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First dinosaur from the Isle of Eigg (Valtos Sandstone Formation, Middle Jurassic) Scotland

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Keywords:	Great Estuarine Group, Bathonian, Thyreophora, histology, Sauropoda, Theropoda		
Abstract:	Dinosaur body fossil material is rare in Scotland, previously known almost exclusively from Great Estuarine Group on the Isle of Skye. We report the first unequivocal dinosaur fossil from the Isle of Eigg, belonging to a Bathonian (Middle Jurassic) taxon of uncertain affinity. The limb bone NMS.Eigg.2017, is incomplete, but through a combination of anatomical comparison and osteohistology we determine it most likely represents a stegosaur fibula. The overall proportions and cross-sectional geometry are similar to the fibulae of thyreophorans. Examination of the bone microstructure reveals a high degree of remodelling and randomly distributed longitudinal canals in the remaining primary cortical bone. This contrasts with the histological signal expected of theropod or sauropod limb bones, but is consistent with previous studies of thyreophorans, specifically stegosaurs. Previous dinosaur material from Skye and broadly contemporaneous sites in England belongs to this group, including <i>Loricatosaurus</i> and <i>Sarcolestes</i> and a number of indeterminate stegosaur specimens. Theropods such as <i>Megalosaurus</i> and sauropods such as <i>Cetiosaurus</i> are also known from these localities. Although we find strong evidence for a stegosaur affinity, diagnostic features are not observed on NMS.Eigg.2017, preventing us from referring it to any known genera. The presence of this large-bodied		

stegosaur on Eigg adds a significant new datapoint for dinosaur distribution in the Middle Jurassic of Scotland.



- 1 First dinosaur from the Isle of Eigg (Valtos Sandstone Formation, Middle Jurassic)
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- 3
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- 28 RH: First dinosaur from the Isle of Eigg, Scotland
- 29 30

ABSTRACT: Dinosaur body fossil material is rare in Scotland, previously known 31 almost exclusively from Great Estuarine Group on the Isle of Skye. We report the 32 first unequivocal dinosaur fossil from the Isle of Eigg, belonging to a Bathonian 33 (Middle Jurassic) taxon of uncertain affinity. The limb bone NMS.Eigg.2017, is 34 incomplete, but through a combination of anatomical comparison and osteohistology 35 we determine it most likely represents a stegosaur fibula. The overall proportions 36 and cross-sectional geometry are similar to the fibulae of thyreophorans. 37 Examination of the bone microstructure reveals a high degree of remodelling and 38 randomly distributed longitudinal canals in the remaining primary cortical bone. This 39 contrasts with the histological signal expected of theropod or sauropod limb bones, 40 but is consistent with previous studies of thyreophorans, specifically stegosaurs. 41 Previous dinosaur material from Skye and broadly contemporaneous sites in 42 England belongs to this group, including Loricatosaurus and Sarcolestes and a 43 44 number of indeterminate stegosaur specimens. Theropods such as *Megalosaurus* and sauropods such as *Cetiosaurus* are also known from these localities. Although 45 we find strong evidence for a stegosaur affinity, diagnostic features are not observed 46 47 on NMS.Eigg.2017, preventing us from referring it to any known genera. The 48 presence of this large-bodied stegosaur on Eigg adds a significant new datapoint for dinosaur distribution in the Middle Jurassic of Scotland. 49

50

Key Words: Great Estuarine Group, Bathonian, Thyreophora, histology, Sauropoda, 51 Perez.

- 52 Theropoda,
- 53

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Dinosaurs first evolved in the Late Triassic, but remained a relatively sparse 55 component of ecosystems until after the end-Triassic mass extinction. During the 56 Middle Jurassic, the group underwent a significant evolutionary radiation and they 57 became the dominant vertebrates on land for the subsequent 100 million years 58 (Benson et al. 2014; Benson 2018). However, our understanding of the mode, 59 tempo, and evolutionary drivers of this radiation are hindered by the globally sparse 60 fossil record for dinosaurs at this time. For example, the Paleobiology Database 61 (www.paleobiodb.org) records just 430 occurrences of Middle Jurassic dinosaurian 62 body fossils globally. In contrast, the much better-known Late Jurassic record 63 preserves 2,100 occurrences of Dinosauria (data downloaded June 2020). This 64 makes all contributions to the Middle Jurassic dinosaur fossil record significant. 65

The Inner Hebrides of Scotland yield rare Middle Jurassic dinosaur remains, 66 but until now these have been exclusively from the Isle of Skye. The Bajocian-67 Bathonian Great Estuarine Group on Skye provides a vivid picture of the diverse 68 Middle Jurassic ecosystem of the Inner Hebrides. It comprises a series of lagoonal 69 and deltaic sedimentary rocks (Andrews 1985) that have yielded a wealth of 70 71 vertebrate material, including marine, terrestrial and flying archosaurs, turtles, 72 squamates, lissamphibians, tritylodontids and mammaliaforms (e.g. Evans et al. 2006; Anquetin et al. 2009, 2010; Wills et al. 2014; Young et al. 2016a; Yi et al. 73 2017; Panciroli 2017a, b, 2018a, b, 2019). 74

Dinosaur body fossils in the Great Estuarine Group remain exceptionally rare 75 and are often fragmentary (see review in Clark [2018]). From the Bathonian Valtos 76 Sandstone Formation they include a sauropod limb bone (Clark et al. 1995; Liston 77 2004), a sauropod tooth (Clark & Gavin 2016), two theropod teeth (Brusatte & Clark 78 2015; Young et al. 2019), and a possible basal coelurosaurian theropod caudal 79 80 vertebra (Brusatte & Clark 2015). Finds from other formations within the Great Estuarine Group and underlying units include a theropod limb bone (Benton et al. 81 1995), an isolated theropod tooth (Young et al. 2019), isolated sauropod teeth 82 (Barrett et al. 2006), and a thyreophoran proximal ulna and radius (Clark 2001). 83 Dinosaur ichnofossil tracks range from isolated tracks on loose boulders (Andrews & 84 Hudson 1984; Clark et al. 2005; Clark & Gavin 2016), to extensive in situ trackway 85 sites, including from the Valtos Sandstone Formation (Clark et al. 2004; Marshall 86 2005; Brusatte et al. 2015; dePolo et al. 2018, 2020). 87

The Isle of Eigg has long been recognised for its fossils, particularly the 'Hugh 88 Miller Reptile Bed' named for the prolific Victorian stonemason turned 89 palaeontologist, geologist and writer, Hugh Miller (1802-1856) who discovered it 90 (Miller 1858). The reptile bed is part of the Bathonian Lealt Shale Formation 91 (formerly 'Estheria Shales', Hudson 1962, 1963), which underlies the Valtos 92 93 Sandstone Formation (Andrews 1985; Barron et al. 2012). Vertebrate fossils from the Lealt Shale Formation mainly comprise isolated skeletal and dental remains of 94 sharks, marine turtles, crocodylomorphs, and plesiosaurs (Hudson 1966; Benton 95 1995). A single purported dinosaur tooth from Eigg was mentioned by Rees and 96 Underwood (2005), but this specimen was not figured and has subsequently been 97 98 lost, so the identification cannot be confirmed. Despite extensive explorations of the

island by Miller and contemporaries, and subsequent attention from geologists and 99 palaeontologists in the latter half of the 20th century (e.g. Hudson 1962, 1963, 1966; 100 Harris & Hudson 1980; Andrews 1985), no archosaur material has been discovered 101 in any of the other exposed sections of the Great Estuarine Group on Eigg until now. 102 Herein we describe the first unequivocal Mesozoic dinosaur specimen to be 103 found in Scotland outside of Skye. The specimen is an indeterminate limb bone-104 probably from a stegosaur-that was found in shoreline exposures of the Valtos 105 Sandstone Formation on the Isle of Eigg. The specimen described here is poorly 106 preserved, hindering higher level taxonomic assignment, but this limitation does not 107 negate the significance of this fossil both in the context of the Scottish dinosaur body 108 fossil record, and for our knowledge of Middle Jurassic dinosaur palaeo-distribution. 109 110

