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2 **New theropod dinosaur teeth from the Middle Jurassic of the Isle of Skye, Scotland**

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15 11448 Words, 102 References, 1 Table, 4 Figures
16

17 Abbreviated Title: Theropod dinosaur teeth from Skye
18

19 **Abstract:** The Middle Jurassic is a largely mysterious interval in dinosaur evolution, as few
20 fossils of this age are known worldwide. In recent years, the Isle of Skye has yielded a
21 substantial record of trackways, and a more limited inventory of body fossils, that indicate a
22 diverse fauna of Middle Jurassic dinosaurs living in and around lagoons and deltas.
23 Comparatively little is known about the predators in these faunas (particularly theropod
24 dinosaurs), as their fossils are among the rarest discoveries. We here report two new isolated
25 theropod teeth, from the Valtos Sandstone and Lealt Shale Formations of Skye, which we
26 visualized and measured using high-resolution x-ray computed microtomographic scanning
27 (μ CT) and identified via statistical and phylogenetic analyses of a large comparative dental
28 dataset. We argue that these teeth most likely represent at least two theropod species—one
29 small-bodied and the other large-bodied—which likely belonged to one or several clades of
30 basal avetheropods (ceratosaurs, megalosauroids, or allosauroids). These groups, which were
31 diversifying during the Middle Jurassic and would become dominant in Late Jurassic, filled
32 various niches in the food chain of Skye, probably both on land and in the lagoons.

Introduction

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Despite the flurry of new dinosaur discoveries across the globe over the last few decades, the Middle Jurassic remains a largely mysterious time for not only dinosaurs, but also terrestrial ecosystems in general. This is because very few Middle Jurassic localities preserve vertebrate fossils (e.g., Weishampel *et al.* 2004). One of these rare places is the Isle of Skye in Scotland, where deltaic and lagoonal sedimentary rocks of the Great Estuarine Group (Bathonian, ca. 168-166 million years old; Harris & Hudson 1980; Hudson 1993) are exposed. These yield trackways and bones of many types of dinosaurs (Andrews & Hudson 1984; Clark & Barco-Rodriguez 1998; Clark *et al.* 1995, 2004, 2005; Clark 2001; Liston 2004; Marshall 2005; Barrett 2006; Wills *et al.* 2014; Brusatte & Clark 2015; Brusatte *et al.*, 2015; Clark and Gavin, 2016; dePolo *et al.* 2018). They are associated with fossils of other tetrapods including mammals, and close relatives, crocodylomorphs, and turtles (Waldman and Savage 1972; Evans 2006; Anquetin *et al.* 2009; Wills *et al.* 2014; Young *et al.* 2016; Panciroli *et al.* 2017a, b, 2018; Yi *et al.* 2017).

Among the rarest dinosaur fossils from Skye are those of theropods, members of the mostly carnivorous group that includes iconic species like *Tyrannosaurus rex* and *Velociraptor*. Most Skye theropod fossils are footprints, made by small-to-mid-sized animals that probably stood about 1.0-2.5 metres tall at the hip. These have been described from several localities in the Lealt Shale, Valtos Sandstone, Duntulm, and Kilmaluag formations (Clark & Barco-Rodriguez 1998; Clark *et al.* 2004, 2005; Marshall 2005; dePolo *et al.* 2018), but provide limited information on the identity of the trackmakers. Bones of these animals are much less common, and thus far the only described theropod body fossils are a single tooth and a caudal vertebra, found separately but described together by Brusatte & Clark (2015), and part of a fragmentary theropod tooth described by Wills *et al.* (2014). A handful of teeth that have been

58 alluded to in the literature or in specimen lists are not yet described (e.g., Evans & Waldman
59 1996).

60 We here augment the patchy theropod record of Skye by describing two new isolated
61 teeth, one of a small individual from the Valtos Sandstone and another of a larger theropod
62 from the Lealt Shale, discovered in recent years during fieldwork conducted by the PalAlba
63 group of collaborative Scottish institutions (Fig. 1). We use x-ray computed microtomographic
64 (μ CT) scanning to visualize and measure the teeth in detail. Comprehensive new datasets of
65 theropod tooth measurements and cladistic characters of the dentition allow us to identify to
66 which theropod groups they most likely belonged. We also use these new analyses to revisit
67 the interpretation and classification of the most complete and best-preserved theropod tooth
68 previously described from Skye, the specimen described by Brusatte & Clark (2015). Our
69 results show that at least one, but probably several, species of theropod were present in Jurassic
70 Skye, belonging to one or several clades of basal avetheropods (i.e., ceratosaurs,
71 megalosauroids, or allosauroids).

72

73 **Anatomical Abbreviations**

74 **AL**, apical length; **CA**, crown angle; **CBL**, crown base; **CBR**, crown base ratio; **CBW**, crown
75 base width; **CH**, crown height; **CHR**, crown height ratio; **CTU**, crown transverse undulation
76 density; **DA**, distoapical denticle density; **DAVG**, average distal denticle density; **DB**,
77 distobasal denticle density; **DC**, distocentral denticle density; **DDT**, dentine thickness distally;
78 **DLAT**, dentine thickness labially; **DLIT**, dentine thickness lingually; **DMT**, dentine thickness
79 mesially; **DSDI**, denticle size density index; **FABL**, fore-aft basal length; **LAF**, number of
80 flutes on the labial surface of a crown; **LIF**, number of flutes on the lingual surface of a crown;
81 **MA**, mesioapical denticle density; **MAVG**, average mesial denticle density; **MB**, mesio-basal
82 denticle density; **MC**, mesiocentral denticle density; **MCE**, mesial carina extent; **MCL**, mid-

83 crown length; **MCR**, mid-crown ratio; **MCW**, mid-crown width; **MDE**, mesiobasal denticles
84 extent.

