal diagrammatic. C, molar measurements (measurements listed in Table 1): C1, lower molar measurements; C2, upper molar measurements. Figures based on lower m3 of holotype BRSUG 20570, and upper M3 of NMS G.1992.47.121.1. D, restoration of complete mandible in medial view; E, restoration of mandible in buccal view. D and E based on composite of specimens herein, incisors in dash-outline based on *Agilodocodon*. [Intended for page width 183 mm]

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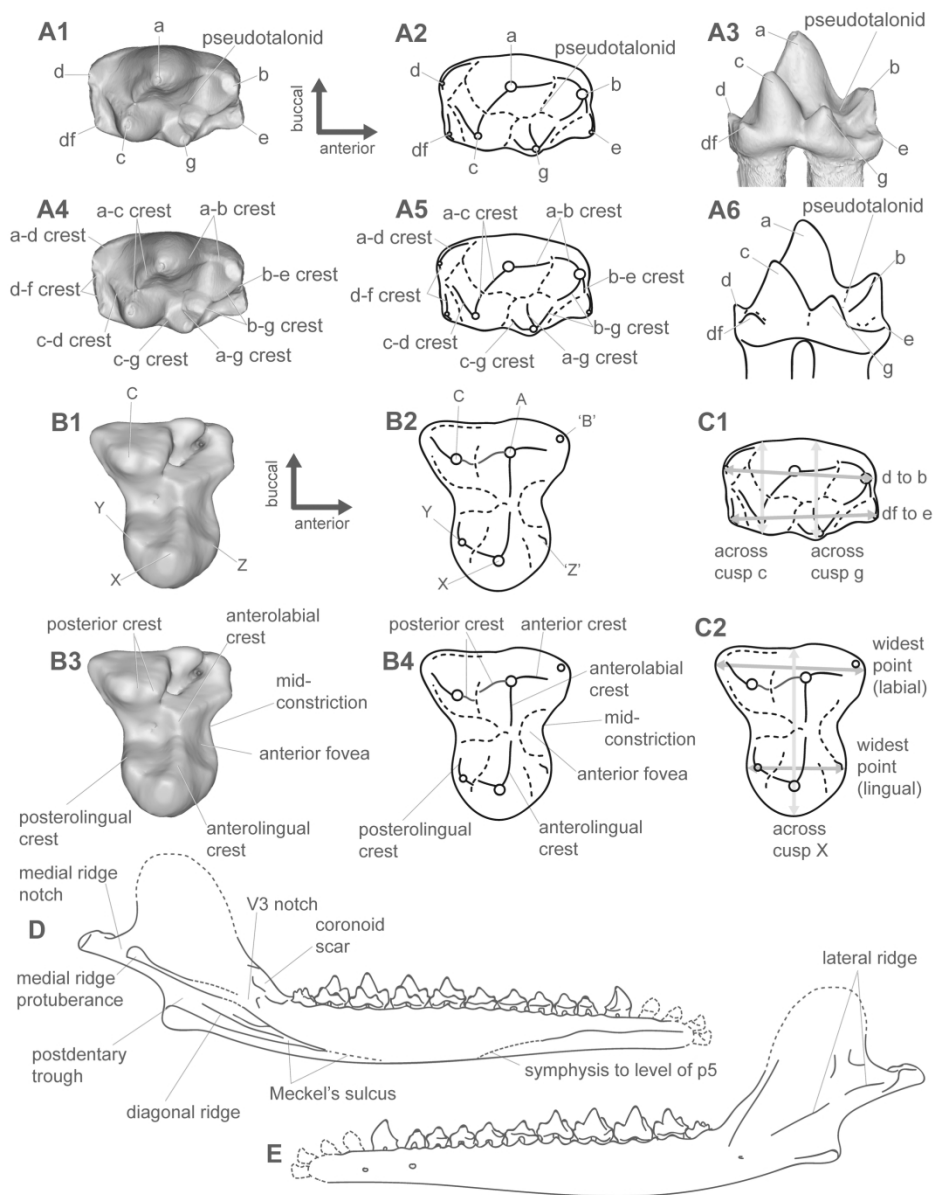


FIGURE 1. Terminology of molar and mandibular morphologies of *Borealestes*. A, lower molar cusp terminology (left molar): A1, occlusal; A2, occlusal diagrammatic; A3, lingual view. Lower molar crest terminology: A4, occlusal; A5, occlusal diagrammatic; A6, lingual view. B, upper molar cusp terminology (right molar): B1, occlusal; B2, occlusal diagrammatic. C, molar measurements (measurements listed in Table 1): C1, lower molar measurements; C2, upper molar measurements. Figures based on lower m3 of holotype BRSUG 20570, and upper M3 of NMS G.1992.47.121.1. D, restoration of complete mandible in medial view; E, restoration of mandible in buccal view. D and E based on composite of specimens herein, incisors in dash-outline based on *Agilodocodon*. [Intended for page width 183 mm]

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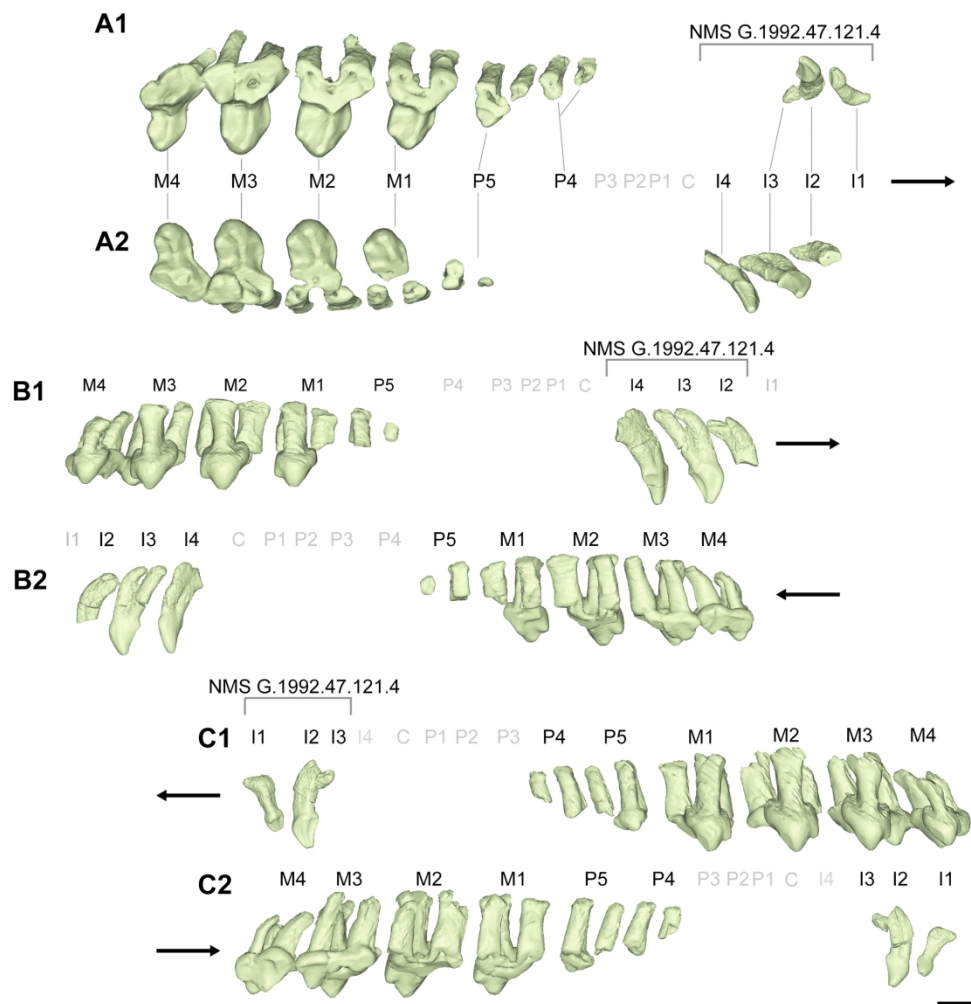


FIGURE 2. *Borealestes serendipitus* upper dentition. Composite upper tooth row from NMS G.1992.47.121.1 (molars and premolars), and from NMS G.1992.47.121.4 (incisors). A1, right tooth row occlusal view; A2, left tooth row occlusal view; B1, left tooth row lingual view; B2, left tooth row buccal view; C1, right tooth row lingual view; C2, right tooth row buccal view. Digital reconstructions from micro CT scans. Letters in grey color indicate tooth positions represented by empty alveoli of lost teeth. Arrows in bold indicate anterior direction. All scale bars equal 1 mm. [Intended for page width 183 mm]

182x187mm (300 x 300 DPI)

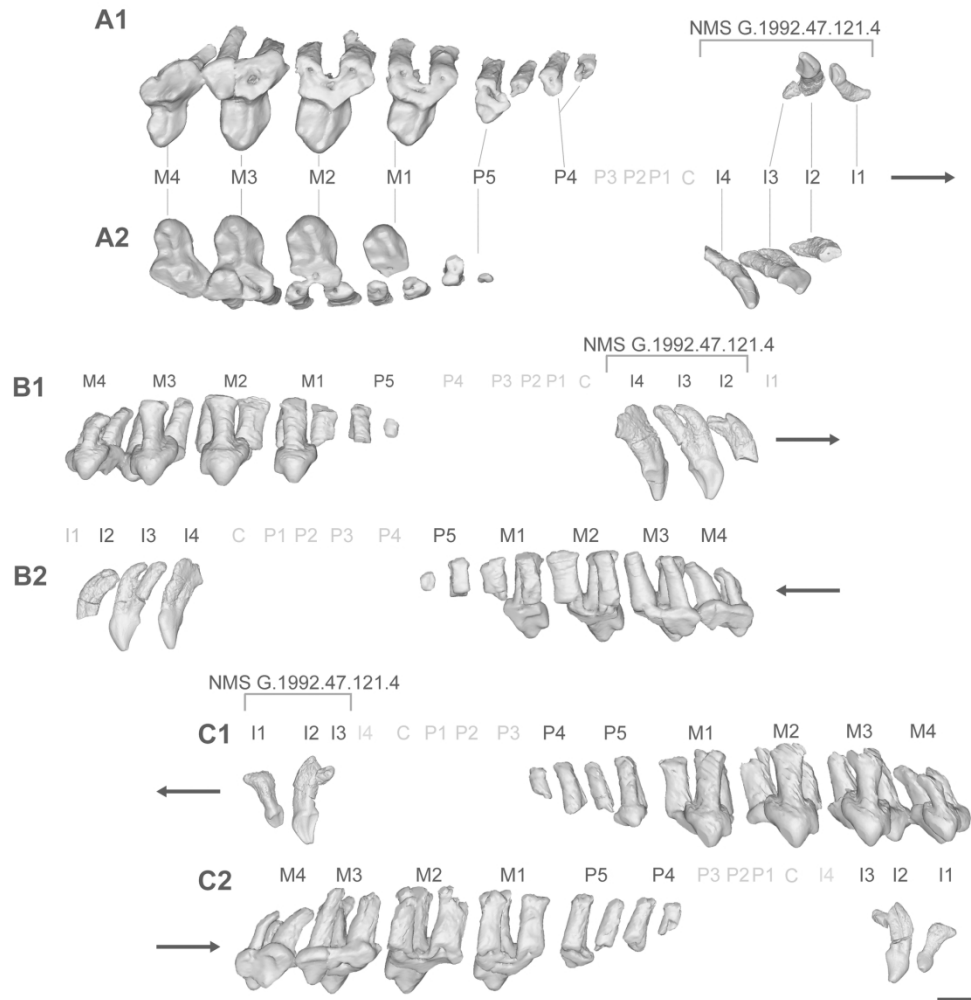


FIGURE 2. *Borealestes serendipitus* upper dentition. Composite upper tooth row from NMS G.1992.47.121.1 (molars and premolars), and from NMS G.1992.47.121.4 (incisors). A1, right tooth row occlusal view; A2, left tooth row occlusal view; B1, left tooth row lingual view; B2, left tooth row buccal view; C1, right tooth row lingual view; C2, right tooth row buccal view. Digital reconstructions from micro CT scans. Letters in grey color indicate tooth positions represented by empty alveoli of lost teeth. Arrows in bold indicate anterior direction. All scale bars equal 1 mm. [Intended for page width 183 mm]

182x187mm (300 x 300 DPI)