111 **1. Geological Setting**

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The Great Estuarine Group (Harris & Hudson 1980; 'Great Estuarine Series' of Judd 113 [1878, p.722]) crops out in the Scottish Inner Hebridean islands of Skye, Muck, Eigg 114 and Raasay (though contemporaneity of formations between the isles is by no 115 means certain) (Fig. 1). It comprises six formations (the Cullaidh Shale Formation, 116 Elgol Sandstone Formation, Lealt Shale Formation, Valtos Sandstone Formation, 117 Duntulm Formation and the Kilmaluag Formation) of Bajocian–Bathonian (Middle 118 Jurassic) age, consisting of sedimentary rocks dominated by sandstone and 119 mudstone, with subordinate shelly, algal and dolomitic limestone beds (Harris & 120 Hudson 1980; Barron et al. 2012). Environments represented include shallow 121 marine, saline, and freshwater lagoons, with tidally influenced littoral lagoons, fluvial 122 delta lobes, and alluvial floodplains and mudflats (Barron et al. 2012). 123

The Valtos Sandstone Formation is named after the village of Valtos on the 124 Trotternish Peninsula on the Isle of Skye, near the type section [NG 517 638 to NG 125 509 653] (Harris & Hudson 1980: 240-243). It is underlain by the Lealt Shale 126 Formation and overlain by the Duntulm Formation. Fossils found include: 127 invertebrates such as the bivalve Neomiodon and gastropod Viviparus; trace fossils 128 Lockeia, Monocraterion, Planolites, Thalassinoides and tridactyl and ovoid footprints; 129 coniferous wood; and fragmentary dinosaur and crocodyliform body fossils (Hudson 130 & Harris 1979; Andrews & Hudson 1985; Clark et al. 1995; Barron et al. 2012; 131 Brusatte & Clark 2015; Clark & Gavin 2016; Young et al. 2016a). The Valtos 132 Formation represents a tidally influenced shallow littoral lagoon, frequently inundated 133 by fluvial delta lobes, and with evidence of periodic emergence (Barron et al. 2012). 134 This interpretation is supported by brackish to freshwater palynomophs such as 135 Botryococcus (Riding et al. 1991). 136 137 A section of the Valtos Sandstone Formation is exposed on the northwestern

shore of the Isle of Eigg at Camas Sgiotaig (the 'singing sands') and the bay of Laig
[NM 468 905 to NM 472 885]. The limb-bone NMS.Eigg.2017 was found in a loose

- block within Camas Sgiotaig, in a broken, but originally sub-spherical, calcite-
- cemented sandstone concretion (sensu Wilkinson 1992). On the Isle of Eigg, such

142 concretions are only known from the Valtos Sandstone Formation, confirming the143 provenance of the specimen.

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146 **2. Materials and Methods**

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The limb-bone NMS.Eigg.2017 is part of the collection at National Museums 148 Scotland (NMS), Edinburgh, UK. It was found by EP on a loose boulder below the 149 high tide line south of Camas Sgiotaig on the Isle of Eigg in May 2017, during 150 fieldwork funded by the National Geographic Society, including team members SLB, 151 EP, TJC, PEdP, DF, and MW. It was subsequently collected under permit by SLB, 152 DR, and DG, using a rock saw to extract the specimen. Preparation was carried out 153 by NL: the bone was consolidated using Paraloid B72 at 5-10% in acetone, then 154 pneumatic circular saws followed by pneumatic pens were used to remove 155 surrounding matrix. A small <1 cm section of the bone was accidentally removed 156 during removal of excess matrix (Fig. 2C). The natural mould of the missing mid-157 section of the bone was filled in with Jesmonite acrylic resin with some fibreglass 158 matting with grey pigment. 159

A photogrammetric model of NMS.Eigg.2017 was created by MH using photographs taken on a Nikon D5300 and uploaded and reconstructed in Agisoft Photoscan Professional Version 1.4.5. The resulting mesh was repaired and optimised in Blender 2.8.1 and then exported in .fpx format. This can be accessed freely on Sketchfab at [LINK].

A portion of the midshaft was removed at a natural break for osteohistological 165 analysis by GFF, and a transverse thin section made following a modified 166 petrographic sectioning procedure (Lamm 2013). The piece was embedded in 167 Buehler Epothin II epoxy resin under a vacuum (-1 bar) and left to cure at room 168 temperature for 24 hours. The block was sectioned in a transverse plane using a 169 Buehler Isomet 1000 Precision Saw with a table saw attachment and a diamond-170 tipped wafering blade. The cut billet was mounted to a polycarbonate plastic slide 171 using Buehler Epothin II epoxy, which was left to cure at room temperature for 12 172 hours. The mounted billet was resectioned to a thickness of 0.7 mm using a Buehler 173 Isomet 1000 Precision Saw. The re-sectioned slide was hand-ground on a glass 174 plate using a sequence of 220-grit, 600-grit, and 1200-grit Silicon Carbide abrasive 175 powders, until the desired optical contrast was achieved. The final slide thickness is 176 ~180 µm. The slide was polished on a short nap cloth and on a nap cloth with 177 mineral oil to improve optical clarity. 178

The slide was photographed using a Nikon D7200 DSLR camera with a Nikkor 60 mm Micro lens and a Nikon SB-600 Speedlight to produce transmitted light. Detailed images were taken using a Leica DMLP Transmitted Light Polarizing Microscope under normal light using Leica Application Suite 4. The polycarbonate sheet used for the slide is anisotropic, which interferes with cross-polarization of the thin-section, so only images under normal light were taken. Images were stitched together using Adobe Photoshop 2020. Where adjustments to contrast, brightness,