85

86 **Institutional Abbreviations**

87 **AMNH**, American Museum of Natural History, New York City, USA; **BP**, Evolutionary
88 Studies Institute (formerly “Bernard Price Institute for Palaeontological Research”), University
89 of the Witwatersrand, Johannesburg, South Africa; **CAGS**, Chinese Academy of Geological
90 Sciences, Beijing, China; **DMNH**, Perot Museum of Nature and Science, Dallas, Texas, USA;
91 **FMNH**, Field Museum of Natural History, Chicago, USA; **GLAHM**, The Hunterian,
92 University of Glasgow, Glasgow, Scotland, UK; **IVPP**, Institute for Vertebrate Paleontology
93 and Paleoanthropology, Beijing, China; **JME**, Jura Museum Eichstätt, Eichstätt, Germany;
94 **MACN**, Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia,’ Buenos Aires,
95 Argentina; **MLP**, Museo de La Plata, La Plata, Argentina; **MNHN**, Muséum national
96 d’Histoire naturelle, Paris, France; **MPC-D**, Institute of Paleontology and Geology, Mongolian
97 Academy of Sciences (formerly IGM), Ulaanbaatar, Mongolia; **MUCPv**, Museo de la
98 Universidad Nacional del Comahue, Neuquén, Argentina; **NCSM**, North Carolina Museum of
99 Natural Sciences, Raleigh, USA; **NHMUK PV**, Natural History Museum, London, UK; **NMS**,
100 National Museums of Scotland, Edinburgh, U.K.; **PVL**, Fundación ‘Miguel Lillo,’ San Miguel
101 de Tucumán, Argentina; **PVSJ**, Museo de Ciencias Naturales, Universidad Nacional de San
102 Juan, San Juan, Argentina; **RTMP**, Royal Tyrrell Museum of Palaeontology, Drumheller,
103 Alberta, Canada; **UMNH**, Natural History Museum of Utah, University of Utah, Salt Lake
104 City, USA; **USNM**, United States National Museum Vertebrate Paleontology, National
105 Museum of Natural History, Washington, District of Columbia, USA; **YPM**, Yale Peabody
106 Museum of Natural History, Yale, Connecticut, USA.

107

Materials and Methods

Computed microtomography scanning

The two teeth are catalogued at National Museums Scotland: the large Lealt specimen as NMS G.2018.17.1 and the small Valtos specimen as NMS G.2018.17.2. We subjected both teeth to X-ray computed microtomography (μ CT) scanning at the School of GeoSciences, University of Edinburgh. Data for NMS G.2018.17.1 and NMS G.2018.17.2 were acquired at peak energies of 130 keV and 70 keV, respectively, each filtered with a 0.3 mm thick Al energy filter. Reconstruction of the scans (both comprising 2000 projection images) used Octopus v8.9 software (Vlassenbroek *et al.* 2010) to yield tomographic slices with a geometric resolution of 68 μ m for NMS G.2018.17.1 and 20 μ m for NMS G.2018.17.2. We used the μ CT slices to construct 3D digital models of both teeth using Mimics 19.0 (Materialize N.V. 2014) and digitally measured them for standard variables (see below). We confirmed these measurements, and assessed other details of the morphology, by examining the teeth under a binocular microscope.

Comparative methodology and terminology

For both teeth, we took up to six measurement variables (i.e., CBL, CH, MA, MC, DC, DA; Table 1) on the crowns, either physically on the specimens with calipers or, for those measurements of portions of the teeth still obscured by matrix, digitally using the models in Mimics 19.0 and calipers. We estimated values of CBL and AL in NMS G.2018.17.1 based on the curvature of the mesial profile. We added these measurements to a comparative dataset, which includes information on the dentition of 155 non-avian theropod species-level taxa,

133 among which 118 were examined first hand in 35 collections in Argentina, France, Belgium,
134 Germany, Italy, Portugal, Qatar, Switzerland, the United Kingdom, South Africa, China,
135 Canada and the USA by C. Hendrickx (Supplementary Appendix 1). In constructing this
136 dataset, C. Hendrickx used an AM411T-Dino-Lite Pro digital microscope to observe denticles,
137 crown ornamentations, enamel texture and small teeth. We followed the dental nomenclature
138 and method proposed by Hendrickx *et al.* (2015a) to describe each tooth comprehensively.
139 Morphometric and anatomical terms and abbreviations follow those defined by Smith *et al.*
140 (2005) and Hendrickx *et al.* (2015a). The terminology of anatomical orientations follows the
141 recommendations of Smith & Dodson (2003) and Hendrickx *et al.* (2015a). We also use the
142 specimens observed to construct the dataset to make qualitative comparisons with the Skye
143 teeth in the descriptive section.

144

145 *Cladistic analysis*

146

147 In order to explore their phylogenetic affinities, we scored NMS G.2018.17.1 and NMS
148 G.2018.17.2 separately into an updated version of the dentition-based cladistic data matrix of
149 Hendrickx & Mateus (2014a). The data matrix includes 145 discrete characters scored across
150 95 genus-level operational taxonomic units (OTUs) phylogenetically bracketed between the
151 basal sauropodomorph *Eoraptor lunensis* (Serenó *et al.* 1993, 2013) and the basal avialan
152 *Archaeopteryx lithographica* (Meyer 1861; Howgate 1984; Rauhut 2014; Rauhut *et al.* 2018;
153 Supplementary Appendix 2). We also included a third theropod tooth from the Jurassic of the
154 Isle of Skye, GLAHM 125390a, previously described by Brusatte & Clark (2015), in the data
155 matrix. Because it is not clear if the three Skye teeth are mesial or lateral teeth, we scored each
156 one as a mesial tooth for mesial characters, then separately as a lateral crown for lateral
157 characters, and then conducted multiple phylogenetic analyses. We performed these cladistic