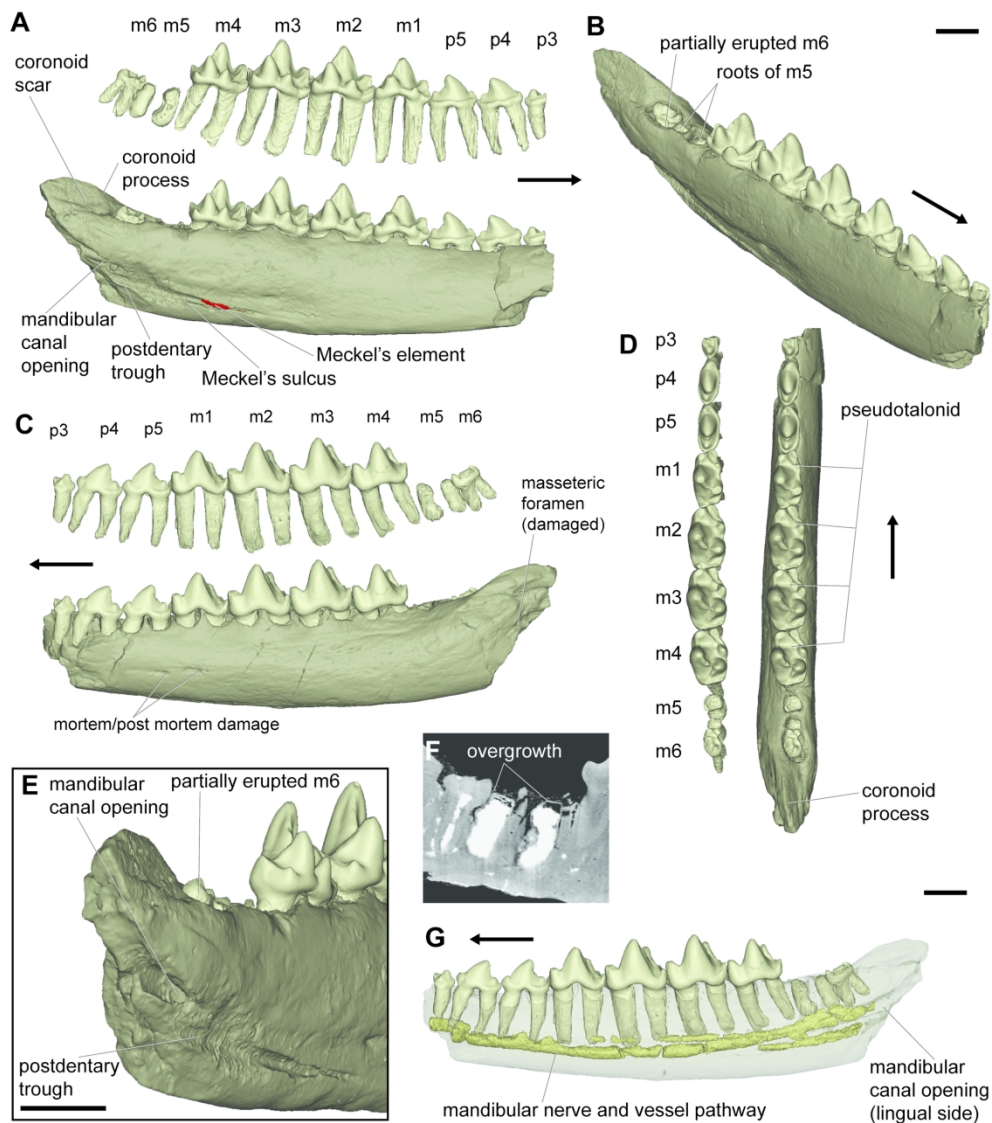


FIGURE 3. *Borealestes serendipitus* BRSUG 20570 (holotype), partial left dentary. A, lingual; B, anterolingual; C, buccal; D, occlusal views of the dentary and dentition; E, posterolingual view showing the opening for mandibular canal and relationship to postdentary trough; F, micro CT scan slice showing the possible overgrowth of m5 roots suggesting pre-mortem tooth loss; G, buccal view of dentary semi-transparent with segmented mandibular nerve and vessel pathway inside the dentary. Digital reconstructions from micro CT scans. Arrows in bold indicate anterior direction. Scale bar same for A–D and G. All scale bars equal 1 mm. [Intended for page width 183 mm]

182x206mm (300 x 300 DPI)

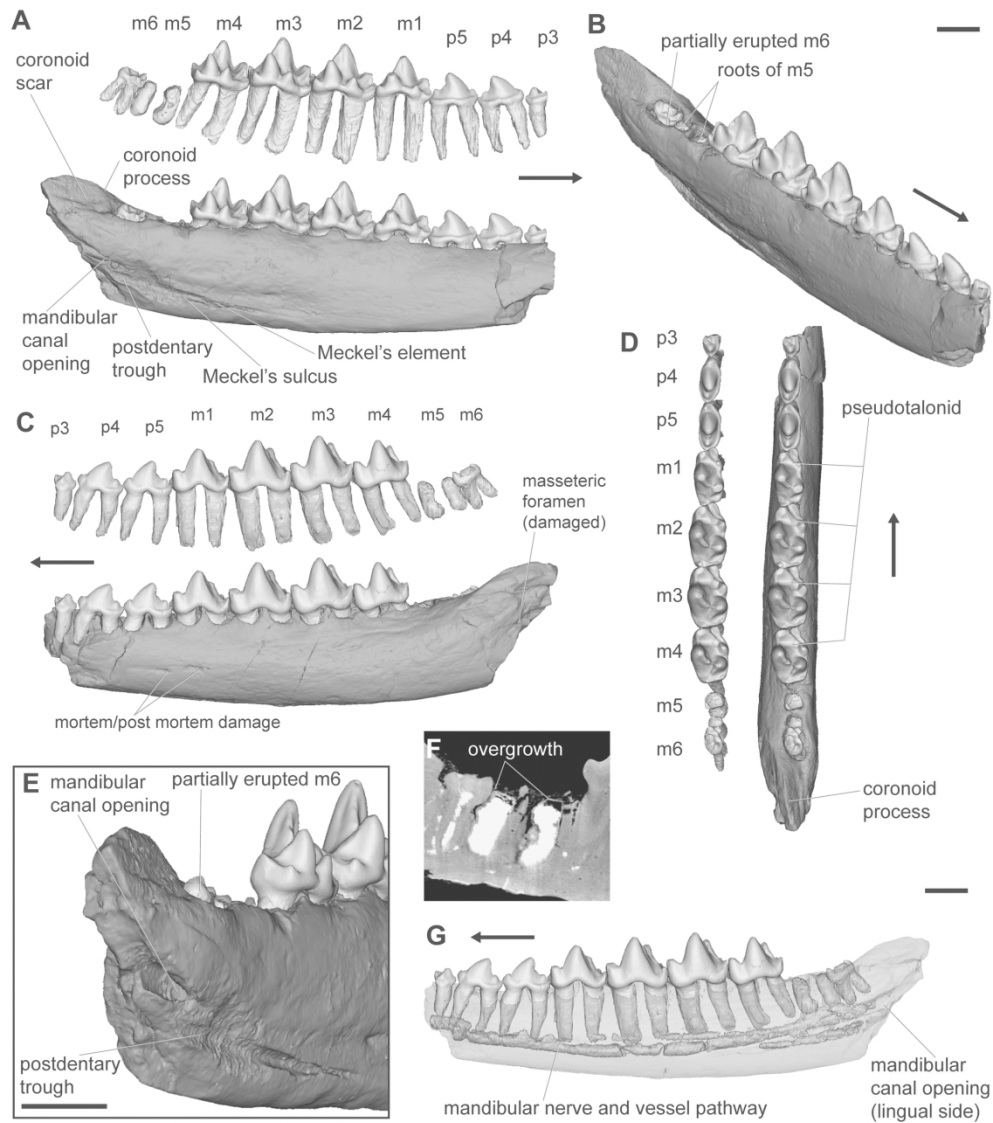


FIGURE 3. *Borealestes serendipitus* BRSUG 20570 (holotype), partial left dentary. A, lingual; B, anterolingual; C, buccal; D, occlusal views of the dentary and dentition; E, posterolingual view showing the opening for mandibular canal and relationship to postdentary trough; F, micro CT scan slice showing the possible overgrowth of m5 roots suggesting pre-mortem tooth loss; G, buccal view of dentary semi-transparent with segmented mandibular nerve and vessel pathway inside the dentary. Digital reconstructions from micro CT scans. Arrows in bold indicate anterior direction. Scale bar same for A–D and G. All scale bars equal 1 mm. [Intended for page width 183 mm]

182x206mm (300 x 300 DPI)

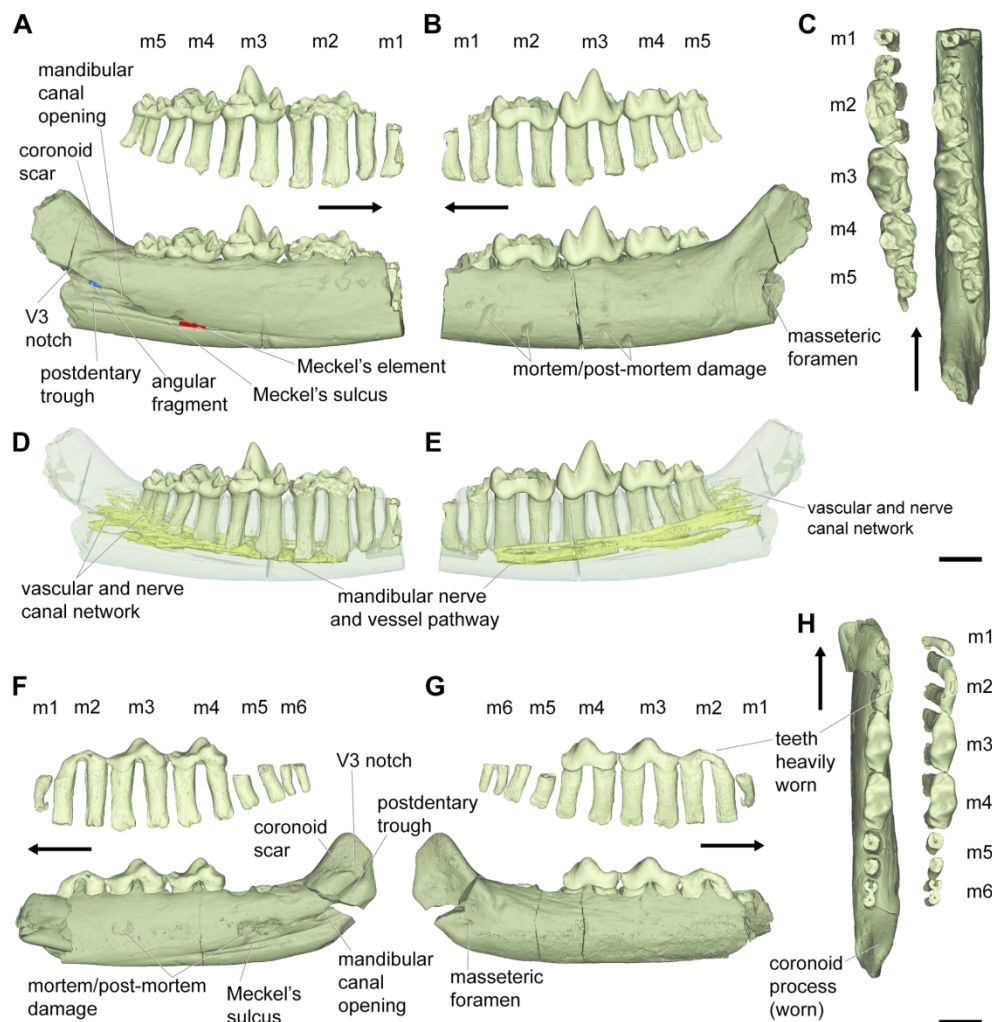


FIGURE 4. *Borealestes serendipitus* BRSUG 20571 (partial left dentary), and BRSUG 29007 (partial right dentary). A, lingual; B, buccal; C, occlusal views of the dentary and dentition of BRSUG 20571. D, lingual; and E, buccal views of the dentary semi-transparent with segmented mandibular nerve and vessel pathway inside the dentary of BRSUG 20571. F, lingual; G, buccal; and H, occlusal views of the dentary and dentition BRSUG 29007. Digital reconstructions from micro CT scans. Arrows in bold indicate anterior direction. Same scale throughout. All scale bars equal 1 mm. [Intended for page width 183 mm]

182x187mm (300 x 300 DPI)

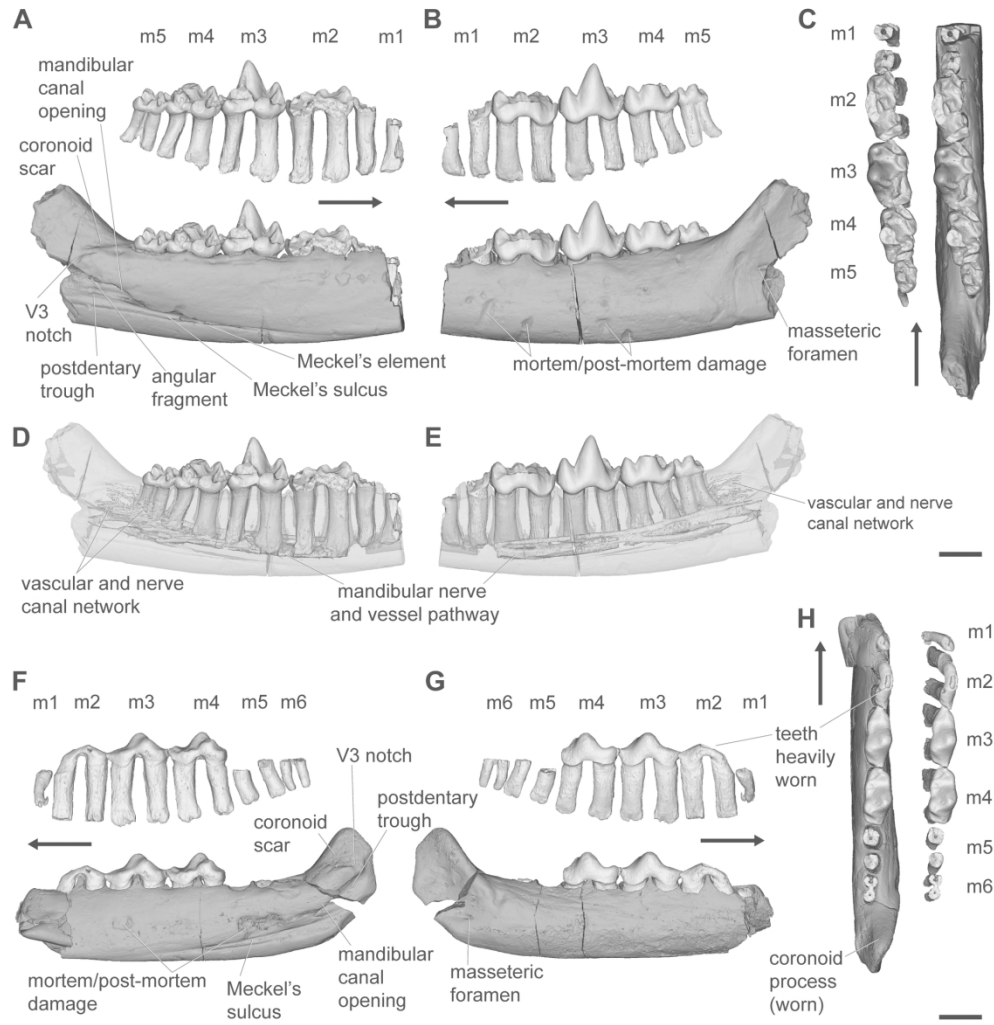


FIGURE 4. *Borealestes serendipitus* BRSUG 20571 (partial left dentary), and BRSUG 29007 (partial right dentary). A, lingual; B, buccal; C, occlusal views of the dentary and dentition of BRSUG 20571. D, lingual; and E, buccal views of the dentary semi-transparent with segmented mandibular nerve and vessel pathway inside the dentary of BRSUG 20571. F, lingual; G, buccal; and H, occlusal views of the dentary and dentition BRSUG 29007. Digital reconstructions from micro CT scans. Arrows in bold indicate anterior direction. Same scale throughout. All scale bars equal 1 mm. [Intended for page width 183 mm]