or colour balance were required, these modifications were applied to the entire 186 image. Osteocyte lacunar density was calculated using the method of Cullen et al. 187 (2014). Histological terminology follows Francillon-Vieillot et al. (1990) and Padian 188 and Lamm (2013). 189 Measurements of NMS.Eigg.2017 were checked using photogrammetry 190 models. Measurements and some figures for the comparative taxa were taken from 191 Benson (2010), Holwerda et al. (in press) and Remes et al. (2009) in combination 192 with the authors' (EP, FH, SCRM) own photographs of specimens. 193 194 Institutional Abbreviations. CGP, Council for Geosciences, Pretoria, South 195 Africa; ISIR, Indian Statistical Institute, Kolkata, India; MACN, Museo Argentino de 196 Ciencias Naturales, Buenos Aires, Argentina; MOR, Museum of the Rockies, 197 Montana, USA; NHMUK (previously BMNH), Natural History Museum, London, UK; 198 NMS National Museums Scotland, Edinburgh, UK; OUMNH, Oxford University 199 Museum of Natural History, Oxford, UK; PVL, Paleontologia de Vertebrados Lillo, 200 Universidad Nacional de Tucuman, Tucman, Argentina; QMF, Queensland Museum, 201 Brisbane, Australia. 202 203 3. Systematic Palaeontology 204 205 SYSTEMATIC PALAEONTOLOGY 206 DINOSAURIA OWEN, 1842 207 Ornithischia Seeley, 1887 208 Thyreophora Nopcsa, 1915 (sensu Norman, 1984) 209 210 Material. NMS.Eigg.2017, an isolated hind limb bone (Fig. 2). 211 Locality. Bathonian (Middle Jurassic) Valtos Sandstone Formation, Great 212 Estuarine Group. Found on a loose boulder on the shoreline south of Camas 213 Sgiotaig, Isle of Eigg, Scotland. 214 **Description.** NMS.Eigg.2017 is badly eroded along most of its length where 215 exposed to weathering by the sea. It is also missing the proximal and distal ends, 216 and is slightly compressed along its length. The total preserved length is 64 cm, and 217 the bone is broken into two halves. Without a definitive identification, it is not 218 possible to say which is the proximal or distal end. One half of the bone has been 219 worn longitudinally, leaving a depth of ~5 cm of bone and exposing the internal 220 structure (Fig. 2). The centre of the shaft is missing, but there was a natural mould of 221 the shaft in the rock, which was used to make a reconstruction (Fig. 2) The moulded 222 section is approximately 14 cm in length and 7.3 cm at the narrowest transverse 223 224 width. There is a longitudinal ridge on the bone shaft, beginning near the break and extending to the margin of one of the broken ends (Fig. 2C), where the bone flares 225 laterally on one side. The extent of this lateral projection is unclear because the rest 226 of the bone is broken and missing. At least two potential tooth marks are visible on 227 the opposite end of the bone, measuring ~2 cm in length and ~0.2 cm deep (Fig. 228

3A). A layer of small molluscs (probably *Neomiodon*) are present on the underside ofthe bone (Fig. 3B).

In the absence of the epiphyses and without a complete shaft of the bone,
 identification presents a challenge. Based on dimensions, comparative anatomy and
 histology (see below) we suggest that NMS.Eigg.2017 is probably a stegosaur fibula.

235

236 4. Possible Identity of NMS.Eigg.2017

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238 4.1 Marine Reptiles and Crocodylomorphs

A variety of marine reptile (ichthyosaurs and plesiosaurs) and various
crocodylomorph fossils are known from the Middle Jurassic formations of the Inner
Hebrides, mostly from the Isle of Skye (Lee & Buckman 1920; Arkell 1933; Hudson
1966; Martill 1985; Clark *et al.* 1993; Benton *et al.* 1995; Brusatte *et al.* 2015; Yi *et al.*2017; Young *et al.* 2016a).Marine reptile remains from the Isle of Eigg comprise
disarticulated plesiosaurian bones from the 'Hugh Miller Bonebed' (Miller 1858;
Hudson 1966).

Despite the presence of marine reptiles and crocodylomorphs in these 246 outcrops, we do not consider NMS.Eigg.2017 to belong to any of these groups. The 247 large size of NMS.Eigg.2017 excludes it from belonging to any of the small-bodied 248 crocodylomorph taxa found in the Middle Jurassic of the Hebrides (e.g. Young et al. 249 2016a; Yi et al. 2017). Although larger-bodied thalattosuchian crocodylomorphs 250 (teleosauroids and metriorhynchoids) have been recovered from contemporaneous 251 Middle Jurassic formations elsewhere (Mannion et al. 2015; Wilberg 2015; Johnson 252 et al. 2019), no thalattosuchians have yet been reported from Scotland. Even the 253 largest thalattosuchian femora are much smaller than NMS.Eigg.2017 (e.g. ~45 cm 254 in Lemmysuchus obtusidens and Machimosaurus mosae; Hua 1999, Johnson et al. 255 2017; Young et al. 2016b). The fibula/tibia is shortened compared to their femur-a 256 modification linked to their aquatic lifestyle (Foffa et al. 2019). In addition, 257 NMS.Eigg.2017 has several features that make it unlikely to belong to this clade. For 258 example thalattosuchian femora have a sigmoidal profile with an oval cross-section, 259 which is not seen in NMS.Eigg.2017 (Andrews 1913; Hua & De Buffrenil 1996), 260 although compression and poor preservation make the cross sectional geometry 261 difficult to assess. In large thalattosuchians the cranial bones attained a length 262 comparable to NMS.Eigg.2017, but the absence of articular facets, alveoli, or dermal 263 ornamentation that characterise most thalattosuchian cranial bones (Andrews 1913) 264 make this identification incompatible with the morphology seen here. NMS.Eigg.2017 265 differs histologically from crocodylomorphs in the predominance of fibrolamellar bone 266 267 with abundant osteons and the absence of parallel-fibered bone in the cortex.

- 268 Whereas fibrolamellar or woven bone is occasionally present in some
- crocodylomorphs (Woodward *et al.* 2014; Cubo *et al.* 2017), their cortices are usually
- 270 formed exclusively of parallel-fibered or lamellar bone with simple vascular canals or
- sparse primary osteons (Hua and De Buffrénil 1996; Andrade and Sayão 2014;
- 272 Sayão et al. 2016; Cubo et al. 2017).

273 274

For these reasons we preclude this bone from being identified as that of a crocodylomorph.

The large size of NMS.Eigg.2017 also rules out attribution to an ichthyosaur 275 or plesiosaur. Furthermore the overall shape of NMS.Eigg.2017 does not match that 276 of marine reptiles. The limbs of the latter are highly modified for underwater 277 propulsion, being reduced or absent compared to terrestrial animals—as in all fully 278 marine tetrapods (Andrews 1910). Plesiosaur and ichthyosaur limbs have short, 279 robust humeri and femora with flared proximal and/or distal ends. The propodeal 280 bones (radius, ulna, tibia, fibula) of these taxa are highly modified into short, often 281 polygonal elements in the paddle (McGowan & Motani 2003; Benson 2013). The 282 microstructure of marine reptile bones is also significantly different from that of 283 terrestrial animals, typically showing either osteoporotic or pachyostotic textures 284 (Hua & De Buffrenil 1996; Houssaye 2013) and does not match that found in the 285 histological section of NMS.Eigg.2017 (see 5.0 Histology). 286

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4.2 Theropoda 288

Theropod dinosaurs were the primary terrestrial carnivores during the Middle 289 Jurassic. They ranged from those with small body masses similar to many extant 290 birds, to medium to large sized genera like Megalosaurus bucklandii (Benson 2010), 291 which reached body masses of ~1.4 tons (Benson et al. 2014) and lengths of ~8-9 292 meters, and Eustreptospondylus oxoniensis (Sadlier et al. 2008). Both of these taxa 293 are well-known basal tetanurans from the Middle Jurassic of England. Medium to 294 large ceratosaurians and potentially mid-sized basal coelurosaurs (tyrannosauroids) 295 were also present globally during this time (see review by Hendrickx et al. 2015). 296

If NMS.Eigg.2017 is a theropod dinosaur, it would belong to a mid-to-large-297 sized taxon. Based on size and proportions, the only theropod skeletal element 298 NMS.Eigg.2017 could be is a femur. The length to width ratio is similar to the femur 299 of Middle Jurassic Megalosaurus bucklandii (Benson 2010: fig 16) and 300

