POSTCRANIA OF BOREALESTES (MAMMALIFORMES, DOCODONTA) AND THE EMERGENCE OF ECOMORPHOLOGICAL DIVERSITY IN EARLY MAMMALS

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Abstract: The Middle Jurassic witnessed the early diversification of mammalian groups, including the stem-mammalian clade, Docodonta. Recent discoveries in China indicate docodontans exhibited ecomorphological diversity akin to small-bodied mammals living >100 million years later, in the Cenozoic. Our understanding of the emergence of this ecological diversity is hindered by a lack of Middle Jurassic fossil material from other parts of the world. The two partial postcranial skeletons of Borealestes described here come from the Kilmaluag Formation, Scotland. These are the most complete Mesozoic mammaliaform skeletons currently known from the UK, and among the best preserved in Europe. As an early member of Docodonta, Borealestes provides key anatomical information for understanding the clade’s evolution, and the emergence of mammaliaform ecomorphological diversity. Using digital reconstructions from micro-CT and synchrotron scans, we describe the postcranial anatomy of Borealestes and provide an updated phylogenetic analysis incorporating cranial and postcranial characters. We find Borealestes species form a sister group to a clade comprising Agilodocodon and Microdocodon. To complement observational analyses of the skeleton, we carry out principal components analyses using 3D landmarks on a comparative dataset of 42 extant mammal taxa. Our results indicate Borealestes lacked specializations for derived locomotor behaviour. We detect some similarity in the humerus between Borealestes and Ornithorhynchus. Borealestes is morphologically intermediate between the robust morphology of fossorial and semi-fossorial/semi-aquatic Haldanodon and Docofosor, and the gracile morphology for scansorial Agilodocodon and Microdocodon. We suggest ecological diversity in Docodonta may arise from an unspecialized basal blueprint, of which Borealestes may be representative.

Key words: mammal, Middle Jurassic, ecomorphology, Bathonian, geometric morphometrics.

One of the most exciting developments in Mesozoic mammal palaeontology in the last 15 years has been the unexpected discovery of high ecological diversity in Jurassic docodontans. Their divergent ecologies include fossorial, semi-aquatic and arboreal specializations (Martin 2005; Ji et al. 2006; Luo et al. 2015a; Meng et al. 2015; Zhou et al. 2019). Docodonta comprise one of the earliest branches of Mammaliaformes (sensu Rowe 1988; Luo 2007), and therefore are a key group for informing our understanding of mammal macroevolution, and the emergence of ecomorphological diversity in early Mesozoic mammaliaforms as a whole. However, a lack of postcranial material for more basal docodontan genera means we currently know little about how this ecomorphological diversity first emerged in this clade, or to what extent it contributed to their overall morphological disparity.

Docodonta were initially identified from mandibular and dental remains, demonstrating unusually complex...
Tooth morphologies for early mammaliaforms (Simpson 1929; Jenkins 1969; Gingerich 1973; Butler 1997). The first docodontan for which extensive cranial and postcranial material was known was Haldanodon exspectatus, from the Upper Jurassic of Portugal (Kühne & Krusat 1972; Lillegraven & Krusat 1991; Martin 2005). Haldanodon exhibits adaptations for a semi-fossorial and/or semi-aquatic lifestyle, with short, robust limb bones, and robust and mediolaterally wide phalanges, a pronounced deltopectoral crest and expanded distal joint of the humerus (Martin 2005). After this discovery, the Chinese docodontan, Castorocauda lutarismilis (Ji et al. 2006), from the upper Middle Jurassic, was found to have adaptations similar to that of the modern beaver or otter. Preserved soft tissue impressions indicate a wide and flattened tail with expanded double transverse processes on wide caudal vertebrae to support it (Ji et al. 2006). Soft tissue impressions around the hind feet suggest webbing between the digits, and its teeth are slightly recurved, perhaps facilitating a diet of aquatic invertebrates or even small fish (Ji et al. 2006). Such specializations were hitherto unknown in Mesozoic mammals. Castorocauda’s plated ribs, a homplastic feature among cynodonts that strengthens the trunk (Jenkins 1971), may be related to digging. Today, a semi-aquatic, semi-fossorial lifestyle of strengthens the trunk (Jenkins 1971), may be related to half-and-half dietary niche space and diversify in dietary ecology (Luo & Martin 2007; Luo 2007; Meng et al. 2015). Because of their early divergence from other mammaliaforms, the postcranial morphology of docodontans can provide key information for understanding the morphological evolution of mammals as a whole (Simpson 1929; Lillegraven & Krusat 1991; Kielan-Jaworowska et al. 2004; Martin 2018).

At least 14 docodontan genera are known from dentomandibular remains from across Laurasia, and spanning in time the Middle Jurassic (Waldman & Savage 1972; Kermack et al. 1987; Sigogneau-Russell 2003) to the Early Cretaceous (Maschenko et al. 2002; Sigogneau-Russell 2003; Averianov et al. 2018), with a peak in taxonomic diversity in the Middle to Late Jurassic (Luo & Martin 2007; Panciroli et al. 2021a). One of the geologically oldest docodontans is Boreales, a genus first discovered in the Kilmaluag Formation in Scotland, which is Bathonian in age, c. 166 Ma (Waldman & Savage 1972; Panciroli et al. 2021a). It was originally known only from dentomandibular remains referred to the type species B. serendipitus (Waldman & Savage 1972), with a more complete skeleton first discovered in 1972, but not studied until recently (Panciroli et al. 2018, 2019, 2021a). The partial skeleton of a second species, Boreales cuillinensis, was identified from the same locality in 2018, and its cranium described alongside those of B. serendipitus (Panciroli et al. 2021a).

The specimens of two species of Boreales currently comprise the most complete skeletons for any Mesozoic mammaliaform in the UK. Boreales has long been considered part of a basal docodontan clade, based on phylogenetic analyses using dentomandibular characters (Sigogneau-Russell 2003; Martin & Averianov 2004; Luo & Martin 2007; Averianov et al. 2010; Panciroli et al. 2019, 2021a). As one of the geologically oldest docodontan genera it provides critical information on the emergence of this clade; their morphology is of particular interest for reconstructing the ecology and early evolution of Docodontata. Herein we describe the postcrania of Boreales serendipitus and B. cuillinensis, and address their phylogenetic placement in a more comprehensive dataset including characters from across the skeleton. We analyse the postcrania of Boreales for ecological signatures using comparative morphology, with the addition of 3D geometric morphometrics. This will allow us to maximize the

Although they share some morphological features with the earliest mammaliaforms of the Late Triassic and Early Jurassic, such as Morganucodon (Hopson & Crompton 1969; Jenkins & Parrington 1976; Kirkman et al. 1981), it is now clear that Docodontata exhibit an unusual amount of within-clade ecological diversity, approaching that seen among small-bodied extant therian mammals. It has been hypothesized that the molar complexity of docodontans may be a key factor in their ability to exploit new niche space and diversify in dietary ecology (Luo & Martin 2007; Luo 2007; Meng et al. 2015). Because of their early divergence from other mammaliaforms, the postcranial morphology of docodontans can provide key information for understanding the morphological evolution of mammals as a whole (Simpson 1929; Lillegraven & Krusat 1991; Kielan-Jaworowska et al. 2004; Martin 2018).
information gained from the girdle and limb bones, which are exceptional in being preserved with minimal deformation or compression, making them especially informative for assessment of the morphology of this taxon, with implications for early mammal evolution.

MATERIAL AND METHOD

Specimens

NMS G.1992.47.121.1 is the partial skeleton of *B. serendipitus* (Fig. 1), discovered in 1972 during fieldwork led by R. Savage and M. Waldman on the shoreline south of Cladh a’Ghlinne, Isle of Skye (Fig. 2A). It was collected in 1973 and mechanically prepared by S. Finney at the University of Cambridge between 1994 and 1996, using a sodium bicarbonate airabrasive. It was then consolidated with 2% Paraloid B72. Some portions of the skeleton are detached from the limestone block (it is unclear when this occurred) and are stored separately (see Table 1 for full details). Only the postcranial elements are described herein; a full description of the crania and dentition are already provided elsewhere (Panciroli et al. 2021a).

NMS G.2020.4.1.1 is the partial skeleton of the recently named species *B. cuillinenis* (Panciroli et al. 2021a), found at Cladh a’Ghlinne in 2018 by Prof. Richard Butler during fieldwork by the University of Oxford, National Museums Scotland and University of Birmingham (Fig. 2B). It was removed in the field using a rock saw, and reduced in size by brittle fracture, without loss of material. We used using an iterative process of pilot x-ray micro-computed tomography (μCT) scanning to facilitate minimum-loss block-splitting and removal of excess matrix using lab-based rock cutting equipment (carried out by RBJB) resulting in a specimen composed of several separate, but contiguous blocks that could each be scanned at high resolution (see Fig. 2B and Table 1). Only the postcranial elements are described herein (see Panciroli et al. 2021a for full description of the crania and dentition).

X-ray micro-computed tomography and data processing

The parameters used for each acquisition of μCT are listed in Table 1. NMS G.1992.47.121.1 was scanned at the European Synchrotron Radiation Facility (ESRF, Grenoble, France) using propagation phase contrast μCT. It was scanned at a lower resolution to capture the whole skeleton, and at higher resolution in the area containing the skull. Although the skull was described by Panciroli et al. (2021a), some of the postcranial bones in the area of the skull are newly described herein (Fig. 1).

X-ray μCT data for NMS G.1992.47.121.2, NMS G.1992.47.121.4, NMS G.1992.47.121.5, NMS G.1992.47.121.6, NMS G.1992.47.121.7, NMS G.1992.47.121.8, NMS G.1992.47.121.9, NMS G.1992.47.121.10, NMS G.1992.47.121.11, and NMS G.1992.47.121.12 were obtained at the University of Edinburgh by Dr I. Butler, School of Geosciences Experimental Geoscience Facility, using their in-house built μCT scanner. The system comprises a Feinfocus 10–160 kV dual transmission/reflection source (Feinfocus Röntgen-Systeme GmbH, Garbsen, Germany), MICOS UPR-160-AIR ultra-high precision air-bearing table (PI miCos GmbH, Eschbach, Germany), Perkin Elmer XRD0822 amorphous silicon x-ray flat panel detector and terbium doped gadolinium oxy-sulfide scintillator (PerkinElmer, Waltham, MA, USA). Data acquisition software was written in-house, and tomographic reconstruction were performed by I. Butler using Octopus 8.7 software (TESCAN Orsay Holding a.s., Brno, Czech Republic).

X-ray μCT data for NMS G.1992.47.121.3 and NMS G.2020.4.1.1 were obtained by RBJB and Dr T. Davies at the University of Bristol using a Nikon XTH 225 ST (Nikon Metrology, Leuven, Belgium) with a 225 kV rotating target.

All tomographic data were segmented and digitally reconstructed by EP using Mimics 19.0 (Materialise NV, Leuven, Belgium) at NMS and the University of Oxford. Where fossils were not covered completely by sedimentary matrix, they were also examined using conventional light microscopy at NMS. Measurements were taken using the measurement tools in Mimics 19.0, and corroborated with manual measurements using fine callipers or a microscope where possible.