182x187mm (300 x 300 DPI)

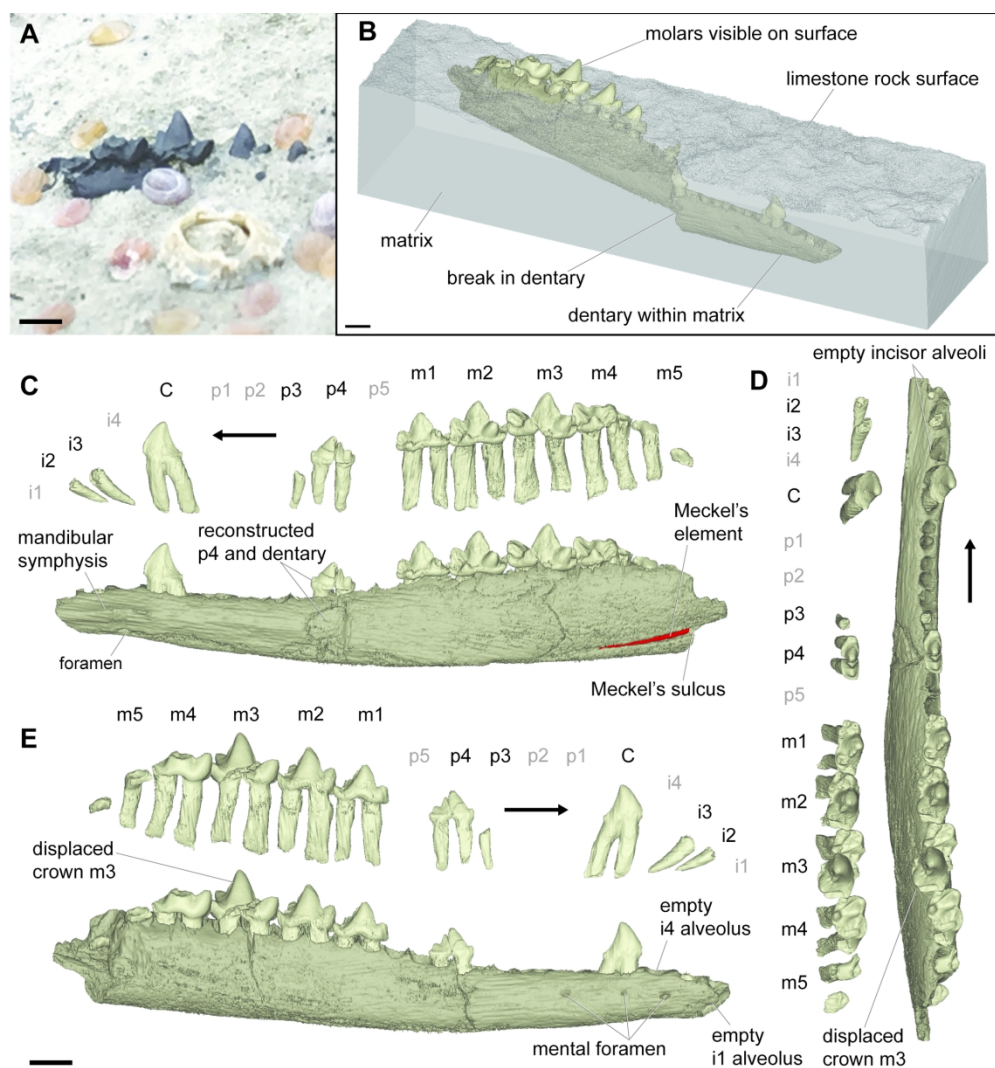


FIGURE 5. *Borealestes serendipitus* NMS G.2018.27.1, partial right dentary. A, the jaw of NMS G.2018.27.1 as found in situ; B, digital reconstruction of dentary in matrix, showing original breakage at p4. Dentary reconstructed from micro CT scans and anterior and posterior portions re-aligned: C, lingual; D, occlusal; and E, buccal view of the dentary and dentition. Letters in grey color indicate tooth positions represented by empty alveoli of lost teeth. Arrows in bold indicate anterior direction. Same scale for C–E. All scale bars equal 1 mm. [Intended for page width 183 mm]

182x196mm (300 x 300 DPI)

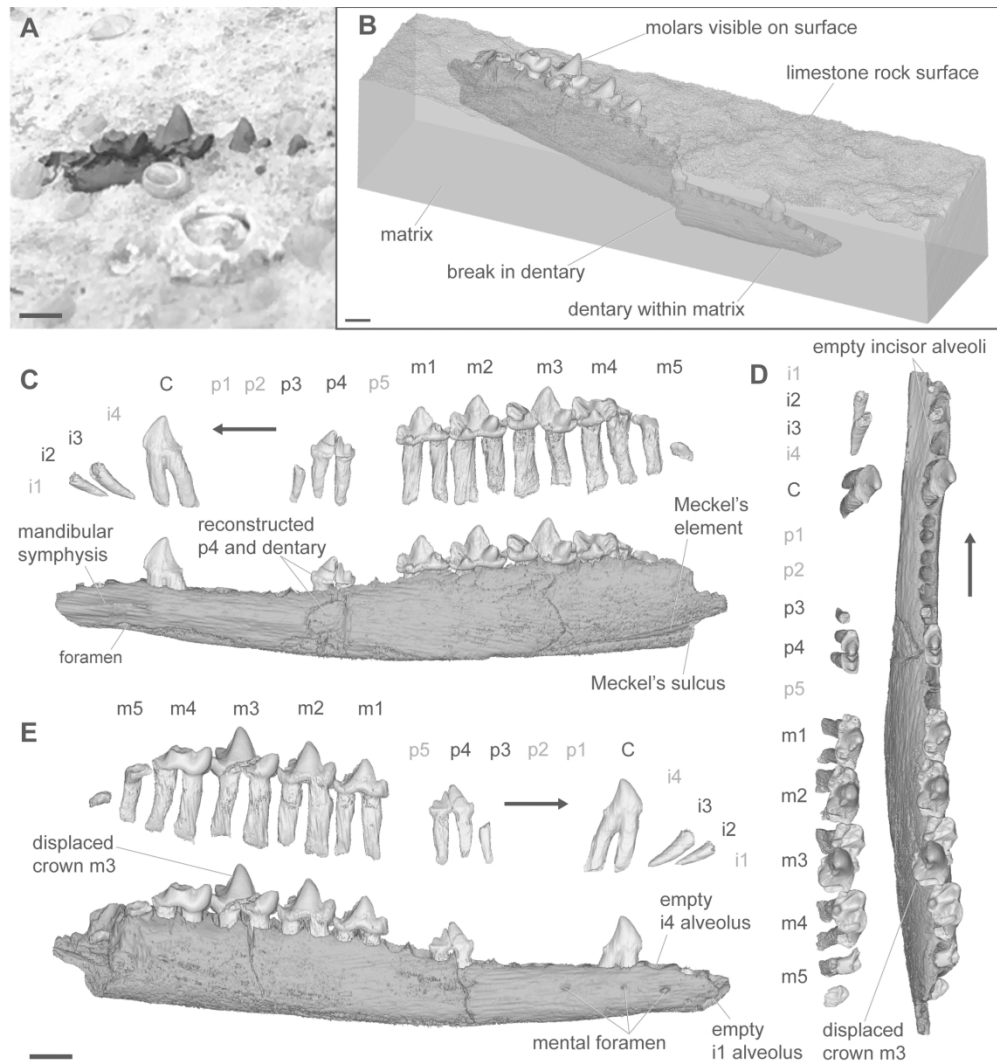


FIGURE 5. *Borealestes serendipitus* NMS G.2018.27.1, partial right dentary. A, the jaw of NMS G.2018.27.1 as found in situ; B, digital reconstruction of dentary in matrix, showing original breakage at p4. Dentary reconstructed from micro CT scans and anterior and posterior portions re-aligned: C, lingual; D, occlusal; and E, buccal view of the dentary and dentition. Letters in grey color indicate tooth positions represented by empty alveoli of lost teeth. Arrows in bold indicate anterior direction. Same scale for C–E. All scale bars equal 1 mm. [Intended for page width 183 mm]

182x196mm (300 x 300 DPI)

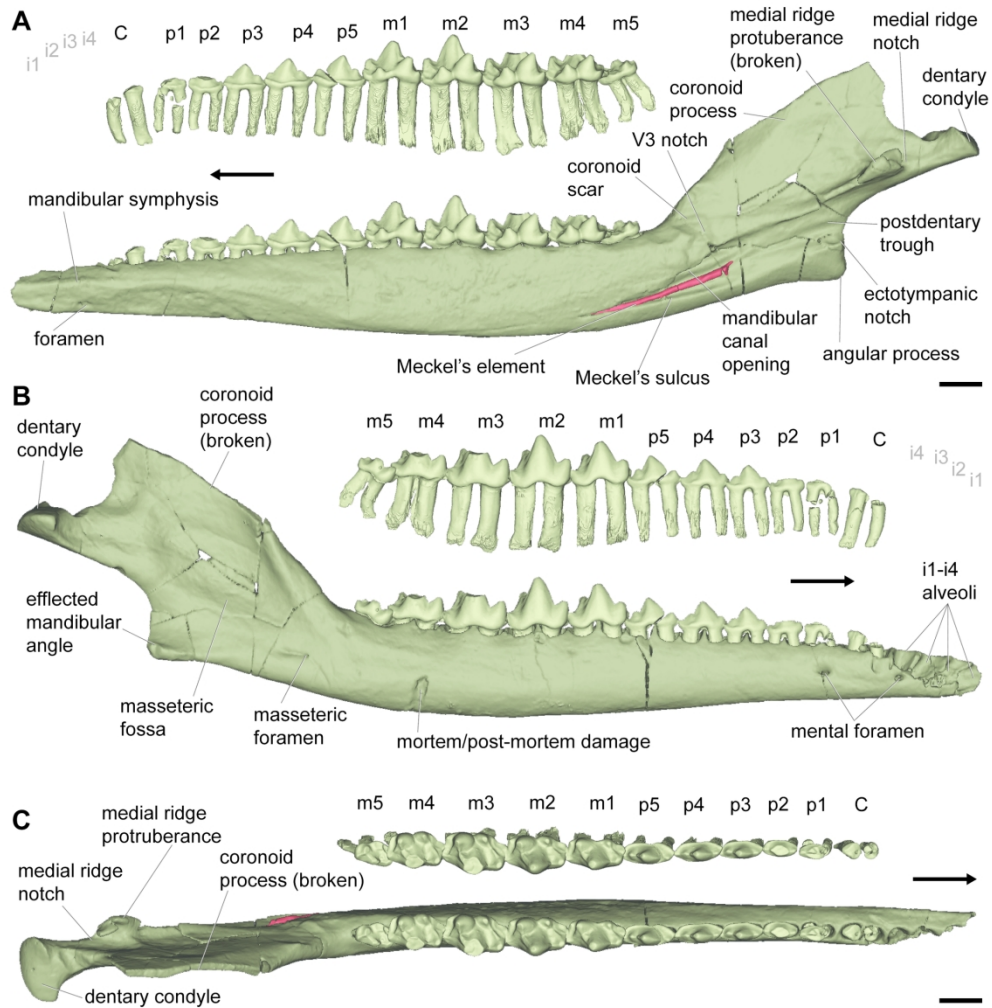


FIGURE 6. *Borealestes serendipitus* NMS G.1992.47.121.3, almost complete right dentary. A, lingual; B, buccal; C, occlusal views of dentary and dentition. Digital reconstructions from micro CT scans. Arrows in bold indicate anterior direction. Scale same throughout. All scale bars equal 1 mm. [Intended for page width 183 mm]

182x186mm (300 x 300 DPI)