- Eustreptospondylus oxoniensis (Sadlier et al. 2008: fig. 19) (Table 1, Fig. 4A-D). The 301
- lateral projection at one end of NMS.Eigg.2017 may correspond to the neck of the 302 femoral head (with the head missing), and the opposite end may represent the distal 303
- end of a femur with the beginning of an epicondylar (flexor or extensor) groove (Fig. 304
- 4). However, the bone lacks the prominent lesser (=anterior) and fourth trochanters 305 that characterize theropod femora. The longitudinal ridge on one half of 306
- NMS.Eigg.2017 may be the base of a lesser trochanter, but the lesser trochanters of 307
- mid-to-large-sized theropods project strongly from the anterior surface of the bone, 308 whereas this ridge is less prominent in NMS.Eigg.2017. Even the less pronounced
- 309 lesser trochanter of *Eustreptospondylus* (Fig. 3C-D) is more pronounced than in 310
- NMS.Eigg.2017. We consider it unlikely that the ridge is a damaged remnant of a 311
- more pronounced trochanter, as its surface is smooth and unbroken. It is also 312
- unlikely that a more prominent lesser trochanter was present in life but not 313
- observable because the bone has broken distal to it. If NMS.Eigg.2017 is a theropod 314
- femur, the lateral projection of the presumed proximal end indicates that only a 315
- 316 moderate portion of the head is missing proximally. Therefore, the region that would

have included the trochanter is preserved, but lacks this predominant feature. The
fourth trochanter should also be visible along the posterior surface of the shaft, but
appears to be absent. Although there is a large portion of the mid-shaft missing—
meaning we cannot completely rule out the presence of a fourth trochanter—overall

we consider the identification of NMS.Eigg.2017 as a theropod femur unlikely.

NMS.Eigg.2017 is much larger, longer and more slender than the humerus, 322 radius or ulna of Megalosaurus bucklandii (Benson 2010: figs 12-13) (Fig. 4E), 323 Eustreptospondylus (Sadlier et al. 2008: fig 16), and other mid- to large-bodied 324 theropods, which were all bipedal animals with much shorter forelimbs than hind 325 limbs. Although NMS Eigg 2017 has a similar length and width as the tibia of 326 Megalosaurus, NHMUK PV OR31809 (Fig. 4F-G), it lacks the twist of the shaft from 327 proximal to distal ends observed in the tibia of *Megalosaurus*, *Eustreptospondylus* 328 (Sadlier et al. 20082008: fig. 20), or other theropods, and also lacks any sign of the 329 prominent cnemial and fibular crests. NMS.Eigg.2017 also does not match the 330 gracile and distally tapering morphology of theropod fibulae. 331

Histological analysis does not support the identification of NMS.Eigg.2017 as 332 belonging to a theropod. The cancellous medullary cavity of NMS.Eigg.2017 is unlike 333 334 the limb bones of most theropod dinosaurs, which are hollow. The pectoral and pelvic girdle elements of theropods have a cancellous medullary cavity, but it is 335 difficult to reconcile the gross morphology of NMS.Eigg.2017 with these bones: 336 theropod scapulae are flat, straplike bones, which is not the case in NMS.Eigg.2017, 337 and there is no evidence of a pubic apron, pubic boot, or obturator process in 338 NMS.Eigg.2017, which eliminates a pubis or ischium as a candidate. 339

340 341

342 **4.3 Sauropoda**

The body fossil record for Middle Jurassic Sauropoda is relatively scarce compared 343 to that of the Late Jurassic or Cretaceous. Material is known from China, India, North 344 Africa, Argentina, and the UK. From the Bajocian-Bathonian of Oxfordshire and 345 Gloucestershire sauropods are represented by *Cetiosaurus oxoniensis* (Upchurch 346 and Martin 2002, 2003). Finds from the northwest of Scotland provide additional 347 indeterminate sauropod material, comprising incomplete limb elements and single 348 teeth (Clark et al. 1995; Liston 2004; Barrett et al. 2006; Clark and Gavin, 2016; 349 Clark, 2018). 350

The small size of NMS Eigg 2017 makes it likely that if it is a sauropod limb 351 bone, it represents a juvenile animal. The femora of contemporaneous sauropods 352 such as Cetiosaurus and Patagosaurus fariasi are more robust than NMS.Eigg.2017, 353 with a lower length to width ratio (Fig. 5A, Table 1). Cetiosaurid femora, even in 354 355 juveniles, are usually anteroposteriorly flattened and mediolaterally wide, creating an elliptical cross-section (Holwerda et al. in press). This shape contrasts with 356 NMS.Eigg.2017, which has a more gracile and rounded midshaft (Fig. 2). However, 357 features congruent with a sauropod femur include the curved, lateral projection at 358 one end of NMS.Eigg.2017, which may correspond to the base of the greater 359 360 trochanter, and the groove visible at the opposite end, which may represent the

epicondylar groove at the distal end of the femur (Fig. 2B-C). The femur of Early
Jurassic sauropod taxon *Barapasaurus tagorei* has closer proportions to
NMS.Eigg.2017 (Table 1, Fig. 5B-C), suggesting that if NMS.Eigg.2017 is a
sauropod femur it belonged to a gracile taxon, and possibly not a cetiosaurid— *Barapasaurus* is currently placed outside of the cetiosaurid clade (Holwerda & Pol
2018).

If NMS.Eigg.2017 belongs to a sauropod, we consider it most likely to be a 367 fibula, as they are similar in length to width ratio to NMS.Eigg.2017 (Table 1). 368 Sauropod fibulae bear a posterior projection on the distal end of the bone above the 369 astragalar articular surface, as seen most clearly in Spinophorosaurus nigeriensis 370 (Remes et al. 2009) (Fig. 5G), but also to a lesser extent in Cetiosaurus oxoniensis 371 (Fig. 5D). This feature may correspond to the lateral projection at one end of 372 NMS.Eigg.2017 (Fig. 3). Moreover, NMS.Eigg.2017 possesses a ridge which may 373 correspond to the ridge for the accommodation of the tibia, similar to those in fibulae 374 of the contemporaneous Cetiosaurus (Fig. 5D), and of the possibly Oxfordian 375 *Rhoetosaurus brownei* (Fig. 5E, F). If that interpretation is correct, it would mean this 376 377 end of NMS.Eigg.2017 corresponds to the proximal half. The somewhat triangular 378 shape of this 'proximal' end of NMS. Eigg. 2017 is similar to that in the juvenile Cetiosaurus OUMNH J.29807 and Rhoetosaurus QMF 1659. 379

The extreme midshaft compression and proximal and distal flaring of the 380 humerus in sauropods is not present in NMS.Eigg.2017. All sauropods show this 381 morphology, even among juvenile individuals such as Tazoudasaurus naimi Pt-1 382 (Allain & Aquesbi 2008) (Fig. 5H, I). Therefore, identification of NMS Eigg. 2017 as a 383 sauropod humerus can be ruled out. There is no proximal flaring of the bone, as 384 seen in the cnemial crest of sauropod tibiae. NMS.Eigg.2017 does not possess the 385 slight sinusoidal curvature or proximal mediolateral widening and distal posterolateral 386 widening seen in the radius of Cetiosaurus oxoniensis OUMNH J.13611 (Fig. 5K). 387 Sauropod radii are oval in cross-section proximally (Upchurch 2004), whereas 388 NMS.Eigg.2017 is more triangular. 389

Although the length to width ratio is similar between NMS.Eigg.2017 and sauropod ulnae (Table 1), and there is a similar triangular cross section near the proximal end of the bone, NMS.Eigg.2017 lacks the narrow distal end, as well as the triradiate anteromedial and anterolateral proximal expansions seen in sauropod ulnae, e.g. *Cetiosaurus oxoniensis* OUMNH J.13611 (Fig. 5J).