Phylogenetic analysis

To assess the phylogenetic placement of *Borealestes* species within Docodonta in light of newly available cranial and postcranial characters, we used the matrix of Zhou et al. (2019), adding scores for *B. serendipitus* and *B. cuillinenis*. This dataset includes 128 taxa scored for 556 characters: 40 mandibular; 187 dental; 145 postcranial; 176 cranial characters and 8 soft-tissue characters. *Borealestes serendipitus* was scored for 278 characters (50%) and *B. cuillinenis* for 250 characters (45%), which is comparable with the other docodontans in this matrix such as *Castroracauda* (42%), *Docofossor* (45%), and *Microdocodon* (52%), but less complete than *Haldanodon* (63%) or *Agiolododon* (63%).

Parsimony analyses were carried out using most of the same search parameters as Zhou et al. (2019), using PAUP v.4 (Swofford 2003). As for Zhou et al., an heuristic search was carried out with characters equally weighted, and unordered, the branch swapping algorithm was tree
bisection reconnection (TBR), with a reconnection limit of 8 and steepest descent option in effect. Our analysis differs from that of Zhou et al. in that trees were obtained using stepwise addition with one tree held at each step and the addition sequence random, with 5000 replicates whereas Zhou et al. used 10,000 replicates, and MulTrees was turned on, because turning it off reduces the ability of branch-swapping to find the best tree.

We carried out four analyses: (1) Zhou et al.’s (2019) original matrix (which did not include Borealesstes); (2) the original matrix without Borealesstes, but amending characters scores for characters 32, 56, 67, 127, 131, 133, 312, 362 and 522 for docodontans, where our interpretation differed from that of the previous authors’ (see Panciroli et al. 2021b); (3) Zhou et al.’s (2019) original matrix with Borealesstes species added; (4) as for analysis 2, adding Borealesstes species. We used PAUP statistical tools to obtain the consistency index (CI), homoplasy index (HI), retention index (RI) and rescaled consistency index (RC) for all analyses (Table 2). See Panciroli et al. (2021b) for more details.

**Geometric morphometric analysis**

The postcrania of Borealesstes species were analysed using principal components analysis (PCA) on 3D landmarks, to compare their shape with extant taxa and provide additional data to make inferences for locomotor and ecological specializations. This approach was not intended to provide an exhaustive analysis, but to augment our comparative analysis and maximize the information gained from the preserved elements. Due to being incomplete, 2D linear measurements and indices of all major limbs (e.g. Chen & Wilson 2015; Meng et al. 2017) cannot easily be implemented, but the limited number of limb bones being preserved with minimal compression/distortion can easily be incorporated into 3D analyses. Using single elements of the limb to infer locomotor function can be successful (e.g. Kilbourne 2017; Janis & Martín-Serra 2020), however relying on single elements can also be uninformative when ecomorphological variation is not adequately captured by such landmark constellations. The 2D landmark analysis of bones such as the humerus and ulna has also proven informative for examining ecomorphology and evolution of pre-mammaliaform therapsids (e.g. Lungmu & Angiecizy 2019).

We applied the 3D landmark and semilandmark scheme of Martín-Serra & Benson (2020) to the radius, pelvis (only the ilum) and femur of B. serendipitus, and the ulna, humerus and scapulacoracoid of B. cuillinensis, because these were the most complete postcranial elements. We analysed these in the context of a dataset of 42 extant mammals held in multiple collections (Table 3). Extant species were selected to include members from different groups of Marsupialia and Placentia in each ecological/locomotor category, also including the platypus, Ornithorhynchus anatinus, as a representative of Monotremata. Based on the mandibular lengths (Table 4), we estimate a body mass of up to 40 g for B. serendipitus, and 16 g for B. cuillinensis (Foster 2009; Panciroli et al. 2021b), this is similar to extant mammals such as Oryzorictes (tenrec) and Neomys (shrew) respectively (Table 3). Therefore we have predominantly selected extant taxa weighing <1 kg (30 out of 42), to minimize the over-representation effect of taxa with larger body mass on the ecomorphological signature, as in previous comparative studies of the locomotor ecomorphology of Mesozoic mammals (e.g. Chen & Wilson 2015; Meng et al. 2017; Grossnickle et al. 2020). We assigned the therian taxa to five categories based on their ecology and locomotion: scratch diggers, swimmers, arboreal, runners (cursorial), gliders and ‘generalists’ (Table 3). The term ‘generalist’, widely used in previous literature, is employed in this study as a category for predominantly terrestrial mammals that, although capable of some of the ecological behaviours identified for other taxa, lack highly derived ecological or locomotor specializations or their associated morphologies (Polly 2007). Our use of the term ‘generalist’ is not intended to imply that these taxa are incapable of performing diverse ecological behaviours. Indeed, many of these taxa may be capable of climbing, scratch digging and other behaviours (e.g. Apodemus sylvaticus or Myrmecobius fasciatus) but nevertheless lack the morphological features of more specialized taxa. This may be widespread in small bodied taxa in which ecomorphological signatures may generally be less pronounced (Weaver & Grossnickle 2020). This decision does not impede our primary aim of identifying ecomorphological specializations in extinct species.

Extant mammals were CT-scanned, digitally segmented, and 3D landmarks and semilandmarks placed using Avizo (FEI Visualization Sciences Group 2015; Panciroli & Benson 2021). Our landmarks and semilandmarks (see Martín-Serra & Benson 2020) were selected to capture traits of the bones such as overall shape and tuberosities that mark the positions of muscle attachments, or edges of articular surfaces. Because of damage and incompleteness,
not all landmarks could be placed on the *Boreales* specimens, but a total of 19 landmarks and 12 semilandmark series were identifiable across all elements (Table 5; Fig. 3). Only those landmarks preserved on the *Boreales* specimens were used from the extant taxa in our analyses, so our analyses effectively include: (1) scapula, the glenoid facet, position of acromion and curve of the scapular neck; (2) humerus, shape of the proximal and distal articular surfaces, shape of the pectoral/deltoid crests and tuberosities, width of the distal humerus; (3) ulna, shape of the proximal articular surface, length and shape of the olecranon process, length of the proximal portion of the ulna vs the distal, overall length of the ulna; (4) radius, shape of the proximal articular surface and its proximal extent; (5) femur, shape of the distal articulation; (6) pelvis, length and shape of the dorsal edge of the ilium. For full details of the 3D landmarking scheme see Panciroli et al. (2021b).

We used R v.3.4.1 (R Core Team 2017) and functions from the R package geomorph (Adams et al. 2017) to analyse morphometric data. We performed a generalized Procrustes superimposition on the three-dimensional coordinates of the landmarks and semilandmarks (Dryden & Mardia 1998) to remove the effects of size, translation, orientation, and the spacing of sliding semilandmarks. We then used the plotTangentSpace function of geomorph (Adams et al. 2017) to perform the PCA on the Procrustes (shape) coordinates. This provides the consensus (mean) shape and three-dimensional coordinates of the extreme shapes of each PC which were visualized using geomorph functions mshape, warpRefMesh and plotReToTarget (Adams et al. 2017), generating three-dimensional surfaces that represent the theoretical shape changes along PC axes. Plots were then finalized in Adobe Illustrator v.20 (Adobe Inc.).

Institutional abbreviation. NMS (formerly RSM), National Museums Scotland, Chambers Street, Edinburgh, UK.

RESULTS

Phylogenetic analysis

The shortest-length trees recovered from each of the four phylogenetic analyses are shown in Figure 4C–F, focusing on relationships within Docodonta (full details can be found in Panciroli et al. 2021b). All four analyses returned a similar topology for the docodontan clade, with *Agilodocodon* and *Microdocodon* as sister-taxa, and *Boreales* species as sister taxa to *Agilodocodon* + *Microdocodon*, but the placement of *Haldanodon*, *Castorocauda* and *Docofossor* is variable among permutations of analyses.

Analyses 1 and 2. We re-analysed the Zhou et al. (2019) matrix with modified search parameters (see Material and Method, above) and returned one tree of 2826 steps (Zhou et al. 2019 recovered a single tree of 2808 steps). *Castorocauda* and *Docofossor* are found in a different arrangement than Zhou et al. (Fig. 4A, C), but *Haldanodon* remains in a similar position, although it is a sister taxon to *Castorocauda* in this analysis. *Agilodocodon* and *Microdocodon* are sister-taxa as in Zhou et al. Analysis 2, in which we modified the character scores for docodontan taxa, returned a single tree of 2835 steps with the same tree topology as the original analysis by Zhou et al. (Fig. 4A, D).

Analyses 3 and 4. We added *B. serendipitus* and *B. cuilinensis* to the original Zhou et al. (2019) matrix (Analysis 3), and with updated characters for docodontans (Analysis 4), returned single trees of 2850 (Analysis 3) and 2841 (Analysis 4) steps (Fig. 4E, F). There is little effect on the overall topology of the docodontan tree: *Haldanodon*, *Castorocauda* and *Docofossor* remain as earlier-branching taxa, whereas *Boreales* species are sister-taxa, closely related to the sister-taxon *Agilodocodon* and *Microdocodon*.

Dental and cranial character states identified in Analysis 4 as unifying the *Boreales* species include: a less developed Meckel’s sulcus than other docodontans (Char. 5(1)); the presence of a pterygoid fossa on the medial side of the ramus of the mandible (Char. 19(1)); presence of a shelf for the pterygoid on the ventral border of the mandible (Char. 20(1)); the presence of a mandibular foramen inside the masseteric fossa (Char. 24(1)); the presence of a diastema posterior to the PM1 (Char. 52(1)); the presence of a cuspule in addition to cusp c in the ultimate lower premolar (Char. 58(2)); the absence of crenulation or cuspules on cingulid row of the lower premolars (Char. 63(0)); the absence of an a–g crest (Char. 99(0)); the interlocking of the molars (Char. 102(1)); the relatively small upper canine (Char. 185(1)); lack of procumbency in the PM1 (Char. 197(0)). Postcranial characters unifying the *Boreales* species include: the expanded and helical articular surface of the clavicle (Char. 248(1)); the short, dorso-ventrally compressed calcaneal tuber without
| Specimen number and part | Element | Publication | CT system | Voxel size (µm) | No. of proj. | Filter (mm) | kV | µA | Power (W) | Exp. (s) | Fr. av. |
|-------------------------|---------|-------------|-----------|----------------|-------------|-------------|----|-----|-----------|---------|--------|
| NMS G.2020.4.1.1, Part AA | Part of whole skeleton, *B. cuillinensis* | Herein & Panciroli *et al.* 2021a | Nikon XTH 225 ST (UoB) | 22.14 | 2201 | Cu 0.5 | 180 | 111 | 19.98 | 0.708 | 4 |
| NMS G.2020.4.1.1, Part AA.2 | Part of whole skeleton, *B. cuillinensis* | Herein | Nikon XTH 225 ST (UoB) | 20.05 | 3141 | None | 130 | 154 | 20.02 | 0.5 | 4 |
| NMS G.2020.4.1.1, Part BB | Part of whole skeleton, *B. cuillinensis* | Herein & Panciroli *et al.* 2021a | Nikon XTH 225 ST (UoB) | 20.05 | 3141 | None | 130 | 154 | 20.02 | 0.5 | 4 |
| NMS G.2020.4.1.1, Part CC | Part of whole skeleton, *B. cuillinensis* | Herein | Nikon XTH 225 ST (UoB) | 29.40 | 3141 | Cu 0.5 | 221 | 131 | 1.415 | 4 |
| NMS G.1992.47.121.1 | Whole skeleton, *B. serendipitus* (section around skull) | Herein | ESRF | 11.90 | 6000 | Al 5.6 Cu 10 | 11.90 | 6000 | 0.3 |
| NMS G.1992.47.121.2 | Left petrosal | Panciroli *et al.* 2018 | In-house built µCT (UoE) | 8.9 | 2000 | Al 0.8 | 70 | 40 | 2.8 | 2 | n.a |
| NMS G.1992.47.121.3 | Right dentary | Panciroli *et al.* 2019 | Nikon XTH 225 ST (UoB) | 12.77 | * | * | * | * | * | * | * |
| NMS G.1992.47.121.4 | Premaxilla & nasal fragment | Panciroli *et al.* 2021a | In-house built µCT (UoE) | 6.43 | * | None | * | * | * | * | * |
| NMS G.1992.47.121.5 | Metatarsal (m3) | Herein | In-house built µCT (UoE) | 8.9 | 2000 | Al 0.8 | 70 | 40 | 2.8 | 2 | n.a |
| NMS G.1992.47.121.6 | Right clavicle | Herein | In-house built µCT (UoE) | 8.9 | 2000 | Al 0.8 | 70 | 40 | 2.8 | 2 | n.a |
| NMS G.1992.47.121.7 | Carpal/tarsal element | Herein | In-house built µCT (UoE) | 8.9 | 2000 | Al 0.8 | 70 | 40 | 2.8 | 2 | n.a |
| NMS G.1992.47.121.8 | Chevrons | Herein | In-house built µCT (UoE) | 8.9 | 2000 | Al 0.8 | 70 | 40 | 2.8 | 2 | n.a |
| NMS G.1992.47.121.9 | ?Cranial fragment | Herein | In-house built µCT (UoE) | 8.9 | 2000 | Al 0.8 | 70 | 40 | 2.8 | 2 | n.a |
| NMS G.1992.47.121.10 | CARPAL/tarsal element | Herein | In-house built µCT (UoE) | 8.9 | 2000 | Al 0.8 | 70 | 40 | 2.8 | 2 | n.a |
| NMS G.1992.47.121.11 | Fragment of ischium | Herein | In-house built µCT (UoE) | 8.9 | 2000 | Al 0.8 | 70 | 40 | 2.8 | 2 | n.a |
| NMS G.1992.47.121.12 | Fragment of rib | Herein | In-house built µCT (UoE) | 8.9 | 2000 | Al 0.8 | 70 | 40 | 2.8 | 2 | n.a |