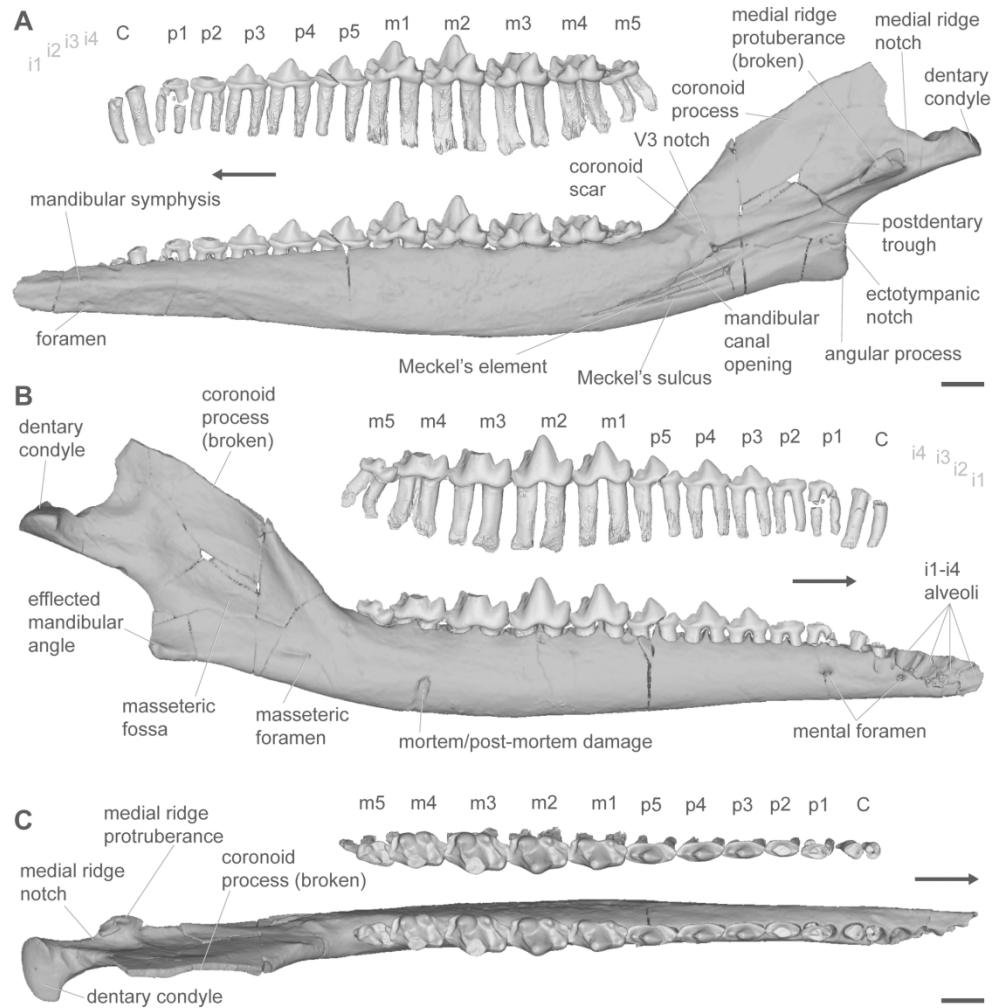


FIGURE 6. *Borealestes serendipitus* NMS G.1992.47.121.3, almost complete right dentary. A, lingual; B, buccal; C, occlusal views of dentary and dentition. Digital reconstructions from micro CT scans. Arrows in bold indicate anterior direction. Scale same throughout. All scale bars equal 1 mm. [Intended for page width 183 mm]

182x186mm (300 x 300 DPI)

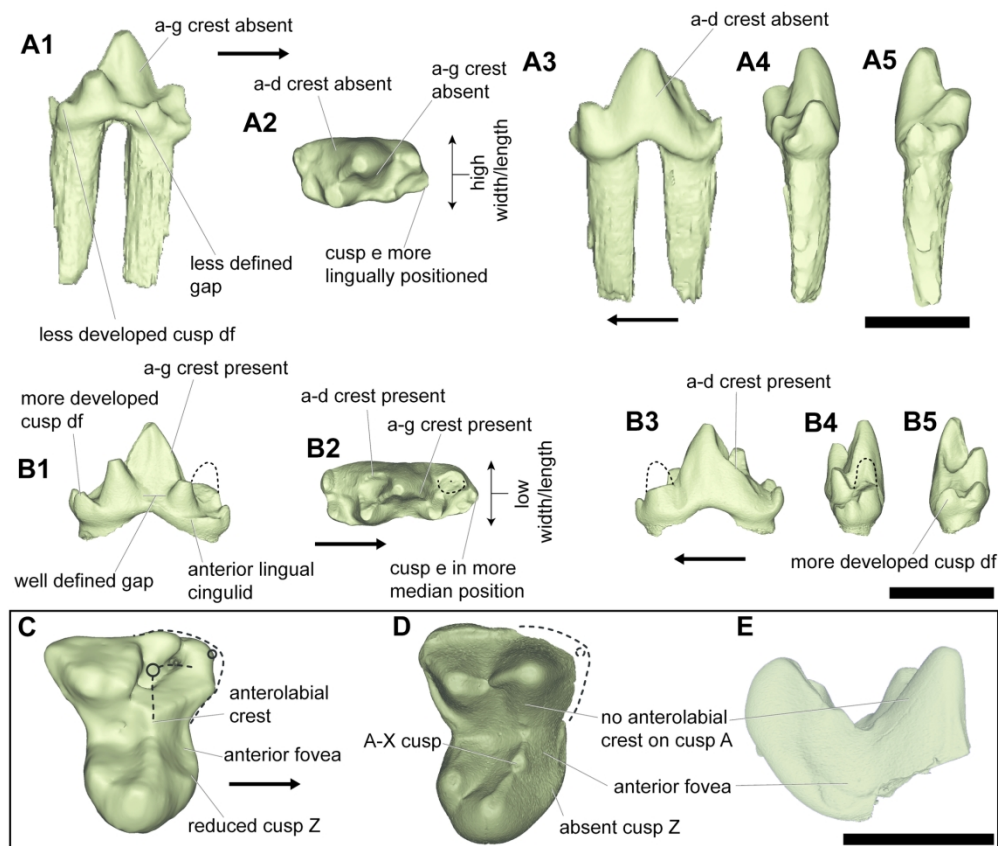


FIGURE 7. Distinguishing characters of *Borealestes serendipitus* and *B. mussettae*. A, and B, lower molar characters. A, *Borealestes serendipitus* based on m1 of holotype BRSUG 20570: A1, lingual; A2, occlusal; A3, buccal; A4, anterior; and A5, posterior views of molar. All B, *B. mussettae* based on holotype NHMUK PV M46495, but crack through cusp a is repaired, and molar mirrored to facilitate comparison: B1, lingual; B2, occlusal; B3, buccal; B4, anterior; and B5, posterior views of molar. C, D and E, distinctive upper molar characters for each species of *Borealestes*: C, M3 of *B. serendipitus*, NMS G.1992.47.121.1; D, *B. mussettae*, NHMUK PV M46871; E, *B. mussettae*, NHMUK PV M46871 anterior view. D and E mirrored to facilitate comparison. Digital reconstructions from micro CT scans. Dotted lines indicate missing portions of tooth. Arrows in bold indicate anterior direction. Same scale for A–B, and same scale for C–E. All scale bars equal 1 mm. [Intended for page width 183 mm]

182x155mm (300 x 300 DPI)

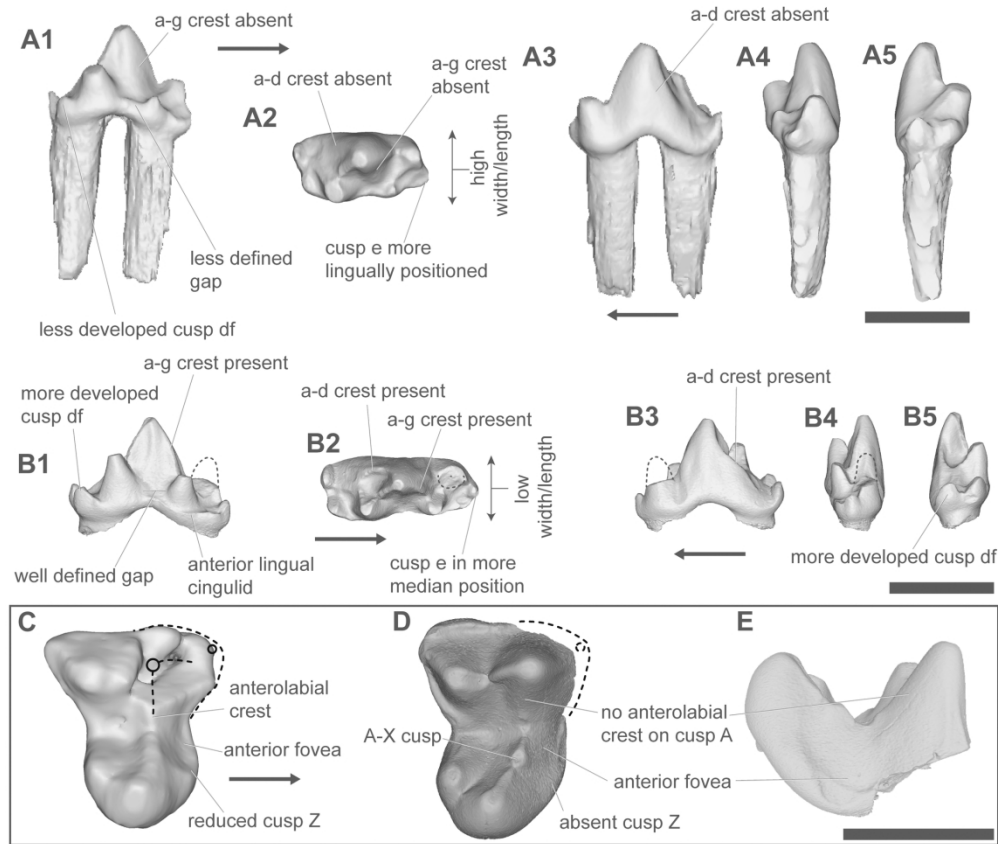


FIGURE 7. Distinguishing characters of *Borealestes serendipitus* and *B. mussettae*. A, and B, lower molar characters. A, *Borealestes serendipitus* based on m1 of holotype BRSUG 20570: A1, lingual; A2, occlusal; A3, buccal; A4, anterior; and A5, posterior views of molar. All B, *B. mussettae* based on holotype NHMUK PV M46495, but crack through cusp a is repaired, and molar mirrored to facilitate comparison: B1, lingual; B2, occlusal; B3, buccal; B4, anterior; and B5, posterior views of molar. C, D and E, distinctive upper molar characters for each species of *Borealestes*: C, M3 of *B. serendipitus*, NMS G.1992.47.121.1; D, *B. mussettae*, NHMUK PV M46871; E, *B. mussettae*, NHMUK PV M46871 anterior view. D and E mirrored to facilitate comparison. Dotted lines indicate missing portions of tooth. Arrows in bold indicate anterior direction. Same scale for A–B, and same scale for C–E. All scale bars equal 1 mm. [Intended for page width 183 mm]

182x155mm (300 x 300 DPI)

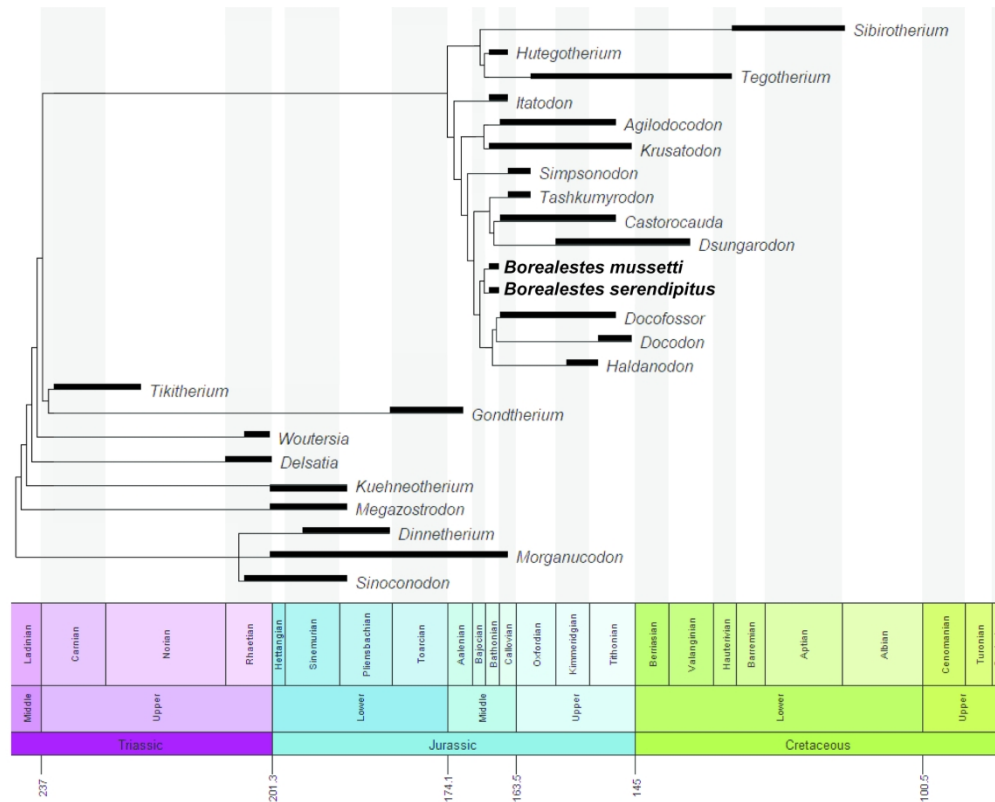


FIGURE 8. Phylogeny of docodonts, with tree-topology based on updated phylogenetic analysis. Results of parsimony branch and bound analysis of docodonts and outgroups, tree of 117 steps. First to last appearances are represented by black box for each taxon (for sources of FAD/LADs see Methods). Nodes uniting taxa do not imply divergence times. [Intended for page width 183 mm]

182x146mm (300 x 300 DPI)