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397 **4.4 Ornithischia**

The Middle Jurassic body fossil record of Ornithischia is restricted to small, bipedal forms (e.g. Ruiz-Omenaca *et al.* 2006), with the exception of the armoured dinosaurs, Thyreophora, which were the first ornithischians to attain large body mass

and quadrupedality (Galton & Upchurch 2004; Barrett & Maidment 2017).

402 Thyreophoran remains are known from Middle Jurassic deposits in the UK, such as

403 Loricatosaurus priscus and Sarcolestes leedsi from the Callovian Oxford Clay

404 Formation (Galton 1983,1985; Maidment et al. 2008), indeterminate stegosaur

remains from the Sharp's Hill Formation of Oxfordshire (Boneham & Forsey 1992),
and body fossils of thyreophorans from the Great Estuarine Group of the Isle of Skye
(Clark 2001). There are also trackways attributed to the ichnogenus *Deltapodus* from
Skye (dePolo *et al.* 2020) and the Middle Jurassic of Yorkshire (Whyte *et al.* 2007),
attributed to a stegosaur trackmaker. Possible larger-bodied ornithopod footprints
have recently been suggested for some of the trackways on Skye (dePolo *et al.*

411 2020), but no conclusive evidence for their presence is currently known.

The femora of thyreophorans are proportionally short and robust with rounded 412 shaft cross-sections (Fig. 6A, B). In contrast, the shaft of NMS Eigg.2017 is slender 413 and elongate, and flattened on one side (although this may have been accentuated 414 by crushing). Humeri in thyreophorans are characterised by prominent deltopectoral 415 crests that occupy much of the length of the bone, and flared distal ends (Fig. 6C, 416 D), unlike the shape in NMS.Eigg.2017. The ulnae of thyreophorans are short, 417 proportionally short and robust and proximally triradiate (Fig. 6E, F), unlike 418 NMS.Eigg.2017, and the radii are shorter and much less slender than 419 NMS.Eigg.2017 (Fig. 6G, H). The cross-sectional geometry of NMS.Eigg.2017 is 420 similar to the tibiae of thyreophorans (Fig. 6I, J) although the proximal and distal 421

422 ends are much more flared than in NMS.Eigg.2017.

NMS.Eigg.2017 is similar in overall proportions and cross-sectional geometry
to the fibulae of thyreophorans (Fig. 6I, K). It is possible, therefore, that
NMS.Eigg.2017 is a fibula of a thyreophoran dinosaur. However, there are no
thyreophoran synapomorphies of the fibula present (Raven & Maidment 2017) and
so NMS.Eigg.2017 cannot be unequivocally referred to Thyreophora by comparative
anatomy alone (but see 5. Osteohistology).

429

430 **5. Osteohistology**

431

A transverse thin section of NMS.Eigg.2017 shows it is extensively fractured and
moderately crushed, which has collapsed some of the internal trabeculae (Fig. 7).
Despite this damage, it is clear that the medullary cavity was not open, and that
trabeculae extended throughout the medullary region. Cortical thickness is relatively
high (~50%) in some regions, but varies around the cortex.

Most of the cortex is heavily remodelled, resulting in dense Haversian bone 437 (Francillon-Vieillot et al. 1990), and combined with expansion of the medullary cavity 438 this feature has obscured all primary bone in the inner cortex. The trabeculae of the 439 medullary cavity are formed of lamellar bone (Francillon-Vieillot et al. 1990) with 440 flattened osteocyte lacunae (Fig. 8D). Within the medullary spaces, linings of 441 endosteally-derived lamellar bone (Bromage et al. 2009) are apparent. The size of 442 the medullary spaces decreases periosteally (Fig. 7B), and close to the cortex, some 443 of the medullary spaces resemble large secondary osteons (Fig. 7A). There is a 444 stark transition between the zone of dense Haversian bone and the trabeculae of the 445 medullary cavity. At this transition, the diameter of vascular spaces decreases 446 significantly and no endosteal lamellar bone is visible between the secondary 447 448 osteons. The zone of dense Haversian bone is defined here as the region where

secondary remodelling completely obscures any intervening primary tissue.

450 Secondary osteons within the zone of dense Haversian bone are longitudinally

oriented and decrease in size periosteally (Fig. 7A). Endosteally, several overlapping

452 generations of secondary osteons can be discerned, and in some areas there are at
453 least three and maybe four generations of secondary osteons (Fig. 8C). The density

of secondary remodelling decreases periosteally, so that there are fewer overlapping secondary osteons, and more primary bone is visible between them (Fig. 7D). We

456 interpret this zone as more representative of abundant secondary remodelling rather

than true dense Haversian bone, because primary tissue is visible between the

458 secondary osteons.

In the thickest part of the cortex an extensive area of primary bone is 459 preserved towards the periosteal surface (Fig. 7C). This primary bone is fibrolamellar 460 with a relatively sparse osteocyte lacunae (~14500/mm³). Osteocyte lacunae are 461 lenticular where they surround primary osteons, but are denser and more globose in 462 the intermittent areas of woven bone (Fig. 8A). The primary bone is relatively poorly 463 vascularized (Fig. 7C) compared to most dinosaurs (Horner et al. 1999; Horner & 464 Padian 2004; Padian et al. 2004; Sander et al. 2011; Woodward et al. 2015), and the 465 density, orientation, and size of vascular canals varies throughout the cortex. In most 466 areas, vasculature is longitudinal in orientation, and these canals are randomly 467 dispersed rather than arranged into circumferential rings (Fig. 7C). Several areas 468 have a higher proportion of anastomosing canals and thus exhibit reticular 469 vascularity, but these are confined to small, randomly distributed patches rather than 470 continuous layers or zones (Fig. 7C). The diameter of the longitudinal vascular 471 canals varies randomly from $\sim 20 \,\mu m$ to $\sim 100 \,\mu m$, and even adjacent canals can be 472 considerably different in size. Vascularity is consistent in density and orientation 473 approaching the periosteal surface, and numerous vascular canals are open to the 474 periosteal surface (Fig. 7C, D, 8F). One line of arrested growth, or LAG, is visible in 475 the primary bone of the cortex, just periosteal to the zone of Haversian bone (Fig. 476 7D). There are no LAGs near the periosteal surface, nor is there development of an 477 external fundamental system (Horner et al. 1999; Woodward et al. 2011, 2015). 478

A region of secondary remodelling is present within the primary cortical bone, 479 about one third of the distance from the zone of dense Haversian bone to the 480 periosteal surface, approximately 0.5-1 mm external to the LAG (Fig. 7D). This 481 region is separated from the Haversian bone by a band of primary fibrolamellar bone 482 (Fig. 7D) with small, longitudinally oriented canals, where the LAG is situated (Fig. 483 8B). The secondary osteons in the zone of remodelling are generally larger than 484 those in the periosteal portion of the Haversian zone, and are more comparable in 485 size to those nearer the medullary cavity. The secondary osteons in the zone of 486 remodelling frequently interconnect, which creates a reticular pattern of vascularity 487 overall (Fig. 7D). No cross-cutting of the secondary osteons can be detected, in 488 contrast with the zone of Haversian bone. Where the primary bone is visible between 489 the secondary osteons in this region of secondary remodelling, some erosive cavities 490 can be discerned (Fig. 8E). These can be differentiated from primary osteons by 491

their scalloped edges, created by Howship's lacunae, which are evidence of
 resorption by osteoclasts (Francillon-Vieillot *et al.* 1990).