158 analyses using TNT 1.1 (Goloboff *et al.* 2008) and a positive constraint (force + command)
159 based on a backbone topology, setting the three Skye teeth as floating OTUs (Supplementary
160 Appendix 2). The backbone tree topology was based on the results obtained by the following
161 analyses: Müller *et al.* (2018) in their fifth analysis (i.e., analysis conducted on the data matrix
162 of Baron *et al.* [2017] using Langer *et al.*'s [2017] modifications) for non-averostran theropods;
163 Rauhut & Carrano (2016) and Wang *et al.* (2017) for Ceratosauria; Carrano *et al.* (2012) and
164 Rauhut *et al.* (2016) for non-coelurosaurian tetanurans; Brusatte & Carr (2016) for
165 Tyrannosauroidae; and Cau *et al.* (2017), in part, based on the dataset of Brusatte *et al.* (2014),
166 for non-tyrannosauroid coelurosaurs. The analyses were conducted using a combination of
167 tree-search algorithms: Wagner trees, TBR branch swapping, sectorial searches, Ratchet
168 (perturbation phase stopped after 20 substitutions), and Tree Fusing (5 rounds), until 100 hits
169 of the same minimum tree length were achieved. The best trees obtained were subjected to a
170 final round of TBR branch swapping (i.e., xmult = hits 100 rss fuse 5 ratchet 20 followed by
171 the bb commands).

172

173

Discriminant analysis

174

175 In order to use measurement data to predict their optimal classifications into major theropod
176 groups, we included NMS G.2018.17.1 and GLAHM 125390a in a quantitative dataset (based
177 on Hendrickx *et al.* 2015b) that we subjected to discriminant function analysis (DFA). NMS
178 G.2018.17.2, consisting of the tip of a crown, was not included in the DFA given that only a
179 single variable (DA) was measurable.

180

181

182

Hendrickx *et al.*'s (2015b) dataset initially included 11 measurements (i.e., CBL, CBW,
CH, AL, CBR, CHR, MCL, MCW, MCR, MC, and DC—see 'Anatomical Abbreviations'
above for definitions) for 995 teeth belonging to 62 non-avian theropod taxa. The dataset

183 combines morphometric data collected by Smith & Lamanna (2006) and Larson & Currie
184 (2013) that incorporate measurements by Smith (2005), Sankey *et al.* (2002), and Longrich
185 (2008) (see Hendrickx *et al.* (2015b) and references therein). We supplemented Hendrickx *et*
186 *al.*'s (2015b) dataset with measurements provided by Longrich *et al.* (2017) for *Chenanisaurus*,
187 Malafaia *et al.* (2017a,b) for *Torvosaurus*, Richter *et al.* (2013) for an indeterminate
188 Spinosaurinae, Currie & Azuma (2006) for *Fukuiraptor*, Hocknull *et al.* (2009) and White *et*
189 *al.* (2015) for *Australovenator*, Gerke & Wings (2016) for *Proceratosaurus*, Zanno *et al.*
190 (2016) for *Eshanosaurus*, Evans *et al.* (2013) for *Acheroraptor*, and Gianechini *et al.* (2011)
191 for *Buitreraptor*. In all, we added 257 teeth belonging to 39 taxa to Hendrickx *et al.*'s (2015b)
192 dataset, based on first hand measurements of the crowns following the methodology of
193 Hendrickx *et al.* (2015a).

194 The final dataset (here entitled 'whole dataset') includes 15 measurements (i.e., CBL,
195 CBW, CH, AL, CBR, CHR, MCL, MCW, MCR, MSL, LAF, LIF, CA, MDL, DCL) for 1,291
196 teeth belonging to 75 taxa (i.e., 71 species and four indeterminate family-based taxa),
197 representing the most taxon-rich theropod tooth dataset currently available (Supplementary
198 Appendix 1). New measurements in this dataset, relative to Hendrickx *et al.* (2015b), include
199 the extension of the denticulate mesial carina (= mesial serrated carina length: MSL), the crown
200 angle (CA), and the number of flutes on the labial (LAF) and lingual (LIF) surfaces of the
201 crown. We used MDL and DCL instead of the MC and DC metrics of Smith *et al.* (2015) and
202 Hendrickx *et al.* (2015b), to ensure that the dataset mostly includes metric-based variables.
203 Likewise, the variables CA, MCL and DCL were not size-corrected, because the crown angle
204 does not change with tooth dimension and because denticle size varies independently from
205 crown height and thickness. All variables were log-transformed to approach a normal
206 distribution (Samman *et al.* 2005; Smith 2005; Larson & Currie 2013) and a log(x+1)
207 correction was applied to LAF and LIF to account for the absence of flutes on the crown. This

208 formula was also used by Gerke & Wings (2016) for MC and DC to account for unserrated
209 carinae. Nevertheless, a crown without denticles should not be morphometrically closer to
210 those with a low number of denticles (i.e., 5 or 6 denticles per five mm, as present in
211 *Tyrannosaurus* or *Torvosaurus*). This is, in fact, the opposite of what we would expect, because
212 theropods with unserrated teeth appear to evolve from taxa with many minute denticles (n.b.,
213 Parvicursorinae and Caudipteridae with unserrated teeth evolved from *Haplocheirus* and
214 *Incisivosaurus*-like theropods, respectively, with a large number of minute denticles on their
215 carinae; C. H. pers. obs.). As a result, an arbitrary value of 100 denticles per five mm was used
216 for unserrated carinae based on the fact that taxa that possess both denticulated and unserrated
217 teeth in the same jaw (e.g., *Compsognathus*, *Aorun*, *Haplocheirus*, *Incisivosaurus*; MNHN
218 CNJ79, IVPP V15709; IVPP V14988; IVPP V13326) typically bear more than ten denticles
219 per mm on the carinae.