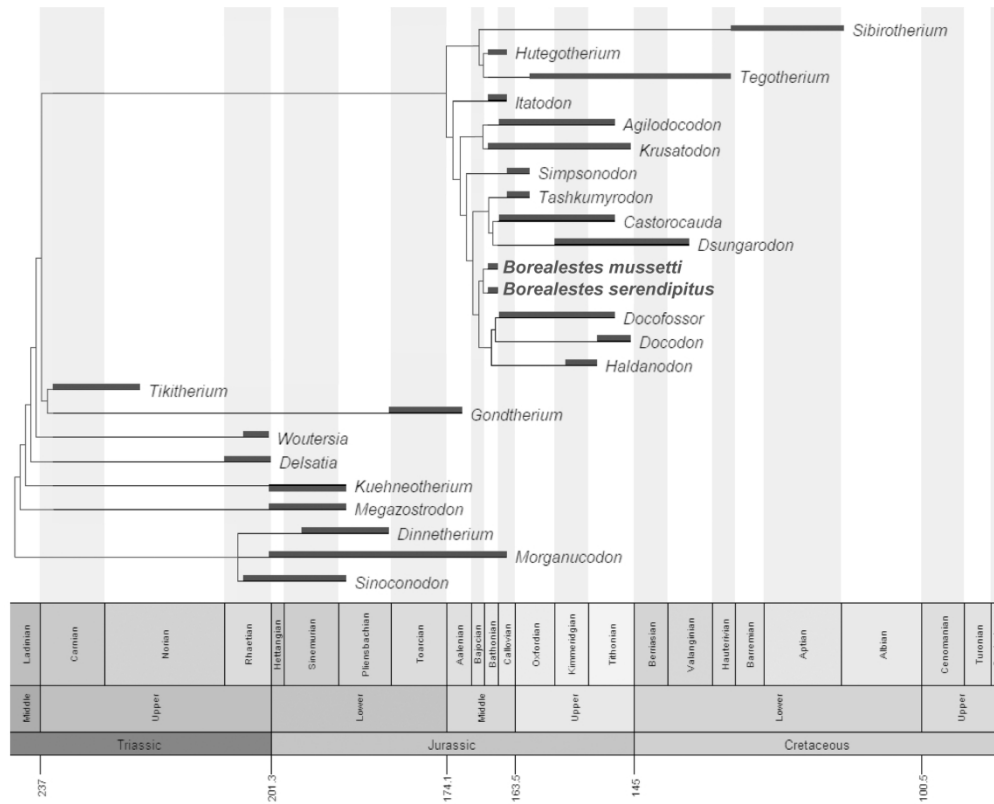


FIGURE 8. Phylogeny of docodonta, with tree-topology based on updated phylogenetic analysis. Results of parsimony branch and bound analysis of docodonts and outgroups, tree of 117 steps. First to last appearances are represented by black box for each taxon (for sources of FAD/LADs see Methods). Nodes uniting taxa do not imply divergence times. [Intended for page width 183 mm]

182x146mm (300 x 300 DPI)

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3 The Journal of Vertebrate Paleontology
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8 The mandible and dentition of *Borealestes serendipitus* (Docodontia) from the
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10 Middle Jurassic of Skye, Scotland
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14 ELSA PANCIROLI,^{1,2*} ROGER B.J. BENSON,³ and ZHE-XI LUO^{4*}
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S6: Data Matrix Used in this Analysis

S7: Cross-reference and Scoring of Other Taxa in Meng et al (2015) Matrix

S8: PAUP Analysis

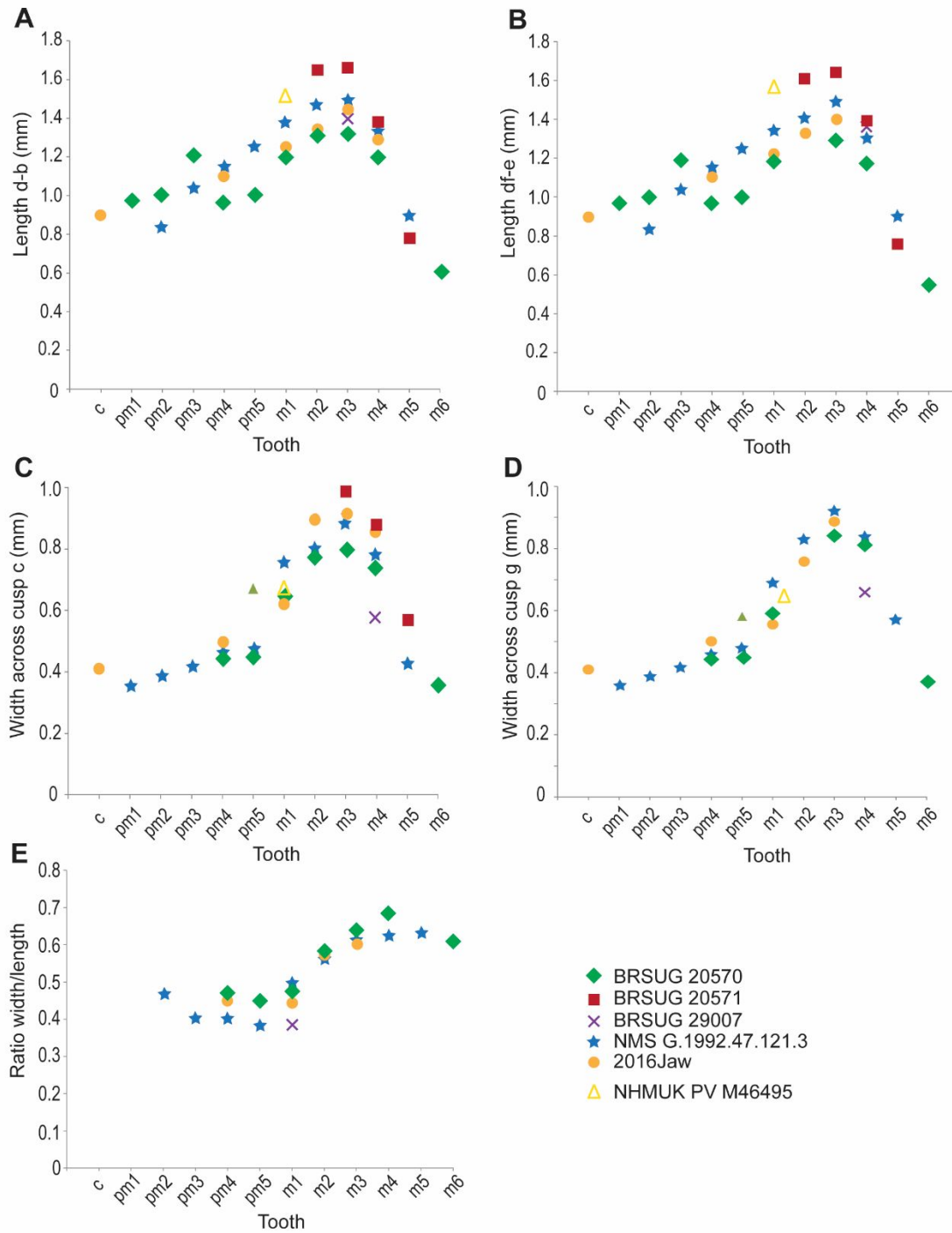
S9: Systematic Character List for Docodontans and Outgroups (see Meng et al
2015)

References

S1: Docodontan Lower molar terminology

Terminology used in this paper	Butler (1997) & Pfretzschner et al. (2005)	Sigogneau-Russell (2003) & Kielan-Jaworowska et al. (2004)	Luo & Martin (2007)
cusp a	cusp a	main cusp	cusp a
cusp b	cusp b	mesiolabial cusp	cusp b
cusp c	cusp c	distolingual cusp	cusp c
cusp d	cusp d	distolabial talonid cusp	cusp d
cusp e	cusp e	cuspule	cusp e / mesiolingual cingulid cuspule
cusp df	cusp df	lingual talonid cusp	docodont cusp f / distolingual cingulid cuspule
cusp g	cusp g	mesiolingual cusp	cusp g
a-b crest			a-b crest / anterior crest
a-c crest			a-c crest / postero-oblique crest
a-d crest		posteromain crest	
a-g crest		anteromain crest	a-g crest / antero-oblique crest
b-g crest		anterobasal crest	
b-e crest		crescent	
c-d crest			c-d crest / Transtalonid crest
c-f crest		posterior crest	
d-f crest		cingulum	d-f crest / Distal-cingulid crest

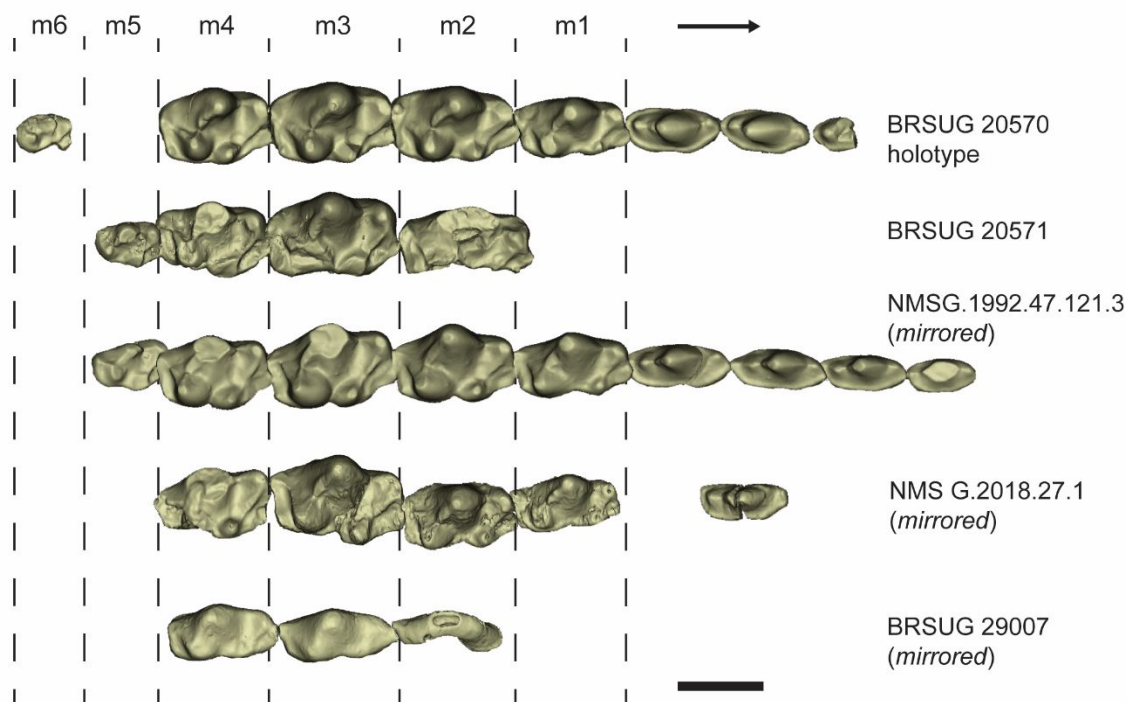
S2: Tooth Row Gradients



Size gradient and width to length ratio of toothrows of *Borealestes serendipitus* and *B. mussettae* holotype. **A**, length measured from cusp d to b; **B**, length measured from cusp df to e; **C**, width measured across cusp c; **D**, width

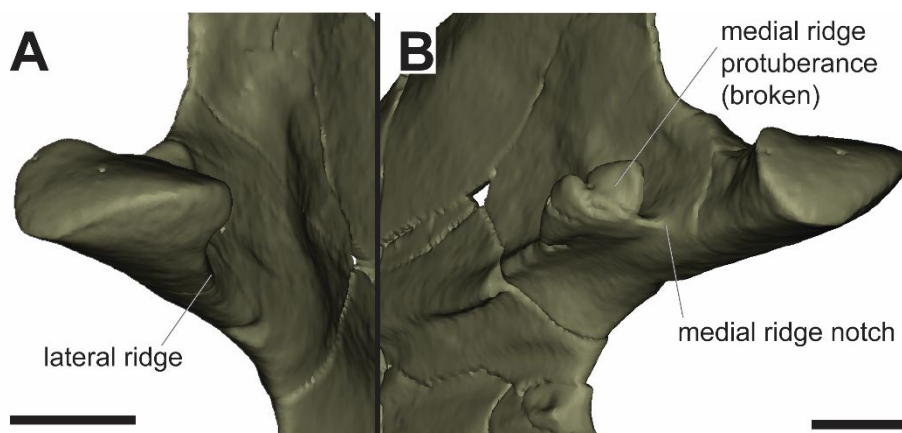
measured across cusp g; **E**, the ratio of width divided by length. All measurements in mm. For measurements see Table 1, and for measurement methodology see Figure 1 and text. [Intended for page width 183 mm]

S3: Comparative Figure of *Borealestes serendipitus* Tooth Rows



Comparison of multiple specimens of *Borealestes serendipitus*. Lower tooth rows in five specimens of *B. serendipitus*, some mirrored to permit easy comparison with the holotype material. NMS G.2018.27.1 m3 crown was displaced post-mortem and is here placed back to correct position to facilitate comparison. The unusually buccolingually narrow teeth of BRSUG 29007 are caused by post-mortem erosion. Same scale throughout. All scale bars equal 1 mm. [Intended for page width 183 mm]

S4: Dentary Condyle of *Borealestes serendipitus* NMS G.1992.47.121.3



The dentary condyle of specimen NMS G.1992.47.121.3, *Borealestes serendipitus*, showing **A**, the spindle-shaped condyle, and **B**, the broken and displaced flange of the medial protuberance.

S5: Notes on *Borealestes* Species

Specimens were re-examined in light of refined diagnosis for both species of the genus *Borealestes*. Justification for identifications given (see main text for details of diagnoses).