Exp., exposure time; Fr. av., frame averaging; No. of proj., number of projections.

ESRF, European Synchrotron Radiation Facility; UoB, University of Bristol; UoE, University of Edinburgh.

For ESRF parameters, the voltage column (kV) indicates the detected total integrated energy in keV.

*Missing data.
TABLE 2. Results of statistical analyses on phylogenetic analyses.

| Analysis | Tree length | CI   | HI  | RI  | RC  |
|----------|-------------|------|-----|-----|-----|
| 1        | 2826        | 0.3181 | 0.6819 | 0.7968 | 0.2535 |
| 2        | 2850        | 0.3154 | 0.6850 | 0.7988 | 0.2520 |
| 3        | 2835        | 0.3171 | 0.6829 | 0.7959 | 0.2524 |
| 4        | 2841        | 0.3164 | 0.6836 | 0.7998 | 0.2531 |

Cl, consistency index; Hi, homoplasy index; RI, retention index; RC, rescaled consistency index.

Geometric morphometrics

The results for PC1, PC2 and PC3 are given in Table 6 (for fully labelled PCA results see Supporting Information or Panciroli et al. 2021b). Across all analyses ≥59% of the variation is explained by the first two PC axes, and ≥70% of the variation is explained by the first three PC axes (Figs 5, 6). Borealestes mostly falls in or near the morphospace occupied by extant tharian mammals on PC1 and PC2, and most often within that occupied by taxa with un specialized morphology (so-called ‘generalists’) but is separated from all taxa in the analysis of the femur, and most extant taxa on PC3 in analyses of the scapula, humerus (along with Ornithorhynchus) and ulna (Fig. 6A–C). PC3 in these analyses may therefore describe the difference between extant tharians and Borealestes as a stem-group mammal outside the extant radiation (crown/stem terminology used herein sensu Budd & Jensen 2000).

Borealestes and Ornithorhynchus occupy a similar position on the positive PC1 of the PCA of the radius (Fig. 5A), but other extant taxa plot nearby, so the similarity of Borealestes and Ornithorhynchus in this regard is not unique; unlike the similarity of their humeri (see below). Only one landmark and one semilandmark series are included for the radius (Fig. 3D), and positive scores on PC1 reflect a rounder proximal articulation, whereas negative scores reflect a more oblong proximal articulation. Scores for PC2 and PC3 capture very slight elongation in the shape of the proximal articulation relative to the proximal tip of coronoid process (landmark L1, Fig. 3D) in PC2. This effectively separates the arboreal (and gliding) taxa, from the scratch diggers and swimmers, with Borealestes scoring similarly to the latter two groups.

In the PCA of the pelvis, Borealestes falls near extant taxa on all three axes (Fig. 5B). Our analysis for this bone only captures the medial and dorsal edge of the ilium (Fig. 3F). PC1 scores reflect changes in the dorsal edge of the ilium, being either convex dorsally (positive scores) or concave (negative scores). PC2 reflects the position of the intersection of the ventral and anterior edge of iliac crest, which flares laterally relative to the rest of the anterior edge of the crest in taxa that score positively on this axis. PC3 reflects the shape of the anterior edge of the iliac crest: a more anteriorly expanded crest in taxa scoring negatively, and a reduction or virtual absence of the anterior edge of the crest in those scoring positively.

The PCA of the femur (which only incorporates the distal articulation because the proximal part is not complete in these fossils, see Fig. 3E) places Borealestes in a completely separate area of morphospace to that of all extant mammals in our dataset (Fig. 5C). Borealestes and Ornithorhynchus score negatively on PC1, which captures their wider mediolateral width of the distal articulation. However, Ornithorhynchus scores similarly on PC2 to extant therian mammals, whereas Borealestes scores more positively, reflecting the comparatively large anteterventral articulating surface of the distal femur. Although scoring more similarly to extant tharians than Borealestes, Ornithorhynchus falls outside of their morphospace, scoring more negatively on PC1 and PC3.

Borealestes and Tarsipes have a negative score on PC3 in the analysis of the scapula (Fig. 6A). Our analysis is essentially confined to the shape of the glenoid facet, curvature of the edge of the scapular neck, and position of the acromion (Fig. 3A). Negative scores on PC3 reflect a dorsoventrally elongate glenoid facet (rather than round), a more dorsoventrally located acromion, positioned at mid-height relative to the glenoid facet, and the point of maximum curvature of the anterior edge of the scapular neck ventral relative to the posterior edge of the scapular neck (Fig. 6A). Ornithorhynchus plots at the extreme negative PC2 and positive PC3 in this analysis, completely separating it from both the extant tharians, and Borealestes.

Borealestes and Ornithorhynchus occupy somewhat similar positions in morphospace on PC3 of the PCA of the humerus (Fig. 6B), where they both fall well outside the area occupied by other extant taxa. Borealestes falls at an intermediate location between the well-defined cluster for tharian mammals (with positive PC3 scores), and the position occupied by Ornithorhynchus (with negative PC3 scores). The humerus is one of the two most completely landmarked bones in our analysis (along with the ulna), each incorporating almost all the landmarks from Martín-
| Taxon                        | Specimen number | Common name                      | Order          | Family            | BM (g) | E/L |
|-----------------------------|-----------------|----------------------------------|----------------|-------------------|--------|-----|
| Acrobates pygmaeus          | NHMUK 82.7.29.23-24 | Feathertail glider              | Diprotodontia  | Acrobatidae       | 12     | GL  |
| Amblysomus hottentotus      | UMZC 2010.15a   | Hottentot golden mole            | Afrosericida   | Chrysocloridae    | 53     | FD  |
| Antechinomys laniger        | NHMUK 32.2.11.23 | Kultarr                          | Dasyuromorpha  | Dasyuridae        | 27     | R   |
| Apodemus sylvaticus         | NHMUK unnumbered | Wood mouse                       | Rodentia       | Muridae           | 22     | G   |
| Calorimysios interruptus    | FMNH 60698      | Black-shouldered opssum           | Didelphimorpha  | Didelphidae       | 250    | A   |
| Castor canadensis           | AMNH 150136     | North American beaver            | Rodentia       | Castoridae        | 21820  | S   |
| Dromicia concinna           | NHMUK 1897.11.18.1 | Western pygmy possum            | Notroctemorpha  | Didelphidae       | 1091   | A   |
| Dasyprocta punctata         | FMNH 60569      | Central American agouti          | Rodentia       | Dasyproctidae     | 2675   | R   |
| Dendrohyrax arbor5s         | FMNH 163770     | Southern tree hyrax              | Hyracoidea     | Procaviidae       | 2950   | A   |
| Dendrolagus dorianus        | UMMZ 2006.38    | Doria’s tree-kangaroo            | Ditudontia     | Macropodidae      | 9581   | A   |
| Desmana moschata            | FMNH 124125     | Russian desman                   | Eupotiophyla    | Talpidae          | 383    | S   |
| Didelphis marsupialis       | NHMUK 1948.7.12.5 | Common opossum              | Didelphimorpha  | Didelphidae       | 1091   | A   |
| Diplomesodon pulchellum     | FMNH 137436     | Piebald shrew                    | Eupotiophyla    | Soricidae         | 11     | G   |
| Elephantulus roseti         | NHMUK 1891.10.15.11 | North African elephant shrew    | Macroscelidea  | Macroscelidae     | 48     | R   |
| Enhydra lutris              | NHMUK 80.879    | Sea otter                        | Carnivora      | Mustelidae        | 23500  | S   |
| Euroscaptor micruna         | NHMUK 99.10.25.1 | Himalayan mole                   | Eupotiophyla    | Talpidae          | 60     | FD  |
| Glis glis                   | UMMZ 1996.325   | Edible dormouse                  | Rodentia       | Gliceridae        | 125    | A   |
| Hemiichinus auritus         | UMMZ 156626     | Long-eared hedgehog              | Eupotiophyla    | Erinaceidae       | 342    | G   |
| Idiurus zenkeri             | UMZC E.1421     | Pygmy scaly-tailed flying squirrel | Rodentia      | Anomuridae        | 100    | GL  |
| Leopardus wiedii            | NMS 2016.12.1   | Margay                           | Carnivora      | Felidae           | 3250   | A   |
| Limnogale mergulus          | FMNH 165440     | Web-footed tenrec                | Afrsericida     | Tenrecidae        | 80     | S   |
| Lutreolina crassauaudata    | UMMZ 134562     | Lutrine opossum                  | Didelphimorpha  | Didelphidae       | 537    | S   |
| Macroscelides proboscisius  | FMNH 137045     | Round-eared elephant shrew       | Macroscelidea  | Macroscelidae     | 38     | R   |
| Macrotris lagotis           | NHMUK 73.6.21.4 | Greater bilby                    | Peramelemorpha  | Peramelidae       | 1350   | R   |
| Microgale thomasi           | UMMZ 172202     | Thomas’s shrew tenrec            | Afrsericida     | Tenricidae        | 23     | G   |
| Mysorex kihaueli            | FMNH 209072-209073 | Khauale’s mouse shrew          | Eupotiophyla    | Soricidae         | 10     | G   |
| Myrmecobius fasciatus       | UMZC A6.41/8    | Numbat                           | Dasyuromorpha   | Myrmecobiadae     | 472    | G   |
| Nandinia binotata           | UMZC A.4922     | African palm civet               | Carnivora      | Nandiniidae       | 2000   | A   |
| Neomys fodiens              | NHMUK 1973.917  | Eurasian water shrew             | Eupotiophyla    | Soricidae         | 14     | S   |
| Notoryctes typhlops         | UMMZ A.5.1/1    | Southern marsupial mole          | Notoryctemorpha | Notoryctidae      | 55     | FD  |
| Ornithorhynchus anatinus     | AMNH A.2.10/1   | Platypus                         | Monotremata     | Ornithorynchidae  | 2000   | S   |
| Oryctolagus cuniculus       | NHMUK 1849.6.20.9 | European rabbit                 | Lagomorpha     | Leporidae         | 1767   | R   |
| Oryzorictes tetradactylus   | UMZC E.5453c    | Four-toed rice tenrec            | Afrsericida     | Tenricidae        | 36     | FD  |
| Petasurus breviceps         | FMNH 129430     | Sugar glider                     | Diprotodontia  | Petauridae        | 106    | GL  |
| Petinomys sagitta           | UMZC A.1499     | Arrow flying squirrel            | Rodentia       | Sciuridae         | 50     | GL  |
| Procapia capensis           | FMNH 147999     | Rock hyrax                       | Hyracoidea     | Procaviidae       | 3030   | G   |
| Solenodon paradoxus         | FMNH 51068      | Solenodon                        | Eupotiophyla    | Solenodontidae    | 900    | G   |
| Sylvisorex howelli          | FMNH 198206     | Howell’s forest shrew            | Eupotiophyla    | Soricidae         | 4      | G   |
| Tarsipes rostratus          | UMMZ A.2547     | Honey possum                     | Diprotodontia  | Tarsipidae        | 9      | A   |
| Trichosurus vulpecula       | UMZC A.9.16/7   | Common brushtail possum          | Diprotodontia  | Phalangeridae     | 2650   | A   |
| Tupaiia glis                | UMZC E.4057E    | Common Treeshrew                 | Scandentia      | Tupaiidae         | 170    | A   |