Assuming NMS.Eigg.2017 is a hind limb bone, the bone matrix and internal 494 structure exclude certain identifications. Fibrolamellar bone is known only in 495 amniotes (Francillon-Vieillot et al. 1990), specifically in synapsids (Chinsamy-Turan 496 2012), some marine reptiles (de Buffrénil & Mazin 1990; Klein 2010; Kolb et al. 2011; 497 Houssaye et al. 2014; Klein et al. 2015; Wintrich et al. 2017), and archosaurs 498 (Horner et al. 2001; de Ricqlès et al. 2003; Padian et al. 2004). The large size of the 499 bone precludes a synapsid identification, while the lack of highly porous 500 (osteoporotic), or compacted (pachyostotic) bone rules out marine reptiles, which 501 have these features as adaptations for a marine lifestyle (Houssave 2009; Houssave 502 et al. 2014). Additionally, the cortical thickness of NMS.Eigg.2017 is greater than 503 would be expected of pelagic animals like ichthyosaurs. 504

505 The histology of NMS.Eigg.2017 is most similar to that of dinosaurs, which 506 typically have highly vascularized fibrolamellar zonal bone with LAGs (Horner *et al.* 507 1999; Padian *et al.* 2004; Padian & Lamm 2013). In contrast, crocodylomorphs and 508 pseudosuchians more commonly show lamellar-zonal bone with lower vascularity 509 and less fibrolamellar tissue (de Ricqlès *et al.* 2003; Andrade & Sayão 2014; Sayão 510 *et al.* 2016; Cubo *et al.* 2017), whereas pterosaurs have extensive medullary cavities 511 with extremely thin cortical walls (De Ricqlès *et al.* 2000; Padian *et al.* 2004)

Detailed comparative anatomy suggests that NMS Eigg 2017 is most likely to 512 be either a thyreophoran or sauropod fibula. The distinctive combination of 513 osteohistological features in NMS.Eigg.2017 provides further clues, but uncertainty 514 over the identity of the element makes the significance of certain features—like 515 vascular orientation—unclear. Different bones of the same individual, and even 516 different regions within the same bone, can produce markedly different histological 517 signatures (Horner et al. 1999; Cullen et al. 2014; Woodward et al. 2014; Nacarino-518 Meneses et al. 2016). Smaller bones tend to grow at slower rates and may 519 experience more rapid secondary remodelling (Horner et al. 1999), and fibulae 520 especially tend to show more remodelling. The pervasive remodelling in 521 NMS.Eigg.2017 may therefore be the result of the element rather than taxonomic 522 identity. However, as NMS.Eigg.2017 likely represents a large hind limb bone, its 523 histology probably generally reflects the overall growth of the individual rather than 524 solely exhibiting a biomechanical signal. 525

The microstructure of NMS.Eigg.2017 differs from theropod limb bones in that 526 the medullary cavity is not hollow (Chinsamy, 1990; Horner & Padian 2004; Bybee et 527 al. 2006; Lee & O'Connor 2013; Cullen et al. 2014). In theropods, some sparse 528 trabeculae can be present in the medullary cavity where the diaphysis grades into 529 the metaphysis. However, it is unlikely that the closed medullary cavity in 530 NMS.Eigg.2017 is attributable to this phenomenon, because trabeculae completely 531 fill the medullary cavity, and because the section was taken relatively close to the 532 midshaft (Fig. 2). Sauropod osteohistology is well studied, and their limb bone 533 cortices are characterized by a laminar vascular arrangement indicative of rapid 534 535 growth (Sander 2000, 2004; Klein & Sander 2008; Woodward & Lehman 2009;

Sander et al. 2011a and b), even in smaller forms (Sander et al. 2006; Stein et al. 536 2010). This arrangement is not the case in NMS.Eigg.2017, where vasculature is 537 arranged randomly rather than into circumferential rows (Fig. 7C). Neosauropods 538 tend to lack distinct LAGs (Sander et al. 2011), and in many cases growth marks are 539 preserved instead as polish lines visible in reflected light (de Ricglès 1983). The 540 presence of a LAG in NMS. Eigg. 2017 therefore argues against a neosauropod 541 affinity for the specimen. The low osteocyte lacunar density of NMS.Eigg.2017 is 542 further evidence against a sauropod affinity, as sauropods typically have much 543 denser osteocyte lacunae than other comparably-sized animals (Stein & Werner 544 2013). 545

Of the possible dinosaur groups, the histology of NMS.Eigg.2017 is most 546 similar to that of thyreophoran dinosaurs. The combination of predominantly 547 longitudinal vascularity indicative of a relatively low growth rate and abundant 548 secondary remodelling is seen in this group (Hayashi et al. 2009; Redelstorff & 549 Sander 2009; Redelstorff et al. 2013; Stein et al. 2013; Maidment et al. 2018). Most 550 osteohistological work on thyreophorans has focused on their osteoderms (e.g. 551 Hayashi et al. 2009; Burns & Currie 2014; Horner et al. 2016), but a few studies have 552 sampled long bones. In a review of ankylosaur osteohistology, Stein et al. (2013) 553 noted abundant structural fibres within the primary and secondary bone of the limb 554 elements of derived North American ankylosaurs. In contrast, stegosaurs lack 555 structural fibres and have slightly less—but still abundant—secondary remodelling at 556 equivalent ontogenetic stages (Hayashi et al. 2009; Redelstorff & Sander 2009; 557 Redelstorff et al. 2013; Stein et al. 2013). Hayashi et al. (2009) sampled fibulae from 558 an ontogenetic sequence of Stegosaurus, and Maidment et al. (2018) sampled a 559 fibula of the stegosaur *Hesperosaurus*. Both showed that vasculature in medium to 560 large sized individuals was predominantly longitudinal with extensive secondary 561 remodelling and the development of LAGs. 562

The histology of NMS.Eigg.2017 is remarkably similar to the medium to large-563 sized Stegosaurus fibulae described by Hayashi et al. (2009), except that an external 564 fundamental system is not developed. This difference could be explained by a 565 slightly younger ontogenetic stage in NMS.Eigg.2017, as the external fundamental 566 system is only developed late in life (Horner et al. 1999; Woodward et al. 2011, 567 2015). In this aspect, NMS.Eigg.2017 is more like the fibula of *Hesperosaurus* MOR 568 9728 described by Maidment et al. (2018), which also lacks an external fundamental 569 system. The two specimens are virtually identical in cross-sectional shape, and 570 although the cortical thickness of MOR 9728 is greater than NMS.Eigg.2017, this 571 could be because the samples were taken at different locations of the midshaft. 572 MOR 9728 is more extensively remodelled than NMS.Eigg.2017, but where primary 573 bone remains near the periosteal surface, the vasculature is sparse and 574 longitudinally oriented, as in NMS.Eigg.2017. 575

576 The osteohistological signal of slow growth with extensive remodelling is 577 evident in *Kentrosaurus*. Based on the femora, *Kentrosaurus* had a slightly faster 578 growth rate than *Stegosaurus* or NMS.Eigg.2017, but still lower than other 579 comparably sized ornithischians (Redelstorff & Sander 2009; Redelstorff *et al.* 2013). 580 NMS.Eigg.2017 shares with stegosaurs the abundant secondary remodelling (Fig. 581 7A, 2C), randomly arranged longitudinal–reticular vasculature (Fig. 7C), and the 582 absence of the structural fibres, as present in ankylosaurs. Of the dinosaurian 583 candidates, the histology of NMS.Eigg.2017 is therefore most consistent with 584 stegosaurs.