NHM PV specimen	<i>B. serendipitus</i>	<i>B. mussettae</i>	Docodonta	Notes on identification
M.44301	yes			The c and g cusp close together, no a-d or a-g crest.
M.46039	yes			Very worn, but lacks a-g or a-d crest.
M.46058	yes			Lacks a-d crest.
M.46116	uncertain			Heavily worn, ID uncertain but probably <i>B. serendipitus</i> .
M.46316	yes			No cusp on the A-X crest.
M.46396	yes			Strong A-X crest as expected for <i>B. serendipitus</i> .
M.46400			yes	The tooth doesn't match morphology of molar of <i>Borealestes</i> : too

				anteroposteriorly elongated, with large cingulid cusps B and C. Not <i>Borealestes</i> .
M.46445			yes	Cusp Y too large, indent too deep, A-X crest too distinct. This incomplete tooth is probably a labial wing of <i>Krusatodon</i> right upper molar.
M.46521	yes			No a-g and a-d crest (not even on cusp d). Posterior cingulid cusps almost non-existent.
M.46549	yes			No a-d crest.
M.46580		yes		Cuspule on the A-X crest, and distinct cusp Y. No cusp Z.
M.46607			yes	Resembles M46400, but does not resemble <i>B. serendipitus</i> .
M.46610	yes			No a-g, no a-d, has all diagnostic morphology of <i>B. serendipitus</i> .
M.46632	probably			Very worn, but nothing contradicts an ID as <i>B. serendipitus</i> .
M.46728	probably			Not any major diagnostic features, but nothing contradicts an ID as <i>B. serendipitus</i> .
M.46791	yes			No a-g, or a-d. Has diagnostic morphology of lower molar <i>B. serendipitus</i> , with very small cusp g far from cusp c, indicating an m1.
M.46841	yes			No a-d or a-g crest.
M.46869	yes			Anteriorly very worn, no a-d crest or a-g crest.
M46246	no	unlikely	Probably	This was labelled as <i>Borealestes</i> cf. <i>mussettae</i> , but it almost certainly neither as it has none of the diagnostic features.
M46845	likely			Referred to 'Docodonta', but likely <i>B. serendipitus</i> , indicated by a very weak a-g crest.
M46842	yes			Referred to 'Docodonta', but likely <i>B. serendipitus</i> , no a-g crest.
M. 46001		yes		Has strong a-g crest and a-d crest.

M. 46066		yes		Has a-g crest.
M.46224		yes		Has a-g crest and well defined pseudotalonid by a-g and b-g crests.
M.46239		yes		Has a-g, a-c, and a-b crests. Longer length/width ratio.
M.46319		yes		Worn, but has a-d crest and wide space between cusps c and g.
M.46389	yes			No a-g crest, the tooth is bucco-labially wide.
M.46394		yes		The A-X crest weak to non-existent.
M.46399	yes			Strong c-d cusp and no a-d cusp.
M.46401	yes			No a-d crest.
M.46404	no	probably not	yes	Very fragmentary; the preserved part is probably the labial wing of upper molar. Could be <i>Krusatodon</i> , certainly not <i>B. serendipitus</i> as there is a cusp on the A-X crest - if it is an A-X crest.
M.46448		yes		Cusp on A-X crest and a more distinct cusp Y than in <i>B. serendipitus</i> .
M.46495		HOLOTYPE		See main text and figures.
M.46588	yes			No a-d crest, buccolingually wide.
M.46809		yes		Has a-g crest.
M.46835		yes		Worn and enamel broken, but seems to show an a-g crest; c and g cusps far apart, and the overall morphology buccolingually narrow.
M.46836		yes		Has strong a-g crest and a-d crest.
M.46871		yes		See main text and figures.
J.79446			yes	Has an a-g crest, not a tooth of <i>B. serendipitus</i> ; cusps c and g close together and strong a-g and a-c crests, but not matching <i>B. mussettae</i> . Likely an anterior lower molar of <i>Krusatodon</i> or <i>Simpsonodon</i> .
J.79474	yes			No a-g crest, but all other features are diagnostic of <i>B. serendipitus</i> .
J.79475	yes			No a-g or a-d crest
J.79497			yes	Has an a-g crest, wrinkled enamel on posterior of molar, probably a tooth of <i>Simpsonodon</i> .
J.79498	maybe	maybe	maybe	Probably a premolar, not diagnostic features for ID.
J.79514			yes	Strong a-g crest and a-d crest, cusp a conical, very tall and pointed, strong lingual cingulid, large cusp b. Doesn't match <i>Borealestes</i> . No wrinkled enamel. Cusps c and g missing, but resembles <i>Krusatodon</i> .

S6: Data Matrix Used in this Analysis

#NEXUS

Begin data;

Dimensions ntax=25 nchar=47;

Format datatype=standard symbols="01234" gap=-;