BM, body mass; E/L, ecological/locomotor categories: A, arboreal; FD, forelimb digger; G, generalist; GL, glider; R, runner; S, swimmer.

AMNH, American Museum of Natural History, New York, USA; FMNH, Field Museum of Natural History, Chicago, USA; UMMZ, University of Michigan Museum of Zoology, USA; NHMUK, Natural History Museum, London, UK; NMS, National Museums Scotland, Edinburgh, UK; UMZC, University Museum of Zoology, Cambridge, UK.

Body mass data from Geiser (1986), Nowak (1999), Smith et al. (2003).
TABLE 4. Measurements of dentary and select elements of the appendicular skeletons of Borealestes.

| Taxon                | Specimen number          | Dentary | Humerus | Radius | Ulna   | Femur | Ilium |
|----------------------|--------------------------|---------|---------|--------|--------|-------|-------|
| Borealestes serendipitus | NMS.G.1992.47.121.1 &   | 23.3    | –       | 12.3   | –      | 12.82*| 9.8   |
|                      | NMS.G.1992.47.121.3      |         |         |        |        |       |       |
| Borealestes cuillinensis | NMS.G.2020.4.1.1         | 17.3    | 10.396* | –      | 11.2*  | –     | –     |

Measurements in mm.

*Estimate (where bone is broken/part missing).

Serra & Benson 2020) (Fig. 3B; Table 5). Negative scores on PC3 reflect a narrower radial and ulnar condyle in Borealestes and Ornithorhynchus, and a larger, flared deltopectoral crest without clear distinction between the edges of the deltid and pectoral crests (captured by SL2 and SL3). The proximal articular surface of the humerus is also much larger. PC1 in the PCA of the humerus effectively separates the specialist digging taxa from the rest of the dataset. These taxa score negatively on this axis, reflecting a much sturdier, wider humerus along the length of the bone, but particularly distally, a much larger distal articulation, and flared deltopectoral crest (Fig. 6B). Meanwhile PC2 captures the position of the most medial point of the medial epicondyle (entepicondyle), the position of the proximal origin of the lateral epicondylar crest, the amount of elongation in the proximal portion of the humerus, and the relative position of the humeral head (displaced laterally in taxa scoring negatively on this axis).

In the analysis of the ulna, Borealestes scores negatively on PC3, as do Enhydra and Euroscaptor (Fig. 6C). Along with the humerus, the ulna is one of the two most completely landmarked bones in our analysis (Fig. 3C). Negative scores on PC3 reflect a relatively straight medial edge of the olecranon process, the ulna being mediolaterally wide medial to the articular surface of the olecranon, and the distal portion of the olecranon itself being dorsoventrally wide, with a dorsoventrally elongate articular surface of the olecranon. PC1 in the analysis of the ulna captures the overall length of the ulna, and the relative length of the proximal versus distal portions of the ulna. Negative scores on this axis reflect an elongate, wide olecranon process and relatively short distal ulna, as seen in digging taxa, which score negatively on this axis, separating most of them from the remainder of the dataset. PC2 reflects the extent of mediolateral flaring of the olecranon process, and the size of the proximal articular surface of the ulna. Scoring negatively on PC2, Ornithorhynchus is separated from both the extant therians, and Borealestes.

DESCRIPTION

NMS.G.1992.47.121.1 is a block of blue-grey limestone measuring approximately 183 mm in length, 105 mm in width, and between 148 and 340 mm in thickness (Fig. 1A). NMS.G.1992.47.121.1 was substantially larger when collected (c. 240 mm in length, c. 170 mm in width and c. 50 mm in depth) and was reduced in size by curators at NMS when it became clear the block required trimming to obtain successful scans at high resolution for study. All offcuts were retained. The surface is undulating, with hairline cracks in the prepared upper surface, also visible in synchrotron scan data. Skeletal elements are scattered on the surface of the block, including the palate and elements of the skull, left ilium and left radius (Fig. 1A). Synchrotron scans revealed other parts of the skeleton within the block (Fig. 1B). The surface bones sit on ‘platforms’ of rock, the result of acid and mechanical preparation to remove the surrounding rock. At least seven such platforms no longer contain fossil material, and probably indicate the original positions of bones that have been removed or detached during handling, such as the petrosal (NMS.G.1992.47.121.2; Panciroli et al. 2018) and the dentary (NMS.G.1992.47.121.3; Panciroli et al. 2019, 2021a).

NMS.G.2020.4.1.1 comprises four parts containing the skeleton of B. cuillinensis (Fig. 2B). It measures approximately 8 cm by 6 cm, and <3 cm in depth. The original specimen recovered in the field was much larger (approximately 35 cm by 30 cm by 15 cm) and was iteratively reduced in size to obtain successful scans at high resolution for study (see above). All offcuts (including those not containing bone) were retained. Some bones are visible on the surface (left dentary, occipital condyles, parts of the ribs and metacarpals), but most of the skeleton is below the surface and only visible in the CT-data (Panciroli & Benson 2021).

Axial skeleton

Atlas arches. Both half neural arches of the atlas (C1) are preserved in NMS.G.1992.47.121.1 (Fig. 7A–H) and the left arch is preserved in NMS.G.2020.4.1.1 (Fig. 8A–D). In the former the two halves are located on opposite sides of the palate and majority of cranial elements (Fig. 1B), whereas in the latter the arch is next to the humerus (Fig. 2B). They are intact, with dorsoventrally tall dorsal arches that are convex laterally, and a small ventrolateral projection, resembling closely the morphology of the half
TABLE 5. Landmarks used in PCA analyses.

| Skeletal element | Landmark/semilandmark |
|------------------|------------------------|
| Scapula          | L2. Point of maximum curvature of the anterior edge of scapular neck |
|                  | L3. Point of maximum curvature of the posterior edge of scapular neck |
|                  | L5. Ventral tip of the acromion process |
|                  | SL2. Edge of glenoid fossa; closed row |
| Humerus          | L1. Most posterior point of greater tuberosity |
|                  | L2. Intersection of pectoral and deltoid crests |
|                  | L3. Most proximal point of deltoid crest |
|                  | L4. Most anterior point of lesser tuberosity |
|                  | L5. Most posterior point of lesser tuberosity |
|                  | L6. Proximal origin of lateral epicondylar crest |
|                  | L8. Most medial point of medial epicondyle (entepicondyle) |
|                  | SL1. Edge of the articular surface of humeral head; closed row |
|                  | SL2. Proximal edge of greater tuberosity followed by the edge of pectoral crest; from L1 to L2 |
|                  | SL3. Edge of deltoid crest; from L2 to L3 |
|                  | SL4. Medial edge of lesser tuberosity; from L4 to L5 |
|                  | SL6. Edge of distal articular surface; closed row |
| Ulna             | L1. Most proximal point of olecranon process |
|                  | L2. Most anterior point of olecranon process |
|                  | L3. End of the proximal epiphysis in the medial edge; defined as the perpendicular point to L5 in the medial side |
|                  | L4. End of the proximal epiphysis in the lateral edge; defined as the perpendicular point to L5 in the lateral side |
|                  | L5. Point of maximum curvature in the distal base of coronoid process; this landmark defines the position of L3 and L4 |
|                  | L6. Most anterior point of distal epiphysis |
|                  | SL1. Medial edge of olecranon process; from L2 to L3 |
|                  | SL2. Lateral edge of olecranon process; from L2 to L4 |
|                  | SL3. Edge of proximal articular surface; closed row |
| Radius           | L1. Proximal tip of coronoid process |
|                  | SL1. Edge of proximal articular surface; from L1 to L1 |
| Pelvis           | L1. Intersection of ventral and anterior edges of iliac crest |
|                  | L2. Posterior end of the dorsal edge of iliac crest |
|                  | SL1. Anterior and dorsal edge of iliac crest; from L1 to L2 |
| Femur            | SL3. Edge of distal articular surface; closed row |

The arches of the atlas in *Morganucodon* (*Eozostrodon*; Jenkins & Partridge 1976). The articular areas for the occipital condyle and atlas are preserved, the former being slightly larger than the latter, and both oval in shape and slightly concave. There is a strong medially directed projection where the two articular areas meet. The centrum of the atlas (C1) is not preserved in either specimen of *Borealestes*, consistent with the fact that the half neural arches are not fused at the dorsal midline. The dentition of both specimens shows no sign of ongoing tooth replacement, the posteriormost molars have erupted in both specimens, and the posteriormost molar is aligned with the coronoid process. These are all adult features of other mammaliaforms and docodontans, therefore these specimens are adult individuals (for further support that these represent adult specimens see Discussion). Therefore the lack of fusion of components of the atlas is an adult character of the vertebrae, at least for *Borealestes*, as also interpreted for *Morganucodon* by others (Jenkins & Partridge 1976).