220 We performed six discriminant function analyses (DFAs) on partitions of our dataset.
221 In all cases, only non-ratio variables and taxa that could be assessed for at least four
222 measurement variables were used in our DFAs. A first DFA on the whole dataset used twelve
223 variables (i.e., CBL, CBW, CH, AL, MCL, MCW, MSL, LAF, LIF, CA, MDL, and DDL).
224 Because different authors have measured theropod crowns in slightly different ways (CBL and
225 CH specially; see Gerke & Wings, 2016), we performed a second DFA on a dataset (here
226 entitled ‘personal dataset’) restricted to our own measurements. Our personal dataset includes
227 550 teeth belonging to 71 taxa gathered into 20 groups (i.e., basal-most Theropoda, non-
228 averostran Neotheropoda, non-abelisauroid Ceratosauria, Noosauridae, Abelisauridae, non-
229 megalosaurian Megalosauroidea, Megalosauridae, Spinosauridae, Metriacanthosauridae,
230 Allosauridae, Neovenatoridae, Carcharodontosauridae, basal Coelurosauria, non-
231 tyrannosaurid Tyrannosauroidea, Tyrannosauridae, Compsognathidae, Therizinosauria,
232 Oviraptorosauria, Dromaeosauridae, Troodontidae). Given the large size of NMS G.2018.17.1,

233 a third and fourth DFA were conducted on the whole dataset and our own dataset, but restricted
234 to taxa with large-sized crowns (i.e., CH > 20 mm). These two datasets include 701 and 375
235 teeth belonging to 51 and 44 large-sized theropod taxa, respectively. We finally performed fifth
236 and sixth DFAs based on the datasets of Smith *et al.* (2005), using the variables CBL, CBW,
237 CH, AL, CA, CA2, MC, DC, MAVG, DAVG and DAVG2, and Gerke & Wings (2016), using
238 CBW, CH, AL, MC, DC and CBL or CHR. DFAs were conducted in PAST v3.19 (Hammer et
239 al. 2001) with the Discriminant analysis (LDA) function. NMS G.2018.17.1 and GLAHM
240 125390a were considered as the unknown taxon in each analysis and classified at genus or
241 group-level.

242

243 **Results**

244

245 *Cladistic analysis*

246

247 The cladistic analysis of the dentition-based data matrix (Supplementary Appendix 2) with
248 NMS G.2018.17.1 as the floating OTU yielded twelve most parsimonious trees (MPTs) when
249 scored as a mesial tooth (Consistency Index (CI) = 0.212; Retention Index (RI) = 0.461; Length
250 = 1211) and five most parsimonious trees when scored as a lateral tooth (CI = 0.212; RI =
251 0.461; Length = 1211). Scored as a mesial crown, NMS G.2018.17.1 occupied various
252 positions among non-abelisauroid Ceratosauria and Megalosauridae, or as the basal-most
253 Tetanurae, Megalosauroidea or Avetheropoda. Scored as a lateral tooth, it was placed among
254 Ceratosauria, as the basal-most taxon of the clades *Berberosaurus* + Ceratosauridae or
255 Abelisauroidea, among Megalosauroidea, closely related to *Monolophosaurus* or *Sciurumimus*,
256 or as the basal-most Allosauroidea (Figure 2).

281 Troodontidae (Appendix 4). However, we note that the most common assignments for both
282 teeth are within the non-coelurosaurian groups of Ceratosauria and Allosauroidea (Table 1).

283

284 **Systematic Palaeontology**

285

286 Dinosauria Owen 1842

287 Saurischia Seeley 1887

288 Theropoda Marsh 1881

289 Neotheropoda Bakker 1986

290 Gen. and sp. indet.

291 (Fig. 2)

292

293 *Material.* NMS G.2018.17.2, an incomplete isolated tooth preserving part of the crown apex.

294 The apical-most and basal parts of the crown, as well as the root and most of the lingual portion

295 of the crown apex, are missing (Fig. 2K-P). The outline of the tip is visible as an impression in

296 the matrix. The labial surface is exposed from the matrix, and both mesial and distal edges are

297 visible. Details of the hidden surfaces are observable in the CT scans (Fig. 2N-R). The labial

298 surface is well preserved in most places, but the base of the preserved portion of the crown is

299 highly fractured.

300

301 *Provenance.* The tooth was discovered by T. Challands in an ex-situ block of the Middle

302 Jurassic Valtos Sandstone Formation at Brothers' Point (Rubha nam Brathairean), NG

303 573513.20N 692.98W.

304

305 *Description.* NMS G.2018.17.2 is the apex of a medium-size crown, likely more than 15
306 millimetres in apicobasal height (Fig. 2). Its key measurements are listed in Supplementary
307 Appendix 1. The crown is nearly triangular in shape, with a slight distal recurvature. The mesial
308 edge is weakly convex and the distal edge is ever so slightly concave. The labial side of the
309 crown apex is asymmetrically convex in apical view; i.e., the surface is gently convex on the
310 distal two-thirds of the crown and strongly convex on the mesial third (Fig. 1Q). The distal
311 carina is serrated along its entire length, whereas the mesial carina is smooth and lacks
312 serrations (Fig. 1Q, P). The distal carina is strongly labially displaced and appears to extend
313 closer to the labial surface basally (Fig. 1Q, O). We counted 20 denticles per five millimeters
314 on the preserved portion of the distal carina. The distal denticles are labiolingually elongated,
315 perpendicular to the distal margin, and separated by broad interdenticular spaces. The external
316 margin of each denticle is symmetrically to asymmetrically convex, but not apically hooked.
317 No interdenticular sulci extend from between the denticles. The external enamel surface is
318 smooth and lacks any substantial ornamentation, texturing, ridges, grooves, flutes, or
319 undulations.