Matrix

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Megazostrodon 100000000000000010000??0000?00000001000?2000000
Kuehneotherium 1001?000000000000?00??0000?00020001000?2010000
Delsatia ?????????????1021000??0000?00000001000?20100??
Woutersia ?????1000010101021000??0000?00000001000?201000?
Gondtherium ?????110000020?????????0????????????????????
Tikitherium ?????110000021?????????0????????????????????1?
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Docodon 21111111121121113131111011102102101001114012011
Docofossor 211111111211211131311100101021021110?1114012011
Dsungarodon ?????111110121103112100110102101010012101111111
BorealestesS 111011111101211030111200101?1112111011103011111
BorealestesMUp ?????110?1012110302201001020111111101110?1101??
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Castorcauda 211?1?????????1031121010102011020100121010111?1
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Simpsonodon ?????11111101101041121?101120111101101210301111?
Krusatodon ?????11?01011110312212011021101101101210301111?
Agilodocodon 2111111101 011110412212111211011011012103011111
Tegotherium ???111111011110412200111020000101102210311111?
Hutegotherium ??111111011110412200111020000101102210311111?
Sibirotherium ???1111110111103122001010200001011022103111111
;
End;

```

S6: Characters Scores for *B. serendipitus*

Characters were scored using the Meng et al (2015) matrix – see S5 for full character list. The following scores were added or changed.

Additional characters added:

1
2
3 48: Presence of an anterior fovea on the upper molars: (0) absent, (1) present
4 and positioned at mid-line constriction of upper molar, (2) present and lingually
5 offset from the midline of the upper molar.
6

7
8 This character is absent in all docodonts except *Docodon* (2) and *Borealestes*
9 (1).
10

11 1-5: characters can now be scored thanks to new material
12

13 8 and 9: defined as mesio-lingual and mesio-labial crests (Meng et al 2015), but
14 meaning anterolingual and anterolabial. Supplementary of Meng et al (2015)
15 gave character states for character 9 as (0) and (2), this has been amended to
16 (0) and (1).
17
18

19 18: cusp c re-scored, from (1) sub-equal to cusp g, to (0) much larger than cusp
20 g.
21

22
23 19: the anterior border of the pseudo-talonid was scored as (1) present and
24 bordered by the b-g crest. In Meng et al 2015 the score for this character differed
25 between the character list (2), the matrix table (3), and the Nexus file (1).
26

27 20: a-g crest re-scored from (2) raised with v-notch, to (1) present or lower.
28 Although there is no a-g crest on cusp a in *B. serendipitus*, there is a very a small
29 portion of crest variably on cusp g, and so this cannot be scored as absent.
30

31
32 21: the b-g crest has been rescored from (0) absent or weakly developed, to (1)
33 present.
34

35 27: the a-d crest was re-scored from (2) connected by a crest with a v-notch, to
36 (1) incomplete. This is because the a-d crest is only present on the d cusp, where
37 it runs labially below the a cusp, and is not present on the a cusp.
38
39

40 28: the alignment of the a-d cusp was re-scored from (0) present and straight to
41 (?) not applicable, because it is not present on cusp a.
42

43 32: The mesio-lingual cingulid from cusp e was re-scored from (1) extending
44 posteriorly below cusp g to (2) absent or limited to mesial part of the tooth. This
45 cingulid does not extend below cusp g in *B. serendipitus*.
46
47

48 42: the placement of cusp e was re-scored from (1) cusp e labially shifted to (0)
49 lingual position.
50

51 44: the degree of triangulation of cusps g-a-c was re-scored from (0) >80
52 degrees to (1) < 80 degrees.
53
54
55
56
57
58
59
60

1
2
3 47: the number of canine roots was scored in the matrix of Meng et al 2015 as
4 (1), but listed in their character descriptions as (?). We can confirm it is (1).
5
6
7

8 S4: Characters scores for *B. mussettae*
9

10 Characters were scored using the Meng et al (2015) matrix – see S5 for full
11 character list. The following scores were added or changed.
12

13 1 to 5: the dentary is not yet known for *B. mussettae*.
14

15 8: the transverse antero lingual and anterolabial crest was scored as (0) absent,
16 unlike *B. serendipitus*.
17

18 9: the transverse antero lingual and anterolabial crest in the posterior molar was
19 scored as (?) unknown, as we believe only the anterior upper molars are known
20 for *B. mussettae*.
21
22

23 19: the anterior border of the pseudo-talonid was scored as (2) present and
24 bordered by the b-e crest, unlike in *B. serendipitus*. This is because of the weaker
25 b-g crest in *B. mussettae* and the subsequent slight shift in the position of the
26 pseudotalonid.
27
28

29 20: unlike *B. serendipitus*, *B. mussettae* has (1) a raised a-g crest and it has a v-
30 notch.
31
32

33 21: the b-g crest was scored (0) absent or weakly developed because it is poorly
34 developed compared to *B. serendipitus*.
35

36 22: the c-d crest was scored as present with the c-d crest being straight, unlike
37 the angle in *B. serendipitus*.
38
39

40 27: the a-d crest is (2) present and connected with a v-notch in *B. mussettae*.
41

42 32: The mesio-lingual cingulid from cusp e was scored as (1) extending
43 posteriorly below cusp g, in contrast to *B. serendipitus*.
44

45 41: this was scored as (?) because the interlocking between lower molars is not
46 yet known for *B. mussettae*.
47
48

49 42: the placement of cusp e was scored as (1) cusp e labially shifted to for this
50 species, in contrast to *B. serendipitus*.
51

52 44: the degree of triangulation of cusps g-a-c was scored as (0) >80 degrees, in
53 contrast to *B. serendipitus*.
54
55
56
57
58
59
60

1
2
3 46 and 47: the number of roots in the canine and upper molars is not yet known
4 for *B. mussettae*.
5
6
7

8 **S7: Cross-reference and Scoring of Other Taxa in Meng et al (2015) Matrix**

9

10 Character lists in Meng et al (2015) differed between the NEXUS file, the matrix
11 table provided for score verification, and the example scores in the character list.
12 We compared these data matrices, and where scores differed we scored those
13 characters based on our own observations of specimens, predominantly from the
14 literature.
15

16 *Sinoconodon*

17 21: crest b-g (?) not applicable

18 32: changed to (?) not applicable
19
20

21 *Morganucodon*

22 3: changed to (0) facing medially
23
24

25 *Dinnetherium*

26 3: changed to parallel to ventral margin (through observation of specimen MCZ
27 20870)
28

29 *Megazostrodon*

30 3: changed to (0) convergent to ventral margin
31
32

33 *Kuehneotherium*

34 21: changed to (?) not applicable

35 32: changed to (2) limited to the mesial part of the tooth
36
37

38 *Woutersia*

39 9: changed to (0) absent
40

41 *Gondtherium*

42 9: changed to (0) absent
43
44

45 *Tikitherium*

46 9: changed to (0) absent

47 14: changed to (1) present
48

49 *Haldanodon*

50 17: changed to (3) distinctive and anteriorly positioned

51 34: changed to (1)
52
53

54 *Docodon*

55 17: changed to (3)
56
57
58
59
60

1
2
3 34: changed to (0)

4 37: changed to (0)

5
6
7 *Docofossor*

8 17: changed to (3)

9 31: changed to (0)

10
11 *Dsungarodon*

12 1 and 2: changed to (?), although *Acuodulodon* and *Dsungarodon* have been
13 suggested to be synonymous by Martin et al 2010, we consider the material too
14 poorly preserved to be certain, and the synonymisation relies too heavily on
15 premolar characters, which are similar among some docodontans genera (and
16 therefore may be similar in this case). We therefore choose not to use this
17 interpretation for this analysis.

18 17: changed to (3)

19 31: changed to (0)

20
21
22 *Borealestes*

23 See S1 and S2 for new scores

24
25
26 *Tashkumyrodon*

27 17: changed to (3)

28 19: changed to (3)

29
30
31 *Castorocauda*

32 17: changed to (3)

33 19: changed to (1)

34
35
36 *Itatodon*

37 17: changed to (4)

38 19: changed to (3)

39 And extra character removed from end

40
41 *Simpsonodon*

42 17: changed to (4)

43 19: changed to (1)

44 22: changed to (?) not applicable due to enamel folding

45 31: changed to (1)

46 32: changed to (1)

47
48
49 *Krusatodon*

50 17: changed to (3)

51 23: changed to (0)

52 31: changed to (1)

53
54
55 *Agilodocodon*

1
 2
 3 Woutersia ?????1000010101021000??0000?00000001000?201000?0
 4 Gondtherium ?????110000020????????????0????????????????????0
 5 Tikitherium ?????110000021????????????0????????????????????1?0
 6 Haldanodon 21111111211211031311100111021111110111140120110
 7 Docodon 2111111121121113131110111021021010011140120112
 8 Docofossor 21111111211211131311100101021021110?11140120110
 9 Dsungarodon ?????111110121103112100110102101010012101111110
 10 BorealestesS 11101111101211030111200101?11121110111030111111
 11 BorealestesMUp ?????110?101211030220100102011111101110?1101??1
 12 Tashkumyrodon ?????????????103?3211101020?0110110121111111??0
 13 Castoroconda 211?1?????????103112101010201102010012101011?10
 14 Itatodon ???11?????????10413201?0102011010110121030111?10
 15 Simpsonodon ???11111101101041121?101120111101101210301111?0
 16 Krusatodon ?????11?01011110312212011021101101101210301111?0
 17 Agilodocodon 211111110101111041221211112110110110121030111110
 18 Tegotherium ???111111011110412200111020000101102210311111?0
 19 Hutegotherium ???111111011110412200111020000101102210311111?0
 20 Sibirotherium ???11111101111031220010102000010110221031111110
 21
 22
 23
 24
 25

26 paup> BandB mulTrees=no;

27
28
29 Branch-and-bound search settings:

30 Optimality criterion = parsimony

31 Character-status summary:

32 Of 48 total characters:

33 All characters are of type 'unord'

34 All characters have equal weight

35 All characters are parsimony-informative

36 Gaps are treated as "missing"

37 Initial upper bound: unknown (compute heuristically)

38 Addition sequence: furthest

39 Initial 'Maxtrees' setting = 100

40 Branches collapsed (creating polytomies) if maximum branch length is zero

41 'MulTrees' option not in effect; only 1 tree will be saved

42 No topological constraints in effect

43 Trees are unrooted

44
45
46
47
48 Maxtrees reset to 200

49
50 Branch-and-bound search completed:

51 Score of best tree found = 117

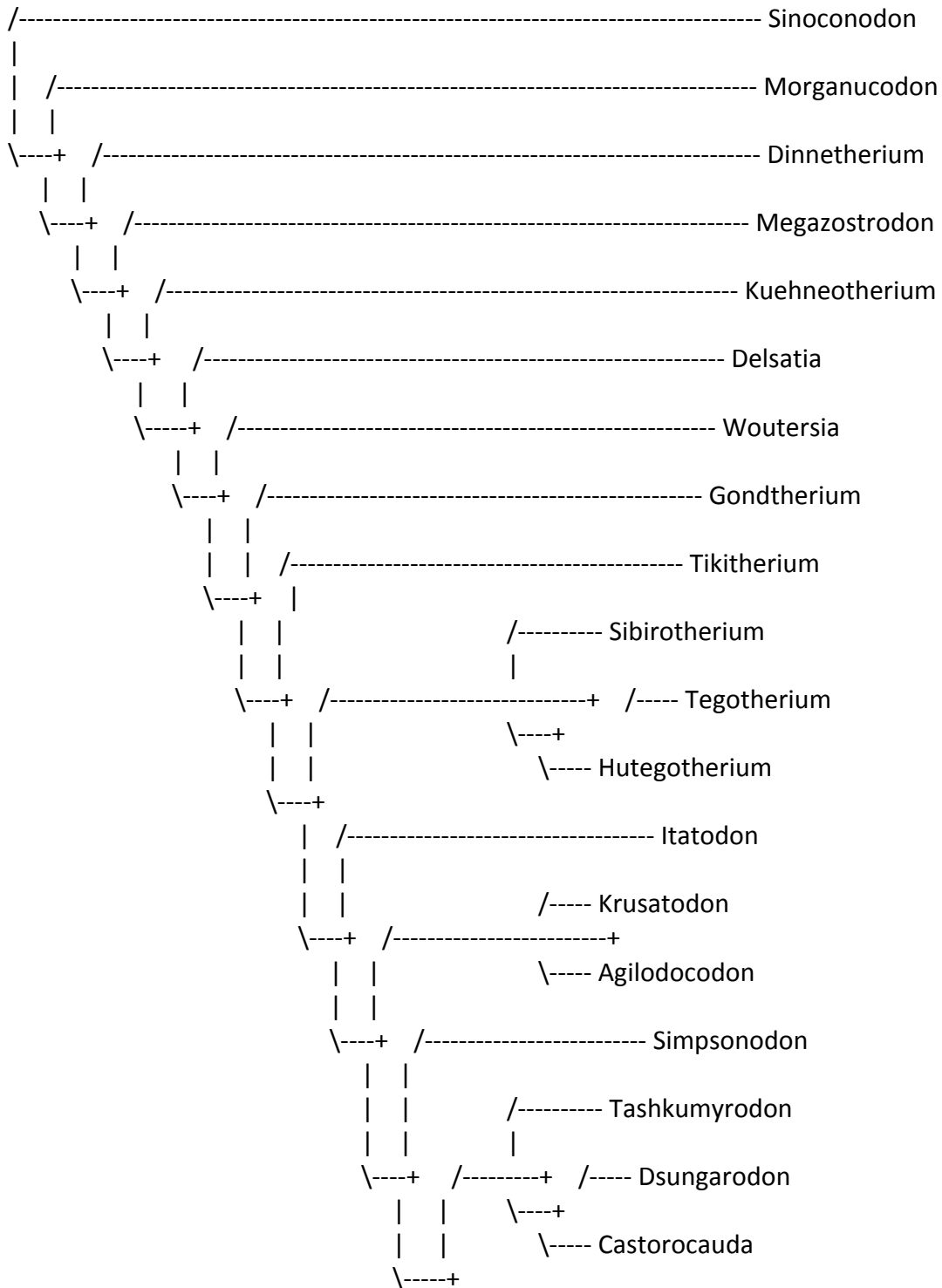
52 Number of trees retained = 1

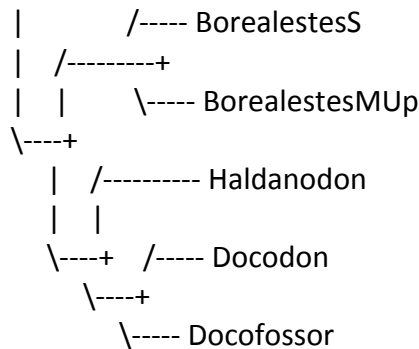
53 Time used = 00:03:09 (CPU time = 00:02:45.5)

paup> ShowTrees / tOrder=right;

Note: No outgroup has been defined; tree is (arbitrarily) rooted at first taxon.

Tree 1 (rooted using default outgroup)





paup> DescribeTrees / xout=internal apoList;

Tree description:

Unrooted tree(s) rooted using outgroup method

Note: No outgroup has been defined; tree is (arbitrarily) rooted at first taxon.

Optimality criterion = parsimony

Character-status summary:

Of 48 total characters:

All characters are of type 'unord'

All characters have equal weight

All characters are parsimony-informative

Gaps are treated as "missing"

Character-state optimization: Accelerated transformation (ACCTRAN)

Tree 1 (rooted using default outgroup)

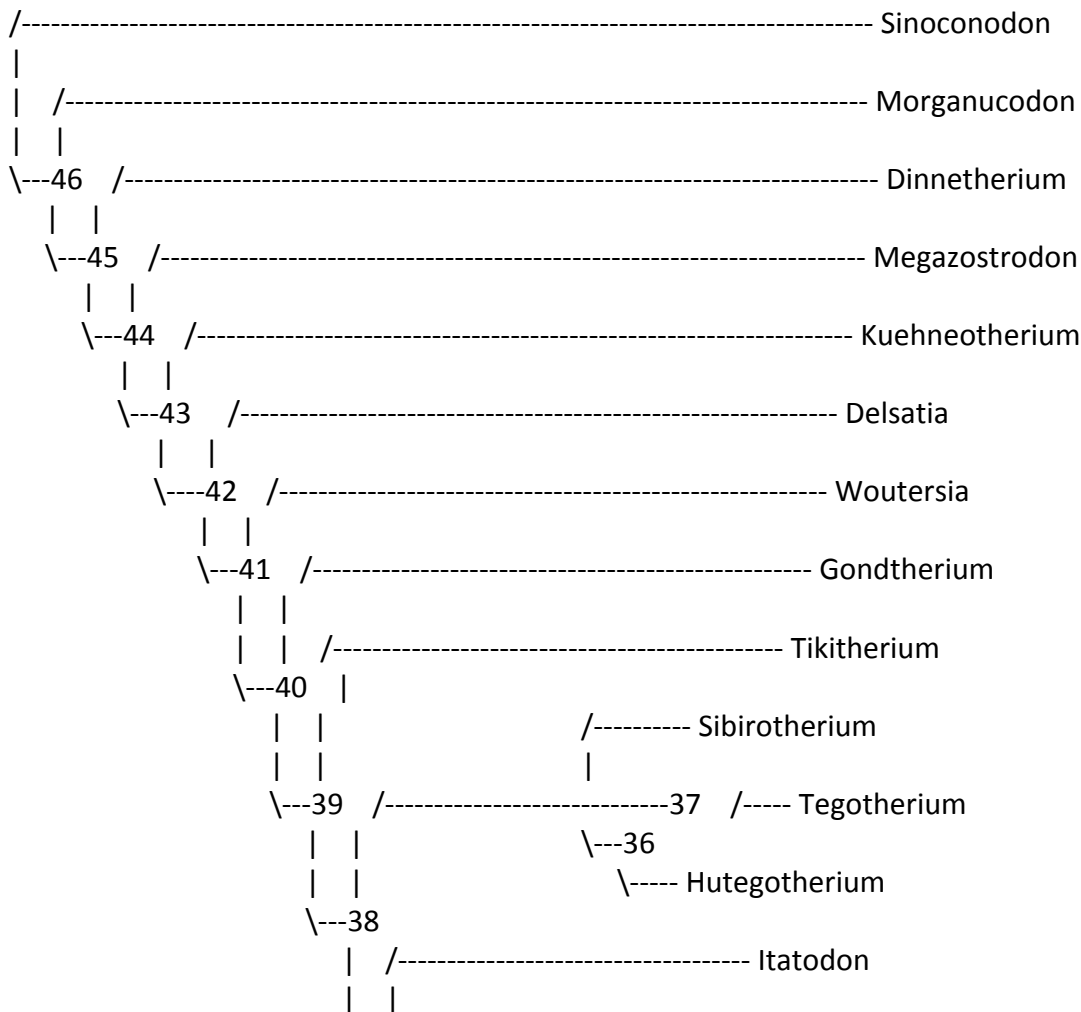
Reconstructed states for internal nodes:

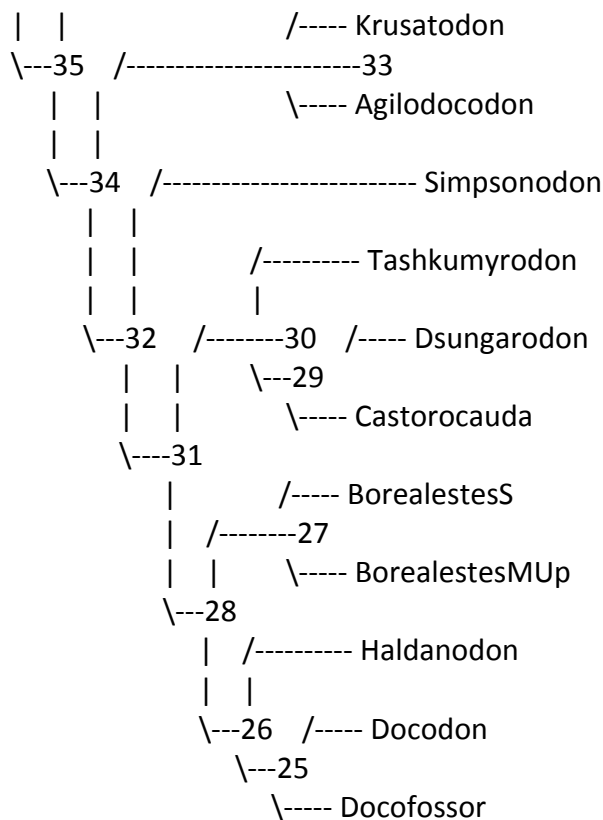
Node	1	2	3	4	4
25	21111111211211131311100111021021110011140120110				
26	21111111211211031311100111021111110111140120110				
27	111011111101211030111100101011111110111030111111				
28	211111111101211031111100101011111110111030111110				
29	211111111101211031121010102011010100121011111110				
30	211111111101211031121110102011110110121011111110				
31	211111111101211031121110102011110110121030111110				
32	211111111101111041121110102011110110121030111110				
33	211111110101111041221211102110110110121030111110				
34	211111111101111041221110102011110110121030111110				
35	211111111101111041220110102011010110121030111110				

```

36      21111111101111041220011102000010110221031111110
37      21111111101111041220010102000010110221031111110
38      21111111101111041220010102000010110121030111110
39      211111100000211041220010102000010110121030111110
40      211111100000201041220010102000010110121030111110
41      211111000000101021000010000000000001000020100010
42      211111000000101021000010000000000001000020100010
43      100110000000000001000010000000000001000020100000
44      1001000000000000010000010000000000001000020000000
45      1001000000000000010000010000000000000000010000000
46      0001000000000000010000010000000000000000010000000
    