Vertebrae. In NMS.G.1992.47.121.1 there are two cervical, three thoracic and four caudal vertebrae preserved (Fig. 7I–Q). None are completely preserved. In addition, there are two chevrons (haemal arches), one almost complete and the second a smaller, worn fragment (Fig. 7R–S). The post-axial cervical vertebrae of NMS G.1992.47.121.1 are represented only by their centra (Fig. 7J–L). The exact position of these vertebral centra in the vertebral column is uncertain, but one is noticeably smaller than the other and may be cervical 2 or 3, while the larger is more likely to be cervical 3 or 4. The centra are amphicoelous, oval when viewed anteriorly or posteriorly. The bases of the neural arch can be discerned on both vertebrae, but the arch and the dorsal portion of the vertebrae are not preserved. Both vertebrae are slightly distorted, but it is clear they are only slightly longer anteroposteriorly than they are wide mediolaterally. The middle part of the centrum is bilaterally constricted on both. There is one possible cervical vertebra in NMS.G.2020.4.1.1, but it is represented only by a fragment of the right transverse process and neural arch (Fig. 8E). However, its position in the cervical series is not clear, and it could instead be a thoracic vertebra.

There are at least three thoracic vertebrae represented in NMS G.1992.47.121.1 (Fig. 7K–M). One thoracic vertebra shows a distorted and poorly preserved centrum lacking processes or arch; one vertebra has a preserved neural spine with transverse processes but no centrum; and the third has a dorsoventrally compressed almost complete vertebra, with centrum, arches and neural spine. Their exact position in the vertebral column is not certain. The centrum is badly distorted in both vertebrae preserved with a centrum, making the original shape difficult to interpret. It appears to be anteroposteriorly shorter than it is mediolaterally wide or dorsoventrally tall. As with the cervical vertebrae, it is amphicoelous and constricted at the middle part of the centrum, and shows a distinct rim around the edge of the centrum. The neural spines of
the thoracic vertebra are long and slant diagonally posteriely from the neural arch (Fig. 7L–M). The postzygapophyses are at the base of the neural arch, and on the right side of one vertebra the articular facet for the rib is preserved, posterolateral to the base of the prezygapophysis (which is not preserved). The neural canal is preserved in the largest of the vertebrae, but it is compressed.

The six thoracic vertebrae preserved in *B. cuillinensis*, NMS.G.2020.4.1.1 are all incomplete (Fig. 8F–K), but the two largest are relatively complete, although compressed dorsoventrally (Fig. 8J–K). Their centra, neural spines
and transverse processes resemble those in NMS G.1992.47.121.1. The largest of the thoracic vertebrae in NMS.G.2020.4.1.1 (Fig. 8K), is probably from a more posterior position in the thoracic series than the others, based on its size.

No caudal vertebrae are preserved in B. cuillinensis, but in B. serendipitus there are four: one proximal (Fig. 7N), one from a position distal to this (Fig. 7O), and two from still further along the tail length (Fig. 7P–Q). The most proximal caudal vertebra is incomplete, comprising the left transverse process, a portion of the centrum, and the base of the incomplete right transverse process. The centrum is compressed dorsoventrally, and lacks the dorsal and ventralmost portions, including the base of the neural arch. The size and structure of this vertebra suggests that it is from the proximal section of the tail, probably one of caudals 3–7. The preserved transverse process projects quite far laterally, similar to the proximal caudals of Microdocodon (Zhou et al. 2019) and also somewhat similar to that seen in Castorocauda (Ji et al. 2006) but less extreme.

The next vertebra preserved in the caudal series in B. serendipitus is from mid-way along the tail, probably between caudals 8 and 12 (Fig. 7O). It is amphicoelous and strongly constricted at the midline, especially dorsoventrally. It is longer anteroposteriorly than it is wide mediolaterally, presenting a rectangular profile in dorsal and ventral view.

FIG. 4. Results of phylogenetic analyses of docodontans using: A, dental, cranial and postcranial characters from Zhou et al. (2019); B, dental and cranial characters presented in Panciroli et al. (2021a), based on analysis originally published in 2019; C, Zhou et al.’s (2019) original matrix (which did not include Boreales); D, Zhou et al.’s (2019) original matrix, with modified parameters (see Material and Method), without Boreales, but amending characters scores for characters 32, 56, 67, 127, 131, 312, 362 and 522 for docodontans, where our interpretation differed from the previous authors’ (see Supporting Information); E, Zhou et al.’s (2019) original matrix with Boreales species added; F, as for Analysis 3 (E), adding Boreales species. See Material and Method, and Supporting Information, for full details of analyses.
There is no neural canal. The ventral side is smooth and convex, while the dorsal side of the vertebra has a strong ridge running anteroposteriorly, flanked by deep indentations laterally. There are no complete preserved transverse processes or zygapophyses, although there appears to be the base of a possible zygapophysis on the dorsal surface of the vertebra at the posterior and anterior ends.

The two distalmost caudal vertebrae comprise one posterior end of a vertebra (Fig. 7P) and a second almost complete vertebra (Fig. 7Q), probably from somewhere between caudals 14 and 18, by comparison to Microdocodon (Zhou et al. 2019). They are positioned together on the surface of the limestone block, beside the fragments of the left dentary and left humerus (Fig. 1A). The almost complete caudal vertebra is much longer anteroposteriorly than it is wide mediolaterally. It is damaged on the right anterior side, and what is preserved on the left includes a distinct ridge, projecting dorsolaterally. There is no corresponding projection on the poster end of the vertebra. The less complete vertebra matches the morphology of the posterior portion of the more complete vertebra, and was therefore likely to have originally been of similar proportions and shape. Both of the posteriormost caudal vertebrae have a smooth ventral surface, and a ridge along the dorsal surface. Unlike in the caudal 8–12 vertebrae, this ridge comprises most of the body of the bone, with no lateral indentations. The vertebrae flare bilaterally at the anterior and posterior ends, forming mediolaterally wide articulation surfaces with the next vertebra. Unlike the other vertebrae described here for Borealestes, there is no concavity on the centrum.

**Chevrons.** The two chevrons preserved in *B. serendipitus*, NMS G.1992.47.121.1, are very different in size, the larger and more complete chevron coming from a more anterior position and the smaller from a distal position on the tail (Fig. 7R–S). The smaller chevron is part of the main limestone block, positioned near the main portion of the skull, whereas the larger chevron, NMS G.1992.47.121.8, was dislodged from the main block and scanned separately. NMS G.1992.47.121.8 is almost intact, and is diamond shaped when viewed dorsally or ventrally (Fig. 7R). It flares laterally at the midline, and these flares project dorsally to their position between the caudal vertebrae, and enclose a dorsal canal along the anteroposterior length of the chevron. There is a protuberance at the elongated anterior end of the chevron (Fig. 7R), but damage makes it unclear if the same protuberance was present on the posterior end. By comparison to Microdocodon, the shape of this larger chevron is similar to those

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**TABLE 6.** Results of principal components analysis on postcranial elements.

|          | PC1       | PC2       | PC3       |
|----------|-----------|-----------|-----------|
| Humerus  | Standard deviation | 0.095172  | 0.060462  | 0.042376  |
|          | Proportion of variance | 0.47198   | 0.19049   | 0.09357   |
|          | Cumulative proportion | 0.47198   | 0.66247   | 0.75604   |
| Pelvis (Ilium) | Standard deviation | 0.101515  | 0.098648  | 0.078901  |
|          | Proportion of variance | 0.30401   | 0.28707   | 0.18365   |
|          | Cumulative proportion | 0.30401   | 0.59108   | 0.77473   |
| Femur    | Standard deviation | 0.134643553 | 0.065358733 | 0.051291991 |
|          | Proportion of variance | 0.50577   | 0.11918   | 0.0734    |
|          | Cumulative proportion | 0.50577   | 0.62495   | 0.69834   |
| Scapula  | Standard deviation | 0.176054  | 0.113473  | 0.086716  |
|          | Proportion of variance | 0.42548   | 0.17675   | 0.10322   |
|          | Cumulative proportion | 0.42548   | 0.60223   | 0.70546   |
| Ulna     | Standard deviation | 0.19311   | 0.069193  | 0.059101  |
|          | Proportion of variance | 0.62958   | 0.08083   | 0.05897   |
|          | Cumulative proportion | 0.62958   | 0.71041   | 0.76938   |
| Radius   | Standard deviation | 0.114379  | 0.094099  | 0.054644  |
|          | Proportion of variance | 0.39695   | 0.26867   | 0.0906    |
|          | Cumulative proportion | 0.39695   | 0.66562   | 0.75622   |

First three PCs only; for complete results see Supporting Information.
FIG. 5. Results of principal component analyses on select postcranial elements in NMS G.1992.47.121.1. A, radius; B, pelvis; C, femur. Legend same throughout. Shape deformation of landmarks shown on PC axes. For more information and full labelling of taxa, see Supporting Information.
FIG. 6. Results of principal component analyses on select postcranial elements in NMS G.2020.4.1.1. A, scapula; B, humerus; C, ulna. Legend same throughout. Shape deformation of landmarks shown on PC axes. For more information and full labelling of taxa, see Supporting Information.
between caudals 6 and 9 in that taxon (Zhou et al. 2019, fig S11C–D).

The smaller chevron, part of NMS G.1992.47.121.1, comprises only a small projection and the central body of the chevron (Fig. 7S). Although superficially resembling a claw, the flared main body of the bone is mediolaterally broad, making it different from ungual morphology. The small size suggests it was a distal chevron from beyond the middle part of the caudal vertebral series.

Ribs and clavicle. There are at least nine ribs preserved in NMS G.1992.47.121.1 (Figs 1A–B, 9A–B), with a rib fragment separated from the rest of the skeleton (NMS G.1992.47.121.12, Fig. 9C). There are approximately eight preserved in NMS.G.2020.4.1.1 (Fig. 9E, F). The ribs are similar in both species, resembling those in most other docodontans for which the ribs are known, but lacking the flattened appearance seen in Castorocauda (Ji et al. 2006).

A portion of the right clavicle, NMS.G.1992.47.121.6, is separated from the main limestone block (Fig. 9D). The lateral end is slightly concave, and would have articulated with the acromion on the scapulacoracoid (not present in this specimen). The medial end of the clavicle that would have articulated with the interclavicle is missing.

Appendicular skeleton

Scapulacoracoid. There is no scapulacoracoid preserved in B. serendipitus, NMS G.1992.47.121.1. The right scapulacoracoid is present in B. cuillinensis, NMS.G.2020.4.1.1, preserved next to the remnants of the skull (Figs 2B, 10). The preserved part consists of a nearly complete coracoid, the glenoid facet, and ventral part of the scapula that bears the intact acromion. The dorsal half of the scapula is missing, and was also damaged by the saw during extraction of the specimen (Fig. 10). What is preserved of the scapulacoracoid of B. cuillinensis resembles Haldanodon (Martin 2005). It shows a wide, saddle-shaped glenoid facet with an oval outline, relatively larger than the glenoid facet in Microdocodon (Zhou et al. 2019). The anterior margin of the scapula is strongly curved. The acromion forms the ventralmost part of the anterior scapular margin, and doesn’t extend beyond the level of the margin of the glenoid facet, as in Haldanodon.

The scapula-coracoid suture runs through the dorsalmost portion of the glenoid facet (Fig. 10). The procoracoid and procoracoid foramen are absent in Borealestes, as in Haldanodon (Martin 2005). The coracoid consists of a glenoid component and a peg-like coracoid process. The ventral margin of the glenoid is marked by a crest and there is a tubercle, which we interpret as the attachment area of the coracobrachialis muscle. The ventralmost tip of the coracoid process would be for the origination of the biceps brachii, it is either damaged, or its tip was not ossified and therefore not fossilized in NMS.G.2020.4.1.1. A similar muscle attachment pattern was also interpreted for the cynodont Massetognathus (Lai et al. 2018). This corresponds to the muscle pattern of the living monotremes (Gambaryan et al. 2015). The coracoid process flares slightly at the end where the coracoid head of the triceps would have attached in life.