320

321 *Identification.* NMS G.2018.17.2 is assigned to a non-sauropodomorph saurischian based on
322 the finger-like shape of its distal denticles, the strongly labially deflected distal carina and the
323 presence of an unserrated mesial carina. To our knowledge, the teeth of ornithischians,
324 sauropodomorphs, marine reptiles, pterosaurs and crocodylomorphs do not share such
325 morphology, a combination of unserrated mesial carina, mesiodistally elongated finger-like
326 distal denticles and broad interdenticular sulci has never been observed in any of these clades,
327 to our knowledge.

328 Based on the large size of the basal distal denticles NMS G.2018.17.2 is likely only a
329 part of the crown apex of a tooth. In non-sauropodomorph saurischians, the mesial and distal

330 denticles typically decrease in mesiodistal height and apicobasal width towards the base of the
331 crown (Farlow et al. 1991). Only some teeth of some theropods (e.g., *Noasaurus*, *Juravenator*,
332 *Microraptor* and *Sinusoasus*; PVL 4061; JME Sch 200; CAGS 20-7-004; IVPP V11527) have
333 the same denticle density at the basal-most and central parts of the distal carinae. However,
334 their basal-most denticles are always apicobasally subrectangular and not mesiodistally
335 elongated as in NMS G.2018.17.2. Given that the preserved portion of the crown of NMS
336 G.2018.17.2 is ~7 mm in height, and based on the size of the denticles, the crown height was
337 likely higher than 15 millimetres. Consequently, accurate measurements are not possible for
338 crown height (CH), crown-base length and width (CBL and CBW), and crown-compression
339 and elongation (CBR and CHR). This makes it more difficult for the quantitative analyses to
340 robustly identify which clade this tooth belonged to.

341 Nevertheless, NMS G.2018.17.2 displays four important features that give insight into
342 its affinities: labiolingually elongated distal denticles perpendicular to the distal margin, a
343 broad interdenticular space separating the distal denticles, a strongly labially deflected distal
344 carina and an unserrated mesial carina.

345 The presence of labiolingually elongated, finger-like distal denticles with
346 symmetrically convex external margins exclude an ornithomimosaur, alvarezsaurid,
347 therizinosaurid, oviraptorosaur, troodontid, or avialan affinity for NMS G.2018.17.2. Many
348 members of these clades lack serrated teeth, but when such teeth are present, they have either
349 many more than 20 denticles per 5 mm on the carinae (e.g., *Falcarius*, *Incisivosaurus*, and
350 *Sinusoasus*; UMNH VP 14545; IVPP V13326; IVPP V11527) or apically inclined/hooks
351 denticles (e.g., therizinosauroids and some derived troodontids; Currie et al. 1990; Currie &
352 Dong 2001; Zanno et al. 2016).

353 Broad interdenticular spaces like those in NMS G.2018.17.2 are also seen in non-
354 averostran theropods (e.g., *Herrerasaurus*, *Dracoraptor*; PVSJ 407; BP/1/5243), non-

355 abelisauroid ceratosaurs (e.g., *Ceratosaurus*, *Genyodectes*; UMNH VP 5278; MLP 26-39),
356 non-megalosaurian megalosauroid (e.g., *Marshosaurus*, *Monolophosaurus*; DMNH 3718;
357 IVPP 84019), allosauroids (e.g., *Sinraptor*, *Allosaurus*, *Acrocanthosaurus*; IVPP V10600;
358 USNM 8335; UMNH VP 6499; NCSM 14345), tyrannosauroids (e.g., *Guanlong*,
359 *Gorgosaurus*; IVPP V14531; RTMP 1991.36.500) and some dromaeosaurids such as
360 *Bambiraptor* (AMNH 30556) and *Deinonychus* (YPM 5232). However, this space is narrow
361 in Abelisauroidea and Spinosauridae, and we consider it unlikely that NMS G.2018.17.2
362 belongs to one of these clades.

363 Teeth with a strongly labially displaced distal carina are present in the mesial and/or
364 lateral dentition of some non-averostran saurischians (e.g., *Ischisaurus*; MACN 18.060), non-
365 abelisaurid ceratosaurs (e.g., *Genyodectes*, *Masiakasaurus*; MLP 26-39, FMNH PR 2476),
366 piatnitzkysaurids (e.g., *Piatnitzkysaurus*; MACN 895), *Monolophosaurus* (IVPP 84019),
367 allosauroids (e.g., *Acrocanthosaurus*, *Giganotosaurus*; NCSM 14345, MUCPv-CH-1),
368 tyrannosauroids (e.g., *Proceratosaurus*, *Alioramus*; NHMUK PV R.4860, MPC-D 100-1844),
369 and dromaeosaurids (e.g., *Sinornithosaurus*, *Linheraptor*; IVPP V12811, V16923). A broad
370 interdenticular space and a strongly labially displaced distal carina appear to be absent in
371 Abelisauridae, Megalosauridae and Spinosauridae, so NMS G.2018.17.2 most likely does not
372 belong to these clades.

373 Finally, the unserrated mesial carina, combined with a denticulated distal carina, is a
374 condition restricted to the mesial and/or lateral dentition of non-neotheropod theropods (e.g.,
375 *Herrerasaurus*, *Ischisaurus*; PVSJ 407, PVSJ 605), noasaurids (e.g., *Masiakasaurus*; FMNH
376 PR 2476), the juvenile megalosaurid *Sciurumimus* (Rauhut et al. 2012), megaraptorans (e.g.,
377 *Megaraptor*; Porfiri et al. 2014), some basal tyrannosauroids (e.g., *Dilong*; IVPP V14242)
378 compsognathids (e.g., Currie & Chen 2001; Peyer 2006; Dal Sasso & Maganuco 2011), basal
379 maniraptoriforms (e.g., *Aorun*, *Ornitholestes*, *Haplocheirus*; AMNH 619; Choiniere et al.