The fibrolamellar bone matrix of NMS.Eigg.2017 is indicative of relatively high 585 growth rates compared to more basal tetrapods (Francillon-Vieillot et al. 1990; 586 Castanet et al. 2000; Padian & Lamm 2013). Based on the vascular canals within the 587 primary cortical bone, the predominantly longitudinal vascularity with small regions of 588 reticular vascularity suggests however that growth in this element was on the low 589 end of the spectrum of fibrolamellar growth rates (Castanet et al. 2000; de Margerie 590 2004). Vascularity at the periosteal surface and the absence of an external 591 fundamental system also suggest this animal was actively growing at the time of 592 death (Horner et al. 1999; Woodward et al. 2011, 2015). The position of the single 593 LAG towards the middle of the cortex indicates considerable growth in the last year 594 of life. The consistent density and orientation of vascularity in the periosteal portion 595 596 of the cortex suggests that growth had not slowed, and that NMS.Eigg.2017 was in 597 the maximum growth phase of its life when it died (Lee et al. 2013).

Establishing the chronological age of NMS.Eigg.2017 is difficult because of 598 the extensive secondary remodelling of the cortex and expansion of the medullary 599 cavity. The combination of active growth and extensive secondary remodelling is 600 unusual, as these typically characterise different phases of growth (Klein and Sander 601 2008; Padian & Lamm 2013). Secondary remodelling usually progresses from the 602 inner cortex outwards (Mitchell & Sander 2014), and therefore Haversian bone in the 603 outer cortex only occurs later in life (Kerley 1965; Klein & Sander 2008). However, it 604 can be induced by biomechanical stress or other environmental factors (Padian & 605 Lamm 2013), which may explain the abundance of secondary osteons in conjunction 606 with high growth rates. It is clear from the single LAG that this individual was at least 607 one year old at the time of death, but it was almost certainly considerably older. The 608 abundance of secondary remodelling and overlapping generations of secondary 609 osteons are typically associated with advanced age (Kerley 1965; Uytterschaut 610 1993; Horner et al. 1999; Klein & Sander 2008; Sander et al. 2011). Unfortunately, 611 retrocalculation of growth marks is not possible with only a single LAG (Cooper et al. 612 2008; Lee et al. 2013), so the exact age of NMS Eigg 2017 at death cannot be 613 determined. 614

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617 6. Conclusion

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This specimen, NMS.Eigg.2017, is the first unequivocal dinosaur fossil found in

620 Scotland outside of Skye. Identification of damaged isolated bones can be

challenging, but finding ways to approach such identification is especially relevant for

the dinosaur fossil record in Scotland, which comprises relatively incomplete material

623 compared to contemporaneous sites in England.

Through detailed anatomical comparison, we find the overall proportions and 624 cross-sectional geometry similar to the fibulae of thyreophorans. The length to width 625 ratio, and certain features such as a longitudinal ridge are similar to features present 626 in a sauropod fibula, and NMS.Eigg.2017 bears resemblance to the fibula of juvenile 627 Cetiosaurus. However, examination of the microstructure of the bone through 628 histological analysis reveals a combination of predominantly longitudinal vascularity 629 indicative of a relatively low growth rate, with abundant secondary remodelling—both 630 strongly indicative of thyreophoran (particularly stegosaur) limb bone microstructure. 631 The vascularity at the periosteal surface and absence of an external fundamental 632 system indicate it belonged to a juvenile animal still rapidly growing at the time of 633 death. We therefore consider NMS.Eigg.2017 most likely to represent a juvenile 634 stegosaur fibula. 635

The presence of a thyreophoran bone on the Isle of Eigg adds a significant new datapoint for dinosaur distribution in the Middle Jurassic. The dinosaur body fossil record is sparse in Scotland, and this specimen provides evidence for a largebodied animal in a locality previously not known for dinosaur fossils. Weathering, tooth marks and a layer of small molluscs on the underside of the femur suggest transport and scavenging of the carcass prior to deposition, which is consistent with its entombment in the fluvio-deltaic Valtos Sandstone Formation.

This specimen increases the palaeontological significance of the Isle of Eigg. The island is already well known for the fossiliferous 'Hugh Miller Reptile Bed' (Miller 1858; Hudson 1966; Benton 1995), and for the distinctive features of its geological landscape, such as the Sgurr of Eigg. Although a theropod tooth fragment from Eigg was mentioned by Rees and Underwood (2005), it has subsequently been lost and this cannot be confirmed. This makes NMS.Eigg.2017 the first unequivocal dinosaur specimen from the island.

This discovery hints that continued exploration of the Valtos Sandstone
 Formation - and other parts of the Great Estuarine Group - could yield further vital
 fossil material. These finds would undoubtedly continue to enrich our picture of
 ecosystem diversity in Middle Jurassic Scotland.

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1217 1218	Figure captions
1218 1219 1220 1221	Figure 1 . The lithostratigraphy of the Great Estuarine Group and location at Camas Sgiotaig on the Isle of Eigg where NMS.Eigg.2017 was found.
1222 1223 1224 1225 1226	Figure 2. NMS.Eigg.2017, a probable thyreophoran limb bone from the Isle of Eigg, Scotland. A, NMS.Eigg.2017 in matrix after initial prep. B-E, NMS.Eigg.2017 removed from matrix and partially reconstructed: B, the eroded 'upper' surface; C, the surface that was downwards into the matrix; D and E, side views of NMS.Eigg.2017. Scale bar B-E same = 100 mm.
1227 1228 1229 1230	Figure 3. Possible bite marks (indicated by arrows) A , and molluscs B on underside of NMS.Eigg.2017

Figure 4. Postcranial elements of theropod dinosaurs *Megalosaurus* and
 Eustreoptospondylus. *Megalosaurus bucklandii* NHMUK PV OR31806 femur 31806
 anterior A, and posterior B, view; *Eustreptospondylus oxoniensis* OUMNH J.13558
 femur in anterior C, and posterior D view; *Megalosaurus bucklandii* OUMNH J.13575
 humerus in anterior view E; and *Megalosaurus bucklandii* NHMUK PV OR31809 tibia
 in anterior F, and posterior G view. All scale bars 100 mm.

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Figure 5. Postcranial elements of sauropod dinosaurs. Cetiosaurus oxoniensis 1238 femur OUMNH J.13615 in posterior view A: Barapasaurus tagorei ISIR741 femur in 1239 anterior view **B** and posterior view **C**; Cetiosaurus oxoniensis OUMNH J.29807 fibula 1240 in anterior view D; Rhoetosaurus brownei QMF 1659 fibula in anterior E and 1241 posterior F view; Spinophrosaurus nigerensis GCP-CV-4429 fibula in anterior view 1242 G; Tazoudasaurus naimi pT-1 humerus in anterior view in anterior H and posterior I 1243 view; Cetiosaurus oxoniensis OUMNH J.13611 ulna J and radius K in anterolateral 1244 view. Scale bar same throughout = 100 mm. 1245

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Figure 6. Postcranial elements of thyreophoran dinosaurs. Anterior views of
Stegosaurus stenops NHMUK PV R36730 femora A, humerus C, ulna E, radius G,
fused tibia and fibula I; anterior view of *Edmontonia* sp. CMN 8531 femur B; anterior
view of *Euoplocephalus tutus* AMNH 5337 humerus D and radius H; anterior view of *Euoplocephalus tutus* AMNH 5403 ulna F; anterior view of *Polacanthus foxii* NHMUK
PV R175 tibia with partial fibula fused to distal end J; posterior view of *Ankylosaurus magniventris* AMNH 5214 fibula K. Scale bar equal to 100 mm.