```

Tree length = 117
 Consistency index (CI) = 0.5812
 Homoplasy index (HI) = 0.4188
 Retention index (RI) = 0.8287
 Rescaled consistency index (RC) = 0.4816





Apomorphy lists:

Branch	Character	Steps	CI	Change
node_46 <-> Sinoconodon	17	1	0.571	1 <=> 0
41	1	0.800	1 <=> 0	
node_46 --> Morganucodon	4	1	0.333	1 ==> 0
node_46 --> node_45	1	1	0.667	0 ==> 1
node_45 --> node_44	36	1	0.500	0 ==> 1
41	1	0.800	1 ==> 2	
node_44 --> Megazostrodon	4	1	0.333	1 ==> 0
node_44 --> node_43	5	1	1.000	0 --> 1
17	1	0.571	1 --> 0	
18	1	0.500	0 --> 1	
43	1	1.000	0 ==> 1	
node_43 --> Kuehneotherium	32	1	0.400	0 ==> 2
node_43 --> node_42	1	1	0.667	1 --> 2
2	1	1.000	0 --> 1	
3	1	1.000	0 --> 1	
6	1	1.000	0 --> 1	
13	1	0.500	0 --> 1	
15	1	1.000	0 ==> 1	

1
 2
 3 17 1 0.571 0 --> 2
 4 47 1 1.000 0 --> 1
 5
 6 node_41 --> Woutersia 11 1 0.500 0 ==> 1
 7 node_41 --> node_40 7 1 1.000 0 ==> 1
 8 13 1 0.500 1 --> 2
 9 17 1 0.571 2 --> 4
 10 19 1 0.500 0 --> 2
 11 20 1 0.667 0 --> 2
 12 25 1 1.000 0 --> 1
 13 27 1 0.500 0 --> 2
 14 32 1 0.400 0 --> 1
 15 34 1 0.500 0 --> 1
 16 35 1 0.500 0 --> 1
 17 36 1 0.500 1 --> 0
 18 37 1 0.667 0 --> 1
 19 38 1 1.000 0 --> 2
 20 39 1 1.000 0 --> 1
 21 41 1 0.800 2 --> 3
 22 44 1 0.667 0 --> 1
 23 45 1 0.500 0 --> 1
 24 46 1 1.000 0 --> 1
 25
 26 node_40 --> node_39 14 1 0.500 0 ==> 1
 27 node_39 --> node_38 8 1 0.500 0 ==> 1
 28 9 1 0.500 0 --> 1
 29 10 1 1.000 0 ==> 1
 30 12 1 1.000 0 ==> 1
 31 13 1 0.500 2 --> 1
 32 node_38 --> node_35 22 1 0.500 0 --> 1
 33 29 1 0.667 0 ==> 1
 34 30 1 0.333 0 --> 1
 35 node_35 --> node_34 21 1 0.500 0 ==> 1
 36 31 1 0.333 0 ==> 1
 37 node_34 --> node_32 19 1 0.500 2 ==> 1
 38 node_32 --> node_31 13 1 0.500 1 ==> 2
 39 17 1 0.571 4 ==> 3
 40 node_31 --> node_28 20 1 0.667 2 --> 1
 41 23 1 0.250 1 ==> 0
 42 27 1 0.500 2 --> 1
 43 33 1 1.000 0 ==> 1
 44 38 1 1.000 2 ==> 1
 45 node_28 --> node_26 10 1 1.000 1 ==> 2
 46 11 1 0.500 0 ==> 1
 47 19 1 0.500 1 ==> 3
 48 26 1 0.250 0 --> 1
 49
 50
 51
 52
 53
 54
 55
 56
 57
 58
 59
 60

1
 2
 3 29 1 0.667 1 ==> 2
 4 40 1 0.500 0 ==> 1
 5 41 1 0.800 3 ==> 4
 6 44 1 0.667 1 ==> 2
 7 45 1 0.500 1 ==> 0
 8
 9 node_26 --> node_25 16 1 1.000 0 ==> 1
 10 31 1 0.333 1 ==> 0
 11 32 1 0.400 1 ==> 2
 12 37 1 0.667 1 --> 0
 13
 14 node_25 --> Docodon 23 1 0.250 0 ==> 1
 15 34 1 0.500 1 ==> 0
 16 48 1 1.000 0 ==> 2
 17
 18 node_25 --> Docofossor 26 1 0.250 1 --> 0
 19 node_28 --> node_27 1 1 0.667 2 --> 1
 20 4 1 0.333 1 --> 0
 21 18 1 0.500 1 ==> 0
 22 48 1 1.000 0 ==> 1
 23
 24 node_27 --> BorealestesS 22 1 0.500 1 ==> 2
 25 32 1 0.400 1 ==> 2
 26
 27 node_27 --> BorealestesMUp 8 1 0.500 1 ==> 0
 28 19 1 0.500 1 ==> 2
 29 20 1 0.667 1 --> 2
 30 21 1 0.500 1 ==> 0
 31 27 1 0.500 1 --> 2
 32 42 1 0.250 0 ==> 1
 33 44 1 0.667 1 ==> 0
 34
 35 node_31 --> node_30 41 1 0.800 3 ==> 1
 36 42 1 0.250 0 --> 1
 37
 38 node_30 --> node_29 22 1 0.500 1 ==> 0
 39 31 1 0.333 1 ==> 0
 40 35 1 0.500 1 ==> 0
 41
 42 node_29 --> Dsungarodon 23 1 0.250 1 ==> 0
 43 24 1 0.333 0 ==> 1
 44 27 1 0.500 2 ==> 1
 45 29 1 0.667 1 ==> 2
 46
 47 node_29 --> Castorocauda 32 1 0.400 1 ==> 2
 48 42 1 0.250 1 --> 0
 49
 50 node_30 --> Tashkumyrodon 19 1 0.500 1 ==> 3
 51 30 1 0.333 1 ==> 0
 52 40 1 0.500 0 ==> 1
 53
 54 node_32 --> Simpsonodon 14 1 0.500 1 ==> 0
 55 26 1 0.250 0 ==> 1
 56
 57 node_34 --> node_33 9 1 0.500 1 --> 0
 58 22 1 0.500 1 ==> 2
 59
 60

```

1
2
3           24      1  0.333 0 ==> 1
4           28      1  1.000 0 ==> 1
5           30      1  0.333 1 --> 0
6
7 node_33 --> Krusatodon  17      1  0.571 4 ==> 3
8           23      1  0.250 1 ==> 0
9
10 node_33 --> Agilodocodon 26      1  0.250 0 ==> 1
11 node_35 --> Itatodon    19      1  0.500 2 ==> 3
12 node_38 --> node_37    37      1  0.667 1 --> 2
13           42      1  0.250 0 ==> 1
14 node_37 --> node_36    24      1  0.333 0 ==> 1
15 node_37 --> Sibirtherium 17      1  0.571 4 ==> 3
16

```

```

17
18 paup> SaveTrees file='F:\Manuscripts\Borealestes dentary\Phylogenetic
19 analysis\PAUP\Tree.txt';
20

```

```

21 1 tree saved to file "F:\Manuscripts\Borealestes dentary\Phylogenetic
22 analysis\PAUP\Tree.txt"
23
24
25

```

S9: Systematic Character List for Docodontans and Outgroups (see Meng et al 2015)

Mandibular Features

From Meng et al. (2015).

1. Mandible --- Angular process shape:

- (0) Pointed angle (two sides of the angular process forming an angle of 90 degrees and higher)
- (1) Obtuse angle (two sides of the angular process forming an angle of less than 90 degrees)
- (2) Rounded angular process

2. Angular process of the mandible with an efflected ventral crest:

- (0) Absent
- (1) Present

3. Mandible angular process – receiving structure for ectotympanic:

- (0) Medially facing concavity for ectotympanic
- (1) Posteriorly facing groove for ectotympanic

4. Meckel's groove to ventral margin of mandible:

- (0) Convergent to the ventral margin
- (1) Parallel to ventral margin

1
2
3
4
5 5. Replacement dental lamina (Crompton's) groove (visible along the
6 lingual alveolar margin of last molars):

7 (0) Present

8 (1) Absent
9

10
11 Upper Molar Characteristics
12

13
14 6. Transversely widening of upper molars:

15 (0) Absent

16 (1) Present
17

18
19 7. Mesiolingual cusp X of upper molars: wear facets on the labial aspect of
20 the cusp:

21 (0) Absent

22 (1) Wear facets present on the labial side of the lingual cusp
23
24

25
26 8. Transverse mesio-lingual and mesio-labial crests between Cusp A and
27 Cusp X on anterior molars:

28 (0) Absent

29 (1) Present and complete
30
31

32
33 9. (New). Transverse mesio-lingual and mesio-labial crests between Cusp A
34 and Cusp X on posterior molars:

35 (0) Absent

36 (1) Present and complete
37
38

39 10. Cusp Y (=upper disto-lingual cusp):

40 (0) Absent or indistinctive

41 (1) Present as a distinctive cusp

42 (2) Present, as crest aligned in antero-posterior line
43
44

45
46 11. Size and development of Cusp C (disto-labial cusp) and its separation
47 from Cusp A (mesio-lingual cusp):

48 (0) Cusp C present and enlarged

49 (1) Reduced cusp C twinned with cusp A
50
51

52
53 12. Posterior transverse crest extending from the disto-labial (C) to the
54 posterior cingulum (modified according to comment by Averianov et al., 2010):

55 (0) Absent
56
57
58
59
60

1
2
3 (1) Present
4
5

6 13. Presence of Cusp E separated from cusp B on posterior upper molars.

7 (0) Present

8 (1) Cusp E present and in labiolingual alignment with cusp B

9 (2) Absent
10
11

12 14. Constricted waist between the labial part and the lingual part of the upper
13 tooth.

14 (0) Absent

15 (1) Present
16
17
18

19 Lower Molar Characteristics 20

21 15. Cusp c on lingual cingulid and in alignment with mesio-lingual cusp g
22 (mesio-lingual):
23

24 (0) Absent

25 (1) Present
26
27

28 16. The a-c v-notch crest (postero-main crest of Sigogneau-Russell,
29 2003):
30

31 (0) Present

32 (1) Absent
33
34

35 17. Presence vs. absence and size of cusp g (mesio-lingual):
36

37 (0) Absent

38 (1) Small

39 (2) Distinctive, opposite to primary cusp a

40 (3) Distinctive, anteriorly positioned (more anteriorly placed than primary
41 cusp a)
42

43 (4) Anteriorly placed and hypertrophied (to the same size as, or larger than
44 cusp c)
45
46

47 18 Cusp c to cusp g size ratio:

48 (0) Cusp c much larger than cingular cusp g (if the latter is present)

49 (1) Sub-equal to the mesiolingual cusp g
50
51

52 19. Development of pseudo-talonid:
53

54 (0) Absent

55 (1) Present and its anterior-border by b-g crest
56
57
58
59
60

- 1
2
3 (2) Present and its anterior-border by b-e crest
4 (3) Present but cusp b is much taller than g so the pseudotalonid
5 appears to be lingually open
6
7
8
9 20. Raised a-g crest:
10 (0) Absent
11 (1) Present or lower
12 (2) Raised, with v-notch
13
14
15 21. Crest b-g:
16 (0) Absent, or weakly developed
17 (1) Present
18
19
20 22. The c-d crest in the posterior basin – presence/absence and alignment:
21 (0) Absent
22 (1) Present, c-d crest or c-f-d crests straight
23 (2) Present, c-d crest angled
24
25
26
27 23. Crest extending from cusp c to cusp df or the cusp df position:
28 (0) Absent
29 (1) Present
30
31
32 24. Placement of cusp d (modified from Sigogneau-Russell 2003: character 7;
33 Luo & Martin 2007 Character 16; assuming homology of the
34 morganucodontan cusp d to docodontan cusp d):
35 (0) Labial position (in alignment with a-b crest, or nearly so)
36 (1) Median placement (nearly halfway along the transverse width of
37 posterior crown)
38
39
40
41
42 25. Distal Cusp d-f (=cusp dd of Hu et al. 2007):
43 (0) Absent
44 (1) Present
45
46
47 26. Folding enamel (on either upper or lower) (Sigogneau-Russell, 2003:
48 character 5; Luo & Martin 2007 Character 17, scored on the posterior face of
49 lower cusp a or lingual face of upper cusps A-C):
50 (0) Absent or weakly developed
51 (1) Present
52
53
54
55 27. Connecting structure of cusps a and d (modified from Luo and Martin
56
57
58
59
60

1
2
3 2007 character 19; Hu et al. 2007, Character 14):

- 4 (0) Not connected
5 (1) Incomplete
6 (2) Connected by a crest with a v-notch
7
8
9

10 28. Alignment of posterior crest of cusp a toward cusp d (postero-main
11 crest of Sigogneau-Russell 2003; as defined in Luo & Martin 2007
12 character 18):

- 13 (0) Present and straight
14 (1) Present and angled
15
16
17

18 29. The b-g Crest - Crest between the mesio-labial cusp and mesio-lingual
19 cusps:

- 20 (0) Absent
21 (1) Present, low and broken (v-valley)
22 (2) Present and continuous
23
24
25

26 30. Size of cusp e:

- 27 (0) Present and distinctive
28 (1) Reduced
29
30

31 31. Mesiolingual cingulid (width would be related with presence/absence of
32 cusp e):

- 33 (0) Narrow or absent
34 (1) Wide
35
36
37

38 32. Mesio-lingual line-like cingulid extending from cuspule e or an
39 equivalent position:

- 40 (0) Connected to cusp g
41 (1) Extending posteriorly to below the cusp g
42 (2) Absent or limited to the mesial part of the tooth
43
44
45

46 33. Size ratio of cusp b and cusp a:

- 47 (0) Large, well separated by a notch from cusp a
48 (1) Small, approximated to cusp a
49
50

51 34. Cusp b position:

- 52 (0) Close to cusp a
53 (1) Well-separated from cusp a by a deep notch
54
55
56
57
58
59
60

1
2
3 35. The “docodont cusp f” (Postero-lingually positioned as defined by Martin
4 and Averianov 2004: figs 3 and 5, and differing from mesio-labially
5 positioned cusp f; Luo & Martin 2007 character 24):

- 6
7 (0) Absent
8 (1) Present
9

10
11 36. The “standard cuspule f” (mesio-labially positioned, as defined by Kielan-
12 -Jaworowska et al. 2004: fig. 5.9: ‘mesiolabial cusp’. We follow Luo & Martin
13 2007 [character 25] in regarding this cusp to be different from cusp g in
14 posterolingual position):

- 15
16 (0) Absent
17 (1) Present
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21 37. The b-e crest:

- 22 (0) Absent
23 (1) Present and continuous from cusp b to the cingulid
24 (2) Present, as a part of the pseudotalonid rim
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27 38. Anterior basin:

- 28 (0) No basin
29 (1) Small concavity
30 (2) Pseudotalonid basin
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34 39. Distal basin:

- 35 (0) Absent
36 (1) Present
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39 40. Width ratio of anterior basin vs. distal basin (modified from Hu et al.
40 2007 character 21, measured at the level of cusps/crests on occlusal
41 surface):

- 42 (0) Posterior basin narrower than anterior basin (or anterior part of the
43 tooth)
44 (1) Posterior basin wider than anterior basin
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48 41. Interlock of lower molars:

- 49 (0) No interlock
50 (1) d-b-e interlock
51 (2) d – ‘standard-f’-e interlock
52 (3) d-“f”-e interlock
53 (4) d-b overlap
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42. Placement of lower cusp E:

(0) Lingual position (lingual to the median axis of the lower molar)

(1) Cusp e labially shifted

43. Cusp triangulation (cusp triangulation between the a-c crest and the a-b crest following Butler 1997; Sigogneau-Russell and Godefroite 1997; Luo & Martin 2007 character 28):

(0) Absent

(1) Present

44. Degree of triangulation of cusps g-a-c:

(0) Broad triangle (>80 degrees)

(1) Sharp-triangled (≤ 80 degrees)

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

46. Number of upper molariform roots:

(0) Two

(1) Three

47. Number of lower canine roots :

(0) One

(1) Two

Additional character in this analysis -

48. Presence of an anterior fovea on the upper molars:

(0) absent

(1) present and positioned at mid-line constriction of upper molar

(2) present and lingually offset from the midline of the upper molar

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