380 2014*b, b*), and many dromaeosaurids (e.g., Currie et al. 1990; Norell et al. 2006; Godefroit et
381 al. 2008) and troodontids (e.g., Currie 1987; Currie and Dong 2001; Norell et al. 2009). These
382 are therefore all candidate clades for NMS G.2018.17.2.

383 The cladistic analysis indicates that NMS G.2018.17.2 may belong to a non-
384 neotheropod saurischian, a noasaurid closely related to *Limusaurus* or a dromaeosaurid. We
385 argue that the first clade is unlikely based on the Middle Jurassic age of NMS G.2018.17.2.
386 Among non-sauropodomorph saurischians, neotheropods such as non-spinosaurid
387 megalosauroids are the only clade present in the Middle Jurassic with a dental morphology
388 similar to that of NMS G.2018.17.2 (Hendrickx et al. 2015*a, b*; Rauhut et al. 2016). To our
389 knowledge, no Jurassic sauropodomorphs have teeth with finger-like denticles and a strongly
390 labially deflected mesial carina. Furthermore, based on current theropod phylogenies (e.g.,
391 Müller et al. 2018; Baron et al. 2017; Wang et al. 2017), non-neotheropod theropods are
392 restricted to the Late Triassic and Early Jurassic.

393 Although Dromaeosauridae might be present in the Middle Jurassic, based on ghost
394 lineages (Hendrickx et al. 2015), a dromaeosaurid affinity for NMS G.2018.17.2 may be
395 unlikely, given that denticles were absent from the teeth of most basal members of the group
396 (Gianechini et al. 2011; Cau et al. 2017). Unserrated teeth are, in fact, likely to be the
397 plesiomorphic condition among the derived clade of bird-like theropods that includes
398 dromaeosaurids and close relatives (Pennaraptora or Paraves), pending the position of
399 scansoriopterygids at the base of Oviraptorosauria or Avialae (Brusatte et al. 2014; Cau et al.
400 2017). We here hypothesize that most, if not all, Middle Jurassic dromaeosaurids, unlike non-
401 maniraptoriform neocoelurosaurs and noasaurids, had unserrated teeth. There have been
402 serrated teeth from Middle Jurassic deposits assigned to dromaeosaurids based on broad
403 resemblance (e.g., Evans & Milner 1994; Metcalf & Walker 1994; Averianov et al. 2005), but

404 these could plausibly belong to non-maniraptoriform theropods with similar dental
405 morphologies, such as basal tyrannosauroids (Rauhut *et al.* 2010).

406 The combination of dental features in NMS G.2018.17.2, the distribution of these
407 features among non-sauropodomorph saurischians, and the results of the cladistic analysis,
408 indicate that NMS G.2018.17.2 may tentatively be attributed to either: 1) a neotheropod
409 theropod other than a member of Abelisauridae, Megalosauria and Maniraptoriformes, or 2)
410 possibly a ceratosaur closely related to Noosauridae.

411

412 Averostris Paul 2002

413 Gen. and sp. indet.

414 (Fig. 2)

415

416 *Material.* NMS G.2018.17.1, an isolated tooth preserving most of the crown but missing the
417 root. The lingual surface of the crown is exposed from the matrix, and both mesial and distal
418 edges are visible. Details of the labial surfaces are observable in the CT scans (Fig. 2F). The
419 lingual surface is well preserved towards the apex, but the base of the crown is highly fractured
420 and much of the enamel layer has been worn away so that the cervix (i.e., the limit between
421 crown and root) cannot be seen (Fig. 2A-B, E). There are no denticles in either the basal two-
422 thirds of the mesial carina or basal one third of the distal carina (Fig. 2A). The reconstructed
423 3D CT model of the tooth shows that the labial surface is more complete than the lingual one.
424 However, the mesial portion and most of the mesiobasal part of the labial surface of the crown
425 are not preserved (Fig. 2F).

426

427 *Provenance.* The tooth was discovered by D. Foffa in an in-situ portion of the Middle Jurassic
428 Lealt Shale Formation exposed as a tidal platform, at Brothers' Point (Rubha nam Brathairean).

429 Much of the labial/lingual side of the tooth was visible on the surface when collected, but the
430 tip of the apex was covered by matrix and later exposed through manual preparation by T.
431 Challands.

432

433 *Description.* NMS G.2018.17.1 is a large (~6 cm in height), ziphodont, and distally recurved
434 crown. Its key measurements are listed in Supplementary Appendix 1. The mesial edge is
435 convex and the distal edge concave in lateral and medial views, whereas the preserved labial
436 and lingual surfaces are symmetrically convex in apical and basal views (Fig. 1I, J). Both
437 mesial and distal carinae are denticulated and extend to the apex, which is crossed by denticles
438 (Fig. 1B, C). The mesial carina is denticulated along its preserved portion, but it is not clear if
439 denticles reached close to the cervix, or terminated at mid-crown. The mesial carina appears to
440 curve slightly mesiolingually towards the base of the crown, as seen in mesial (Fig. 1I) and
441 apical (Fig. 1G) views. The distal carina is apicobasally straight all along the crown, in distal
442 view (Fig. 1H). Although the distal carina appears to be deflected lingually due to the large
443 missing portion of the lingual surface of the crown (Fig. 1I), the carina is centrally positioned
444 on the crown in apical view (Fig. 1I). The distal denticles are better preserved than those on
445 the mesial carina, where denticle apices are largely eroded. We counted 11 denticles per five
446 millimeters on the mesiocentral, distocentral and distoapical portions of the carinae, and 12
447 denticles per five millimeters in the apical-most part of the mesial carina. There is, therefore,
448 no size discrepancy between mesial and distal denticles (i.e., Denticle Size Density Index
449 (DSDI) close to 1; Rauhut & Werner 1995). The distal denticles are weakly mesiodistally
450 subrectangular in the central portion of the carina and subquadrangular more apically. The
451 external margins of the preserved distal denticles are symmetrically convex. There are broad
452 interdenticular spaces between the distal denticles and no interdenticular sulci. The tooth
453 appears to be fairly thin in cross section, although accurate measurements are not possible due

454 to the heavy damage incurred on the exposed surface. There is no strong ornamentation on the
455 exposed enamel surfaces, nor those visible in the CT scans.