Humerus. An almost complete humerus is preserved in B. cuillinensis NMS.G.2020.4.1.1, located near the atlas arch and some scattered metacarpals/tarsals (Figs 2B, 11E–H). Only a fragment of the deltopectoral crest of the left proximal humerus is present in B. serendipitus, NMS.G.1992.47.121.1, located beside the fragment of posterior left dentary (Figs 1B and 11A–D). The abraded broken surface of this fragment of humerus suggests that the bone may have been complete on the surface of the limestone, but was either broken or eroded prior to collection.

The deltopectoral crest of B. serendipitus appears larger than in B. cuillinensis, with a deep fossa for muscle insertion (Fig. 11). However, this may be due to the broken and slightly crushed position of the deltopectoral crest in this specimen of B. cuillinensis, and may not be a true difference between the species. What remains of the greater tubercle and humeral head in B. serendipitus indicates a relatively large head, but there is too little preserved to indicate further details of its morphology.

In NMS.G.2020.4.1.1 (B. cuillinensis) most of the humerus is preserved, with only a small section of the deltopectoral crest and the ectepicondyle missing (Fig. 11E–H). It is relatively shorter and more robust bone than those of Agilodocodon (Meng et al. 2015) or Microdocodon (Zhou et al. 2019) but less robust than that seen in Haldanodon (Martin 2005). The greater tubercle is larger than the lesser tubercle, and the deltopectoral crest is less developed on the lateral aspect of the humerus in B. cuillinensis than in Haldanodon, and terminates halfway down the humeral shaft. Below the lesser tubercle, the teres major tuberosity is well developed on the medial side of the humerus. The humerus has the same ‘hourglass shape’ as Haldanodon (Martin 2005,
FIG. 8. Atlas arches and vertebrae of NMS G.2020.4.1.1, *Borealesstes cuillinensis*. A–D, left arch: A, posterior; B, medial; C, anterior; D, left lateral view. E, cervical vertebra. F–K, thoracic vertebrae. In E–K vertebrae are pictured from top to bottom in: dorsal; left lateral; ventral; and right lateral view. Scale bar represents 5 mm for all elements.

FIG. 9. Ribs and clavicle of *Borealesstes serendipitus* (A–D) and *B. cuillinensis* (E, F). A–B, NMS G.1992.47.121.1: A, ribs as in position in matrix; B, rib from elsewhere in matrix. C, rib fragment NMS G.1992.47.121.12. D, right clavicle NMS G.1992.47.121.6. E–F, ribs belonging to NMS G.2020.4.1.1: E, cluster of ribs from part AA (see Fig. 2B); F, cluster of ribs from part CC. Scale bar represents 5 mm for all elements.
p. 227), caused by the expanded proximal and distal ends of the bone and twisting of the ends relative to one another, known as humeral torsion (Gambaryan & Kielan-Jaworowska 1997; Luo & Wible 2005), a common feature of mammaliaforms, and some crown mammals. The distal end is broad, but less so compared to the humeral length than seen in *Haldanodon* (approximately 57% of humeral length, vs 61.3% in *Haldanodon*; Martin 2005, p. 227). The radial condyle is spherical and large, and the ulnar condyle is smaller and mediolaterally compressed. The large entepicondyle suggests a well-developed area of muscle attachment, for origination of flexor muscles of the wrist and digits, and for flexion and pronation of forearm, by comparison with extant mammals (Evans & de LaHunta 2012; Gambaryan et al. 2015; Regnault et al. 2020).

**Radius.** The left radius of *B. serendipitus* is preserved on the surface of the limestone block in specimen NMS G.1992.47.121.1 (Figs 1A, 12A–D). It is complete with only the distalmost end missing (Fig. 12A–D). There is a relatively wide, cup-shaped and projecting articular fovea, strongly sloping medially in dorsal view.

The radius is somewhat sigmoidal along its length, and in intact anatomy would be positioned alongside the ulna. The ulna is not preserved in NMS G.1992.47.121.1. The distal end of the radius is somewhat expanded, but does not appear to be transversely wider than the proximal end, although the missing styloid process makes this interpretation uncertain. A ridge runs along the distal half of the length of the shaft on the dorsal side, somewhat laterally positioned. This blends smoothly into a groove on the lateral side of the distal radius. This groove would run to the styloid process, but this process is broken and missing. Medially, a much smaller groove is visible on the mediodorsal surface of the distal end of the radius. The long slender morphology resembles the radius of *Microdocodon* (Zhou et al. 2019, fig S10) and *Agilodocodon* (Meng et al. 2015), rather than the more robust (relatively wider and shorter) morphology of *Haldanodon* (Martin 2005) and *Docofossor* (Luo et al. 2015a).

**Ulna.** No ulna is preserved in *B. serendipitus*, but an almost complete left ulna, and proximal portion of right ulna, are preserved in *B. cuillinensis*, NMS.G.2020.4.1.1 (Figs 2B, 12E–L). The left ulna was damaged during extraction of the skeleton, removing a small portion of the shaft of the bone during cutting (Fig. 12E–H). The width of the saw blade is known (c. 1 mm), so the length of the ulna can be reconstructed reliably. The olecranon process is well developed. Its proximal ventral margin (or dorsal if oriented vertically) curves strongly dorsally (Fig. 12E–L),
more so than in other mammaliaforms, a feature typical of other docodontans (Fig. 12M) (Martin 2013; Zhou et al. 2019, suppl. mat.) The olecranon has a rugose proximal surface for tendon insertion. The coronoid process is smaller and the semilunar notch is shallower and smaller than in Haldanodon (Martin 2005, 2013) or Docofossor (Luo et al. 2015a), but larger than in Microdocodon (Zhou et al. 2019). The radial notch is distinct and the styloid process is concave and flared around the rim. The size of the ulna compared to the radius cannot be ascertained for either species of Boreales because neither specimen includes both bones for comparison.
ilium. The right ilium of *B. serendipitus* is preserved on the surface of the limestone block NMS G.1992.47.121.1, and is almost complete (Figs 1A, 13C–F). Overall the ilium appears similar to the described ilia of other docodontans in which it is known: the element is elongate, and the iliac blade is flattened laterally, but convex medially. There is a thin flange on the dorsal edge of the iliac blade, projecting dorsally from midway along the ilium and narrowing slightly anteriorly (Fig. 13C–E). The ventral edge of the anterior end of the iliac blade is also mediolaterally thin, and has no discernible bulging along the rim. There is no discernible rugose ilio-sacral contact on the medial side of the ilium, but some ghosting in the original tomographic slices makes it unclear. Overall, the ilium blade of *B. serendipitus* is wider than the more gracile ilium of *Microdocodon* (Zhou et al. 2019) but much narrower than the robust ilium of *Haldanodon* (Martin 2005). *Borealeses* bears resemblance in the ilium to *Morganucodon* (Jenkins & Parrington 1976).

The acetabular facet is large, triangular when viewed posteriorly, and slightly convex (Fig. 13C). The surface is slightly angled anterodorsally. The preserved part of ilium shows that the suture between the ilium and ischium was not fused in the adult. The articulation with the ischium is damaged; a small piece is broken and missing (Fig. 13C, E), most likely during collection or preparation of the specimen. The articulation with the ischium and pubis are evidently narrow, forming a shallow acetabular facet for the femoral head. Although the cotylar notch on the dorsal aspect of the acetabulum is well documented in other docodontans (Martin 2005; Zhou et al. 2019), it is not feasible to estimate this notch in *Borealeses* because the posterior part of the ilium and the acetabulum as a whole are not preserved in this specimen.

ischium. The bone fragment NMS G.1992.47.121.11 is identified as the dorsal corner of the right ischial blade, the only part of the ischium preserved in this specimen of *B. serendipitus* (Fig. 13A, B, G, H). There is a strong ischial tuberosity, more pronounced than in *Microdocodon* (Zhou et al. 2019), with a concave lateral surface of the ischium. The dorsal edge of the ischium appears wide and flattened, sloping medioventrally (Fig. 13H).

femur. An incomplete right femur is preserved in this specimen of *B. serendipitus* NMS G.1992.47.121.1, located at the opposite end of the limestone block from the rest of the skeleton, near the right ilium (Figs 1B, 13I–M). The distal portion of the femur is well preserved extending from below the third trochanter (trochanter not preserved). A fragment of the proximal portion of the femur is preserved near the broken and crushed end of the distal portion, and has been placed in approximate position in the reconstruction, but it does not preserve the proximal morphology.

The preserved morphology of the distal femur is slender and gracile, similar to *Agilodocodon* (Meng et al. 2015) and *Microdocodon* (Zhou et al. 2019). It lacks the broad profile of the distal femur formed by the lateral and medial condyles in *Haldanodon* (Martin 2005) and *Castorocauda* (Ji et al. 2006). The intercondylar fossa is distinct, and there is a noticeable medial condyle, but the lateral condyle is less distinct and neither condyles flare. The preserved diaphysis of the femur is slender, similar to those of *Agilodocodon*, and other mammaliforms such as *Morganucodon* and *Megalostrodon* (Jenkins & Parrington 1976).

Manus and pes. There are multiple metacarpals, metatarsals and carpal and tarsal elements preserved in both specimens of *Borealeses*, but as none of these elements are in articulation, identification is hindered.

There are seven metacarpal/tarsals, and seven carpal/tarsal elements present in *B. serendipitus*, NMS G.1992.47.121.1 (and associated dislodged material) (Fig. 14). Most are preserved in the main block containing the partial skeleton, but three other autopal elements were preserved separately (NMS G.1992.47.121.5 (Fig. 14C), NMS G.1992.47.121.7 (Fig. 14D) and NMS G.1992.47.121.10 (Fig. 14E)). Two elements are identified as metacarpals: metacarpal 4, by its distinctive proximal asymmetry (Fig. 14F) and metacarpal 5, which has distinctive distal asymmetry (Fig. 14L). The metacarpal 5 is wider and shorter than its counterpart of *Agilodocodon* (Fig. 14L), but not as wide as the block-like metacarpal 5 of *Docofossor* (Luo et al. 2015a), or the extremely short metacarpal 5 in haramiyidans (Meng et al. 2017). It appears that in *Borealeses* the morphology of metacarpal 5 does not indicate the locomotor specializations known in other mammaliforms. One metatarsal can also be positively identified: NMS G.1992.47.121.5 is separated from the skeletal block and represents metatarsal 3 (Fig. 14C), recognizable from the compacted morphology of the proximal joint, and size (compared to other elements,
and to those of Agilodocodon). All of these elements are identified by their resemblance to the corresponding elements in Agilodocodon (Meng et al. 2015). The remaining four autopodial elements lack distinctive features for the further identification, but their shorter length, with broader proximal end suggest that they are intermediate metacarpals or metatarsals. None of the metapodial bones show the epiphyseal suture, thus we interpret these finger bones as not having epiphyses, as in extant therians.