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Figure 7. Overview of the osteohistology of NMS Eigg 2017. A, column through the 1255 cortex, showing medullary spaces endosteally, dense Haversian bone throughout 1256 most of the cortex, and primary fibrolamellar bone in the outer cortex; B, overview of 1257 1258 entire slide, showing the arrangement of the medullary cavity and the cortex, and position of the LAG (arrow) in the middle cortex; **C**, outer cortex, showing primary 1259 fibrolamellar bone with longitudinal-reticular vascularity and consistent vascularity to 1260 1261 the periosteal surface; **D**, outer cortex, showing zone of dense Haversian bone grading into primary fibrolamellar bone with a LAG (arrow), and a second, isolated 1262 zone of secondary remodelling. All images under normal light. Abbreviations: FLB, 1263 fibrolamellar bone; HB, Haversian bone; LAG, line of arrested growth; longvasc, 1264 longitudinal vascularity; Retvasc, reticular vascularity; SOs, secondary osteons; SR, 1265 secondary remodelling. 1266

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Figure 8. Histological details of NMS.Eigg.2017. **A**, primary osteons in the outer cortex, showing fibrolamellar bone matrix and variation in osteocyte shape and density; **B**, primary and secondary osteons with a LAG (arrow) in the outer cortex; **C**, overlapping generations of secondary osteons within the dense Haversian bone of the inner cortex; numbers indicate order of deposition; **D**, trabeculae composed of lamellar bone and infilled with endosteal lamellae in the medullary cavity; **E**, erosive cavities in the fibrolamellar bone separating the two zones of secondary remodelling; **F**, outer cortex, showing consistent vascular orientation and density, localized

1276 secondary remodelling, and erosional cavities. All images under normal light.

Abbreviations: ec, erosional cavity; el, endosteal lamellae; lb, lamellar bone; po, primary osteon; so, secondary osteon; sr, secondary remodelling; vasc, vascular canal; wb, woven bone.

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Table 1. Measurements of NMS.Eigg.2017 and other Middle Jurassic dinosaur limb bones. Data from Benson (2010), Holwerda *et al.* (in press) Remes *et al.* (2009) and author's own photographs of specimens. *Measurements are estimated due to missing proximal and distal ends of NMS.Eigg.2017 and compression and erosion of mid-shaft, and should be considered with caution.

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Taxon	Specimen	Bone	Length (cm)	Width (mid shaft) (cm)	L/W ratio
Eigg Dinosaur	NMS.Eigg.2017	-	64-79*	7.3 *	0.11-0.09
Megalosaurus bucklandii	OUMNH J.13575	humerus	39	6	0.15
Megalosaurus bucklandii	NHMUK PV OR36585	ulna	23	5	0.22
Megalosaurus bucklandii	NHMUK PV OR31806	femur	81	10	0.12
Megalosaurus bucklandii	NHMUK PV OR31809	tibia	65	7	0.11
Cetiosaurus oxoniensis	OUMNH J.13612	ulna 🗸	121	19	0.16
Cetiosaurus oxoniensis	OUMNH J.13615	femur	166	30	0.18
Cetiosaurus oxoniensis	OUMNH J.29807	fibula	57	6	0.11
Cetiosaurus oxoniensis	OUMNH J.13621	tibia	96	17	0.18
Barapasaurus tagorei	ISIR 70	humerus	84	12	0.14
Barapasaurus tagorei	ISIR 72	ulna	60	7	0.12
Barapasaurus tagorei	ISIR 71	radius	55	6	0.11
Barapasaurus tagorei	ISIR 64	fibula	55	4	0.07
Barapasaurus tagorei	ISIR 741	femur	93	13	0.14
Spinophorosaurus nigerensis	NMB-1698-R	humerus	60	8	0.13
Spinophorosaurus nigerensis	GCP-CV- 4229/NMB-1699-R	femur	64	10	0.16
Spinophorosaurus nigerensis	GCP-CV- 4229/NMB-1699-R	fibula	36	4	0.11

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Figure 1. The lithostratigraphy of the Great Estuarine Group and location NMS.Eigg.2017 was found.



Figure 2. NMS.Eigg.2017, a probable thyreophoran limb bone from the Isle of Eigg, Scotland. A, NMS.Eigg.2017 in matrix after initial prep. B-E, NMS.Eigg.2017 removed from matrix and partially reconstructed: B, the eroded 'upper' surface; C, the surface that was downwards into the matrix; D and E, side views of NMS.Eigg.2017. Scale bar B-E same = 100 mm.



Figure 3. Bite marks (indicated by arrows) A, and molluscs B on underside of NMS.Eigg.2017.

685x249mm (72 x 72 DPI)



Figure 4. Postcranial elements of theropod dinosaurs *Megalosaurus* and *Eustreoptospondylus*. *Megalosaurus* bucklandii NHMUK PV OR31806 femur 31806 anterior A, and posterior B, view; *Eustreptospondylus* oxoniensis OUMNH J.13558 femur in anterior C, and posterior D view; *Megalosaurus bucklandii* OUMNH J.13575 humerus in anterior view E; and *Megalosaurus bucklandii* NHMUK PV OR31809 tibia in anterior F, and posterior G view. All scale bars 100 mm.

693x932mm (72 x 72 DPI)



Figure 5. Postcranial elements of sauropod dinosaurs. *Cetiosaurus oxoniensis* femur OUMNH J.13615 in posterior view A; *Barapasaurus tagorei* ISIR741 femur in anterior view B and posterior view C; *Cetiosaurus oxoniensis* OUMNH J.29807 fibula in anterior view D; *Rhoetosaurus brownei* QMF 1659 fibula in anterior E and posterior F view; *Spinophrosaurus nigerensis* GCP-CV-4429 fibula in anterior view G; *Tazoudasaurus naimi* pT-1 humerus in anterior view in anterior H and posterior I view; *Cetiosaurus oxoniensis* OUMNH J.13611 ulna J and radius K in anterolateral view. Scale bar same throughout = 100 mm.

667x1051mm (72 x 72 DPI)



Figure 6. Postcranial elements of thyreophoran dinosaurs. Anterior views of *Stegosaurus stenops* NHMUK PV R36730 femora A, humerus C, ulna E, radius G, fused tibia and fibula I; anterior view of *Edmontonia* sp. CMN 8531 femur B; anterior view of *Euoplocephalus tutus* AMNH 5337 humerus D and radius H; anterior view of *Euoplocephalus tutus* AMNH 5403 ulna F; anterior view of *Polacanthus foxii* NHMUK PV R175 tibia with partial fibula fused to distal end J; posterior view of *Ankylosaurus magniventris* AMNH 5214 fibula K. Scale bar equal to 100 mm.

841x657mm (72 x 72 DPI)



Figure 7. Overview of the osteohistology of NMS.Eigg.2017. A, column through the cortex, showing medullary spaces endosteally, dense Haversian bone throughout most of the cortex, and primary fibrolamellar bone in the outer cortex; B, overview of entire slide, showing the arrangement of the medullary cavity and the cortex, and position of the LAG (arrow) in the middle cortex; C, outer cortex, showing primary fibrolamellar bone with longitudinal-reticular vascularity and consistent vascularity to the periosteal surface; D, outer cortex, showing zone of dense Haversian bone grading into primary fibrolamellar bone with a LAG (arrow), and a second, isolated zone of secondary remodelling. All images under normal light. Abbreviations: FLB, fibrolamellar bone; HB, Haversian bone; LAG, line of arrested growth; longvasc, longitudinal vascularity; Retvasc, reticular vascularity; SOs, secondary osteons; SR, secondary remodelling.



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608x685mm (72 x 72 DPI)