456

457 *Identification.* NMS G.2018.17.1 is identified as a theropod based on a combination of features
458 that, to our knowledge, are restricted to theropods among Middle Jurassic tetrapods: large size
459 (~6 cm in height), distally recurved crown, both carinae bearing denticles (with fewer than 15
460 denticles per 5 mm on both carinae), and weakly linguallly twisted mesial carina.

461 The discriminant function analyses place NMS G.2018.17.1 outside of the
462 morphospace envelope for all other theropod teeth in our dataset, an unexpected finding.
463 However, this is likely due to the limited measurement data available for the tooth, particularly
464 the absence of data for crown compression, combined with estimated values for CBW and AL.
465 Therefore, results of the discriminant analyses should be considered as highly tentative. These
466 place NMS G.2018.17.1 in a variety of possible theropod clades, including as a dilophosaurid
467 (*Dilophosaurus*), a non-abelisauroid ceratosaur, a ceratosaurid, an abelisaurid (*Rugops* or
468 *Arcovenator*), a megalosaurid (*Torvosaurus*), a neovenatorid, a carcharodontosaurid, and even
469 a troodontid.

470 NMS G.2018.17.1, however, does possess several important qualitative features that
471 help constrain its most likely identification (Hendrickx *et al.* 2015b; Hendrickx & Mateus
472 2014). Given that NMS G.2018.17.1 is a ziphodont tooth (i.e., it is a distally recurved crown
473 with denticulated mesial and distal carinae) of particularly large size (i.e., ~6 cm), based on our
474 current knowledge it cannot be from a member of Noasauridae, Compsognathidae,
475 Ornithomimosauria, Therizinosauria, Alvarezsauroidea, Oviraptorosauria, Dromaeosauridae,
476 Troodontidae, or Avialae. To our knowledge, members of these clades all bear finely
477 denticulated or unserrated non-ziphodont teeth (i.e., conodont, folioid teeth) or small
478 ziphodont teeth less than five centimetres long apicobasally.

479 Among ziphodont theropods, NMS G.2018.17.1 displays several key features with
480 taxonomic utility, including broad interdenticular spaces between the distal denticles, a
481 centrally positioned distal carina, a weakly lingually twisted mesial carina, fewer than 15
482 mesial and distal denticles, and a DSDI close to one. Broad interdenticular spaces between
483 distal denticles are present in non-averostran theropods, non-abelisauroid ceratosaurs, non-
484 megalosaurian megalosauroid (i.e., Piatnitzkysauridae, *Monolophosaurus* and *Sciurumimus*),
485 most allosauroids and many tyrannosauroids (Hendrickx and Mateus' (2014) datamatrix).
486 Because the crown is relatively compressed labiolingually (i.e., CBR < 0.65) and because the
487 mesial carina neither twists conspicuously mesiolingually nor is strongly displaced lingually,
488 NMS G.2018.17.1 cannot be from the mesial dentition of Ceratosauria, non-
489 carcharodontosaurid Allosauroida (i.e., Metricanthosauridae and Allosauridae) or
490 Tyrannosauroida. Teeth with fewer than 15 denticles per 5 mm are present in ceratosaurs,
491 megalosauroids, allosauroids, and large-sized tyrannosauroids such as tyrannosaurids. Non-
492 averostran theropods other than herrerasaurids seem not to have teeth with fewer than 15
493 denticles per 5 mm on the distal carina (Hendrickx and Mateus' (2014) datamatrix). Finally,
494 with a DSDI close to one, NMS G.2018.17.1 probably does not belong to a piatnitzkysaurid or
495 a basal tyrannosauroid, as most members of these clades have crowns whose mesial denticles
496 are significantly smaller than those on the distal carina (Rauhut et al. 2010).

497 The combination of dental features displayed by NMS G.2018.17.1, suggests that this
498 large crown may belong to the mesial/lateral dentition of a non-noosaurid and non-abelisaurid
499 ceratosaur; to the mesial dentition of a megalosaurid or a basal
500 tetanuran/megalosauroid/avetheropod; or to the lateral dentition of a non-megalosaurian
501 megalosauroid closely related to *Monolophosaurus* or a basal allosauroid. The results of the
502 cladistic analysis, combined with the Middle Jurassic age and northern European provenance
503 of the tooth, suggest that the specimen almost certainly belongs to an averostran theropod, and

504 we favour a non-abelisauroid ceratosaur, a basal megalosauroid closely related to
505 *Monolophosaurus*, a megalosaurid or an allosauroid as most likely. Nonetheless, it is possible
506 that the tooth belongs to another theropod clade with similar tooth morphologies, such as
507 Tyrannosauroida. Middle Jurassic tyrannosauroids have, been identified recently, albeit of
508 small size (Averianov *et al.* 2010; Rauhut *et al.* 2010), so NMS G.2018.17.1 could conceivably
509 belong to this group.