In NMS.G.2020.4.1.1 there are 11 metacarpals/metatarsals preserved, but none exhibit definitive identifiable features (Fig. 15B–L). There is also a single terminal phalanx, that would bear the horny claw in the intact animal (Fig. 15M), but it is not possible to tell if this is from the manus or pes. It resembles other docodontan unguals in shape, being mediotlaterally narrow with a strong proximal overhanging process and a well-developed proximal flexor process. There is a lateral groove on either side of the claw for attachment of the claw sheath. The terminal phalanx is not bilaterally compressed as the terminal phalanx of Agilodocodon (Meng et al. 2015, fig. 3), a feature indicative of arboreal habits in Agilodocodon and other taxa (MacLeod & Rose 1993). Borealesestes’ terminal phalanx is suggestive of non-specialist locomotor modes (MacLeod & Rose 1993).

Of the seven carpal/tarsal in this specimen of B. serendipitus, two elements remain unidentified (Fig. 14E; F; NMS G.1992.47.121.10), but the remaining elements are identified as an entocuneiform (Fig. 14A), a cuboid (Fig. 14B), a probable navicular (Fig. 14D; NMS G.1992.47.121.7), right calcaneus (Fig. 16A–C) and right astragalus (Fig. 16D, E). The left entocuneiform has a well-formed entocuneiform–metatarsal saddle joint, facilitating movement of metatarsal 1. The cuboid also has a wide distal cuboid–metatarsal facet. The astragalus was positioned deep within the limestone block and as a result the resolution of the scan means surface detail is limited. However the fibio-astragalar trochlea and postastragalar shelf are identifiable. They are less developed than in Docofossor, and like the rest of the pedal and manual elements there is no sign of the anatomical specializations for a fossorial lifestyle as seen in Docofossor (Luo et al. 2015a). Only two carpal/tarsal bones are preserved in NMS.G.2020.4.1.1, B. cuillensis: one is identified as a probable lunate (Fig. 15A) and the other is a left calcaneus (Fig. 16G–J).

The calcanea of Borealesestes exhibit almost identical morphology in both species. The right calcaneus in NMS G.1992.47.121.1, and is located near the ribs on the main skeleton block, below the surface (Fig. 1B). In NMS.G.2020.4.1.1, a left calcaneus is located near the ulnae (Fig. 2B). In both species, the calcaneus is short and curved ventrally with a small calcaneal tuber (Fig. 16F). The morphology shows plesiomorphic features shared with other non-mammalian mammaliaforms such as Morganucodon (Jenkins & Parrington 1976; Szalay 1994; Zhou et al. 2013) and other docodonts for which the calcaneus is known, such as Agilodocodon (Meng et al. 2015), Microdocodon (Zhou et al. 2019) and Docofossor (Luo et al. 2015a). In Borealesestes the calcaneus appears slightly less elongate than in Agilodocodon, being more similar to the morphology of Morganucodon. However, this might be attributed to the damage sustained on the calcaneal tuber of both Borealesestes calcanea, which may make it appear less elongate. In NMS.G.2020.4.1.1, additional bony material is adhered to the tuber; this may be the displaced end of the tuber.

**DISCUSSION**

**Phylogenetic analysis**

All four of our analyses recover a docodontan subclade comprising Borealesestes spp as the sister taxon to a clade of Agilodocodon + Microdocodon (Fig. 4C–F). The taxonomic scope here is limited to those taxa for which cranial and postcranial material is known. However, the two Borealesestes species are recovered as sister taxa, a result that agrees with the analysis of the dentary and mandibular characters in Panciroli et al. (2019, 2021a) (Fig. 4B). Within Docodonta, the placement of Castorocauda, Haldanodon and Docofossor differs slightly between analyses, although these three taxa are consistently placed in various configurations as outgroups to Borealesestes + (Agilodocodon + Microdocodon).

Because of its older geological age (Bathonian, compared to Oxfordian/Kimmeridgian for the other docodontan taxa), it might be expected that Borealesestes would be an early-diverging member of the docodontan clade; Borealesestes species therefore might be expected to represent the plesiomorphic character states for the clade. However, our tree topology of docodontan taxa differs significantly from that of Panciroli et al. (2021a), which employed a much larger sampling of docodontans that are preserved by dental and mandibular material only. That analysis recovered Borealesestes species as sister to a clade comprising Haldanodon + (Docofossor + Docodon), all considered to be ‘basal’ docodontans, but it found this
FIG. 14. Manus and pes elements of NMS G.1992.47.121.1, *Borealestes serendipitus*. A, entocuneiform. B, cuboid. C, metatarsal 3 (NMS G.1992.47.121.5). D, ?navicular (NMS G.1992.47.121.7). E, unidentified element (NMS G.1992.47.121.10). F, unidentified element. G–I, intermediate metacarpals/tarsals (mc/mt). J, metacarpal 4. K, intermediate metacarpal/tarsal. L, metacarpal 5. All elements shown in ventral (left) and dorsal (right) views. M, manus of *Agilodocodon* for comparison (from Meng et al. 2015, fig. S6). Scale bars represent 5 mm (A–L all same scale).
clade to be more deeply nested within Docodonta (Fig. 4B). Taken together, these results suggest that the relationships within Docodonta may be more complex than anticipated, and that tree topology may change depending on available character partitions from cranium and skeleton, in addition to mandible and teeth. Without more cranial and postcranial material from key taxa from Russia and North America, it is difficult to resolve the topology of the clade more conclusively.

Comparative anatomy and ecomorphological inference

Examination of the two species of docodontan *Borealestes* (*B. serendipitus* and *B. cuillinensis*), finds little difference in their postcranial morphologies. Both are adult, as indicated by diagnostic features of their tooth eruption and dentaries (Panciroli et al. 2019, fig. 6; 2021a, fig. 7). In *Docodon victor*, which is known from a relatively complete growth series, the ultimate molar is positioned medial to the anterior
part of coronoid process in juveniles, but in adults is shifted to a position anterior to the coronoid process, in alignment with the coronoid. In successively older adult individuals the coronoid shifts posteriorly as the mandible grows in length, resulting in a retro-molar space between the ultimate molar and the front of coronoid process (Schultz et al. 2017, fig. 4). In Morganucodon and docodontans, the ultimate lower molar of adults also has two roots closely compressed together or even confluent with each other (Kermack et al. 1973; Panciroli et al. 2019, 2021a). These diagnostic adult features are present in specimens of *B. serendipitus* and *B. cuillinensis*, suggesting that they had reached adult stage.

The absence of epiphyses in most long bones and phalanges does not indicate a juvenile ontogenetic stage in mammaliaforms such as *Borealeses*. The adult limb bones of early-diverging mammaliaforms lack epiphyses even at early growth stages, as first observed in morganucodontans (Jenkins & Parrington 1976), and corroborated in almost all preserved limb elements of mature docodontans.

**FIG. 16.** Calcanea and astragali of *Borealeses* species. A–C, NMS G.1992.47.121.1, *B. serendipitus*; A–C, right calcaneus: A, dorsal; B, ventral; C, medial view; D–E, right astragalus: D, ventral; E, dorsal view. F, composite outline drawing of *Borealeses* calcaneus. G–I, NMS G.2020.4.1.1, *B. cuillinensis*, left calcaneus: G, ventral; H, dorsal; I, medial view. Scale bar represents 5 mm.
Haldanodon (Martin 2005; Ji et al. 2006; Luo et al. 2015b; Meng et al. 2015). The single exception is found in the distal tibiae, which are sutured to the diaphysis in Agilodocodon, Microdocodon and Docofossor, probably related to a hypertrophied tibial malleolus hooked to the astragalus (Luo et al. 2015a; Zhou et al. 2019). The well-preserved long bones of Haramiyavia (Late Triassic) lack epiphyses (Luo et al. 2015a), and they are also absent among eutriconodontans, which are crown mammals (Jenkins & Schaff 1988; Ji et al. 1999; Martin et al. 2015; Chen et al. 2017). The absence of epiphyses in long bones and phalanges of Borealestes is therefore a plesiomorphic feature of mammaliforms, which is retained in eutriconodontans.

Some other ossification-related traits of Borealestes species are also different to those crown-group mammals. In particular, the open suture of the acetabulum is shared with adult specimens of Morganucodon, Castorocauda, Docofossor and Microdocodon, as well as ontogenetically mature gobiocodontids. This is different to the fusion of the acetabular suture of the ilium, ischium and pubis in crown mammals. Borealestes and other stem mammaliforms therefore show plesiomorphic features of skeletal fusion, different from most crown mammals including multituberculates, and stem and crown therians (Morris 1972; Kielan-Jaworowska & Gambaryan 1994; Chen & Luo 2013; Yuan et al. 2013).

Taken together, the proportions of the postcranialia of Borealestes are intermediate between the more gracile docodontan taxa Agilodocodon (Meng et al. 2015) and Microdocodon (Zhou et al. 2019), and the more robust Haldanodon (Martin 2005) (Figs 7–16). Borealestes species also lack the extreme ecomorphological specializations seen in Castorocauda (Ji et al. 2006) or Docofossor (Luo et al. 2015a). The results of PCA on the postcranialia of Borealestes species supports this observation (Figs 5, 6). Although there are indications that it was capable of scratch digging and swimming to some extent, both comparative morphology and principal component analyses suggest Borealestes species were non-specialist, lacking highly derived ecological or locomotor specializations or their associated morphologies.

The atlas neural arches of Borealestes species form part of the atlas-axis complex. Although the atlas centrum is not preserved in either specimen and the components of the atlas are not fused, the preserved halves of the arches suggest the atlas would have resembled that of other early mammaliforms and cynodonts. The lack of fusion of components of the atlas is a plesiomorphic feature of cynodonts, similar to that seen in the tritylodontids such as Oligokyphus and Kayentatherium (Kühne 1956; Jenkins & Parrington 1976; Rowe 1988; Sues & Jenkins 2006). The vertebrae preserved in both Borealestes species suggest a similar morphology in the cervical and thoracic vertebrae to other docodontans, and to those of non-mammaliform cynodonts (Sues & Jenkins 2006). In the caudal series of Agilodocodon (Meng et al. 2015) there is a clear change in morphology from caudal 7 to caudal 8: the transverse process is reduced and the more posteriorly positioned vertebrae are more elongated. In Microdocodon (Zhou et al. 2019), this transition occurs from caudal 6 to caudal 7. Using Agilodocodon and Microdocodon for comparison, the single preserved proximal caudal in Borealestes is most likely to be from a position anterior to caudal 7–8, as the transverse processes of this caudal project quite far laterally. This projection is somewhat similar to that seen in Castorocauda (Ji et al. 2006), whereas in Agilodocodon the proximal caudal vertebrae are narrower and less flattened. The well-developed zygapophyses in Agilodocodon suggest a slender and probably more mobile tail than other docodontans, or other mammaliforms such as Megacerops (Zhou et al. 2013, suppl. mat.) The single preserved proximal caudal of Borealestes appears to be intermediate between the morphologies of the proximal caudals of Castorocauda and Agilodocodon (Fig. 7N). The preserved distal caudals are similar to those in Castorocauda, which are essentially little changed from earlier mammaliforms and even some tritylodontids such as Oligokyphus (Kühne 1956). We suggest a sturdy, but relatively mobile tail for Borealestes, supported by the presence of large chevrons which would have increased the dorsoventral depth and robustness of the tail. The isolated caudal vertebrae do not suggest a more specialized ecology in Borealestes.

No material from the posterior thoracic or lumbar regions is preserved in Borealestes. The reduction or loss of the lumbar ribs in mammaliforms is variable among groups, even within subclades of mammaliforms (Chen et al. 2017). For most docodonts for which the lumbar region is known, lumbar ribs of reduced size are retained. The exception is Agilodocodon, which has no lumbar ribs on the last four lumbar vertebrae, and shows a more distinctive thoraco-lumbar transition than Castorocauda (Meng et al. 2015). This can be interpreted to correspond to an increased range of movement in the posterior vertebral column. The ribs of Borealestes are preserved and resemble the morphology of most docodontans, showing no signs of the flattened, reinforced specialization for a semi-aquatic lifestyle seen in Castorocauda (Ji et al. 2006; Meng et al. 2015). However it is not possible to determine whether Borealestes had a distinctive thoraco-lumbar transition from the material preserved here.

In the geometric morphometric analysis, Borealestes was separated from extant taxa along PC3 in analyses of the humerus and ulna, but only the distal femoral articulation in the hind limb. This suggests that extant mammal forelimb shape may differ more significantly from that of early mammaliforms like Borealestes than their hindlimb shape. However, this may instead be the result of the more extensive landmarking possible on the humerus and ulna of Borealestes (due to the relative completeness of
these elements), which may more effectively detect differences in bone shape between Boreales and the extant taxa in our analysis.

The deltopectoral crest of the humerus of Boreales species is flared and appears to be intermediate between the gracile arboreal Agilodocodon (Meng et al. 2015) and the robust semi-aquatic/digger Haldanodon (Martin 2005) and specialist digger, Docofossor (Luo et al. 2015a). This prominent deltopectoral crest would provide attachment for strong muscles (e.g. insertion of the pectoralis and deltoid muscles, and possibly also the origin of the brachialis muscle; Gambaryan et al. 2015) suggesting strength in the forelimb, particularly abduction and forelimb retraction. In Haldanodon the humerus is more robust than the femur. The shaft of the humerus is not preserved in NMS G.1992.47.121.1, however, comparing the morphology of the humerus in B. cuillinensis (Fig. 11E–H) with the femur in B. serendipitus (Fig. 13I–M), and looking at the morphology of the radius and ulna of these taxa (Fig. 12), these elements are all more gracile than those of Haldanodon, again suggesting a less robust morphology overall for Boreales.

These observations are supported by the results of geometric morphometrics. The humerus of Boreales is intermediate between the morphology of monotremes (Ornithorhynchus) and therians. They share negative scores, but the PC3 distance between Boreales and therians is only slightly greater than between Boreales and Ornithorhynchus (Fig. 6B). This captures a narrower radial and ulnar condyle in these taxa, and a larger, flared deltopectoral crest without clear distinction between the edges of the deltoid and pectoral crests (captured by SL2 and SL3). The proximal articular surface of the humerus is also much larger in Boreales and Ornithorhynchus. The platypus, Ornithorhynchus, is often cited as an important taxon for understanding basal mammal postcranial morphology, due to the retention of some plesiomorphic characteristics such as a rigid pectoral girdle (Jenkins 1970). Although monotremes were previously cited as an example of a basal morphology for mammals (e.g. Isidro & Vázquez 2006) the majority of workers consider monotreme morphology and movement to be specialized and derived in its own right, and divergent from both extant therians (e.g. Jenkins 1970; Pridmore 1985; Gambaryan et al. 2002; Gambaryan & Kuznetsov 2013) and stem mammals discovered so far (e.g. Chen & Wilson 2015; Luo et al. 2015a; Meng et al. 2015). The similarity in humeral scores between these taxa may be linked to the more rigid pectoral girdle in both genera, and the position of the limbs (stance), which are not held under directly the body, as well as a shared capability at digging. Pridmore (1985) noted the complex movements of the humerus in Ornithorhynchus, which arcs and rotates considerably around the glenoid during propulsion; early mammaliaforms may have exhibited similar forelimb movements. The more positive score in PC3 for Boreales relative to Ornithorhynchus, and the distinct difference in the scores for the distal articulation of the femur in Boreales from the rest of the dataset, suggests that Boreales had a different posture than monotremes do today, and possibly a distinct hind limb movement that may not be comparable to any living mammal taxa.

The scapulacoracoid of Boreales is not well preserved, but the portion that remains, including the coracoid, gneoid facet and ventral portion of the scapular blade, resembles that belonging to Haldanodon (Martin 2005). In the geometric morphometric analysis of the scapulacoracoid (scapula in the extant taxa), which is essentially restricted to the glenoid and position of the acromion, Boreales scores similarly to Tarsipes rostratus (honey possum) (Fig. 6A). They share a narrower, elongate gneoid fossa that is more concave than in other taxa. Ornithorhynchus meanwhile, scores positively on this axis (PC3). Therefore although the monotremes may provide a useful data point for comparison with mammaliaforms such as Boreales, the comparison is limited.

In Haldanodon, the proximal part of the ulna including the olecranon and articulation facets is approximately the same length as the rest of the ulna (Martin 2005, p. 228). This ratio is similar in Docofossor, which has an olecranon–ulna ratio of 47% (Luo et al. 2015a, suppl. mat.) and Castorocauda (Ji et al. 2006) but is not the case in Microdocodon (Zhou et al. 2019), which has an olecranon–ulna ratio closer to 28%. In B. cuillinensis, the ulna has an olecranon–ulna ratio of 32%, closer to those of Microdocodon and Agilodocodon. This would suggest that B. cuillinensis was neither a specialist digger nor swimmer based on the inferred ecologies for these taxa, although it is still above the 26% average olecranon–ulna ratio recorded in fossorial extant mammals (Chen & Wilson 2015). In the geometric morphometric analysis, the ulna of Boreales plots near taxa that habitually swim (Castor and Enhydra) and dig with their forelimbs (Oryzorictes and Euroscaptor and to a lesser extent Solenodon) (Fig. 6C). They share a more developed olecranon process, and the proximal ulna is mediolaterally relatively wide medial to the articular surface of the olecranon. These morphologies are associated with enhanced muscular attachments for the forelimb to facilitate habitual digging and/or swimming motion. There is also a flange on the medial side of the olecranon (Fig. 12E, I), which is a feature commonly seen in extant mammals that are capable scratch diggers (Salton & Sargis 2008). The placement of Boreales in relation to these taxa suggests that although not as specialized for fossorial or aquatic lifestyles as more ecologically derived docodonians like Docofossor, Haldanodon or Castorocauda, Boreales was probably a capable digger and able to swim, similar to many small-bodied mammals today.
What remains of the ilium and ischium is similar to that seen in other docodontans, but with a slightly more developed iliac blade than in *Agilodocodon*, suggesting more muscle attachment in this area. The proportions of the manus can provide useful ecomorphological inferences among mammals, including mammaliaforms; for example, the proportion of proximal and distal metacarpals/tarsals can be informative, as can multivariate analyses incorporating all limb elements (Chen & Wilson 2015; Meng et al. 2017; Grossnickle et al. 2020). Unfortunately, only disarticulated scattered proximal and distal manus and pes elements are preserved in NMS G.1992.47.121.1. These elements resemble those in *Agilodocodon* (Meng et al. 2015), and are far less robust in morphology than those seen in the specialist digger *Docofosor* (which is also brachydactyloous), or in *Haldanodon* (Martin 2005).

The *Boreales* calcaneus does not resemble extant mammals, being closer to the morphology to other early mammaliaforms such as *Morganucodon*. It is slightly less elongate than in *Agilodocodon* and, perhaps surprisingly, less elongate than earlier tritylodontids such as *Oligokyphus* (Kühne 1956). The tibio-astragalor trochlea and post-astragalar shelf are less developed than in *Docofosor* (Luo et al. 2015a) and, as for the rest of the pedal and manual elements, there is no sign in *Boreales* of the anatomical specializations for a fosorial lifestyle seen in *Docofosor*. The tibio-astragal joint of the pattype, *Ornithorhynchus anatinus*, allows this semi-aquatic monotreme to abduct its feet relative to the limb, and provides a wide range of movement including eversion and hyperextension (Luo et al. 2015a). This appears to resemble the morphology of docodontan *Docofosor brachydactylus*, suggesting a similar posture and range of movement for this Jurassic fosorial taxon. The tibio-astragal contact in *Boreales* is shallow with a smaller astragalar head than in *Docofosor*, but the resemblance in morphology suggests that it would also have been able to abduct its feet relative to the limb, but less so than in *Docofosor*.

**CONCLUSION**

The two species of docodontan *Boreales* (*B. serendipitus* and *B. cuillinensis*) exhibit little difference in their postcranial morphologies. *Boreales* *serendipitus* is larger and fractionally more robust than *B. cuillinensis*, as observable by comparing the humerus and manus and pes elements, but the difference is nominal. Both the observational analysis and principal components analysis support an interpretation of *Boreales* species as ‘generalists’, that is, lacking derived ecomorphologies that would reflect the specialist behaviours that are clear in taxa such as *Docofosor* or *Agilodocodon*. But in some PCAs, *Boreales* plots near extant mammalian scratch diggers and swimming taxa, supporting the interpretation that like many ‘generalist’ extant taxa it was probably capable of both. The more abducted and laterally positioned limbs of *Ornithorhynchus* probably strongly influence its PCA scores, which places the platypus apart from extant therians in the PCA results (Figs 5, 6). Although there is some similarity in the results for the humerus in *Ornithorhynchus* and *Boreales*, overall they do not occupy similar morphospace, so comparative similarity between them is limited. However, their placement in analyses of forelimb elements may reflect shared similarity in limb posture, and capacity for scratch digging and/or swimming. Results for the femur hint that hind limb posture and range of movement in *Boreales* may not resemble that seen in any extant taxa.

The intermediate skeletal morphology of *Boreales* postcrania may be representative of the basal morphology of docodontans as a whole, which like many small mammals today includes a capability for scratch digging. Such morphology could have provided a blueprint that natural selection could then adapt into more specialized fosorial morphologies seen in the Late Jurassic docodontans (Martin 2005; Luo et al. 2015b). However, our phylogenetic analyses incorporating scores for postcranial characters return a novel topology compared to previous analyses using only dentomandibular characters, namely in the placement of *Boreales* species as sister to a clade formed by *Agilodocodon* and *Microdocodon*. This separates them from the ‘basal docodontan’ clade previously formed to include (*Boreales + Haldanodon + (Docofosor + Docodon))*. It suggests that interpretation of which taxa are ‘basal’ among docodontans may be more complex than anticipated. The derived position of *Boreales* in our phylogenetic analysis stresses the necessity of including a wider sampling of postcranial characters for docodontans from outside China. This will not only help to resolve the clades’ relationships, but also reveal broader patterns of ecomorphological specialization in early mammals as a whole.

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DATA ARCHIVING STATEMENT

Scan data and 3D digital files are all available in the Morpho Source repository: https://www.morphosource.org/projects/00000C1092. Supporting information and data files are available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.3vd41ms5r.

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SUPPORTING INFORMATION

Additional Supporting Information can be found online (https://doi.org/10.1111/pala.12577):

Appendix S1. Body mass calculations.
Appendix S2. Geometric morphometrics.
Appendix S3. Phylogenetic analysis.
Appendix S4. Characters used in phylogenetic analysis.
Appendix S5. Phylogenetic analysis results.
Appendix S6. Principal components analyses.
Appendix S7. CT scan data DOIs.

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