510

511 **Revision of GLAHM 125390a**

512

513 This specimen, GLAHM 125390a, the most complete and well-preserved theropod tooth
514 described from the Isle of Skye, was first reported and thoroughly described by Brusatte &
515 Clark (2015). The shed tooth comes from the Valtos Sandstone, the same formation that yielded
516 NMS G.2018.17.2. However, GLAHM 125390a was found at Valtos, approximately one mile
517 north of Brother's Point, where NMS G.2018.17.2 was discovered. Based on a series of
518 quantitative analyses Brusatte & Clark (2015) referred GLAHM 125390a to Theropoda indet.,
519 suggesting that it most likely belongs to a dromaeosaurid, a megalosaurid, a basal
520 tyrannosauroid or a small-bodied basal coelurosaur.

521 We included GLAHM 125390a within our larger datasets and conducted a series of
522 new DFAs and cladistic analyses. The DFAs on our whole dataset, our dataset of personal
523 measurements, and the datasets of Smith & Lamanna (2006) and Gerke & Wings (2016)
524 classify GLAHM 125390a as either a troodontid, ceratosaurid, neovenatorid or a
525 carcharodontosaurid at the group level. At the taxon level, GLAHM 125390a was assigned to
526 the abelisaurids *Rugops* and *Majungasaurus*, as well as *Ceratosaurus*, *Suchomimus*,
527 *Neovenator* and *Megaraptor*. In the cladistic analysis, GLAHM 125390a is positioned as a

528 dromaeosaurid closely related to *Tsaagan* or as the sister taxon of *Megaraptor* within
529 Megaraptora (when coded as a mesial and lateral tooth, respectively).

530 Brusatte & Clark (2015) also used cladistic analysis and, coding GLAHM 125390a as
531 a lateral tooth, recovered a tree with a large polytomy that differs from the well-resolved tree
532 obtained in this study. This is because the specimen was scored slightly differently in our data
533 matrix, having subtle transverse undulations on the crown, a higher number of distal denticles
534 apically than at mid-crown, and distal denticles perpendicular to the distal margin. The apically
535 inclined distal denticles noted by Brusatte & Clark (2015) are an illusion due to interdenticular
536 sulci that curve basally. The presence of a constriction between the root and crown was coded
537 as unknown in our dataset. Although there is indeed no constriction at the cervix on the distal
538 profile of the crown, the mesiobasal portion is not preserved in GLAHM 125390a, so the
539 presence of a mesial constriction, as seen in most solidont theropods, cannot be ruled out.
540 Finally, interdenticular sulci appear to be particularly well-developed between mid-crown
541 denticles of the distal carina, so that both short and long denticular sulci were scored as present
542 in our data matrix.

543 Brusatte & Clark (2015) identified GLAHM 125390a as belonging to an indeterminate
544 theropod, but the clade can now be narrowed to Neotheropoda. Strongly developed and
545 elongated interdenticular sulci appear to be restricted to non-neocoelurosaur averostrans and
546 therizinosaurids. A therizinosaur affinity is excluded on the basis of the presence of mesiodistally
547 elongated distal denticles perpendicular to the distal margin of the crown, the absence of a
548 convex distal profile of the crown, and a distal constriction between crown and root. However,
549 strongly developed interdenticular sulci may be present in neotheropods, such as
550 dilophosaurids. Similar to the wide interdenticular space (see above), an irregular enamel
551 texture is seen in distantly related clades such as herrerasaurids, abelisauroids, allosaurids,
552 metriacanthosaurids, some tyrannosaurids and most non-dromaeosaurid neocoelurosaurids.

553 Because the status of the mesial denticles and a mesial constriction between root and crown
554 are unknown, and given the limited amount of dental information available and the age of the
555 specimen, GLAHM 125390a is, therefore, referred to an indeterminate neotheropod.

556 Unlike Brusatte and Clark (2015), we are not as confident that GLAHM 125390a
557 belongs to one of three groups (a megalosaurid, a non-tyrannosaurid tyrannosauroid, or a
558 dromaeosaurid). The features do not correspond perfectly to any of these three clades. For
559 instance, the crowns of megalosaurids and non-tyrannosaurid tyrannosauroids all display a
560 braided enamel texture, whereas dromaeosaurids do not seem to have elongated interdenticular
561 sulci between distal denticles to our knowledge. Given the combination of dental features
562 displayed by GLAHM 125390a, it is also possible that the specimen belongs to a ceratosaur
563 (i.e., Ceratosauridae, Abelisauridae, and Noasauridae), or a basal allosauroid (i.e.,
564 Metriacanthosauridae, Allosauridae). It is also possible that it belongs to the same taxon as
565 NMS G.2018.17.1 and/or NMS G.2018.17.2 (see below).

566

567 **Theropod Diversity on Skye**

568

569 How many species are represented by the three teeth described above? This question is difficult
570 to answer conclusively, but there are several lines of evidence. The three teeth all differ from
571 each other, most notably in crown height, distal denticle density, the presence of well-
572 developed interdenticular sulci between distal denticles, the denticulation of the mesial carina,
573 and the position of the distal carina on the distal surface of the crown (i.e., strongly displaced
574 in NMS G.2018.17.2, but centrally positioned in GLAHM 125390a and NMS G.2018.17.1).
575 Whether these differences are taxonomically informative is less clear, because many dental
576 features are ontogenetically dependant (e.g., the size of mesial and distal denticles; Carr and
577 Williamson 2004), and the development of interdenticular sulci and position of the carina on

578 the distal surface are variable along the tooth-row of individuals (e.g., Smith 2005; Benson
579 2009; Reichel 2012; Hendrickx et al. 2015). It could be, therefore, that the differences between
580 the three teeth reflect a combination of ontogenetic and/or individual variation among one or
581 two species, rather than signifying three distinct theropod species.

582 There are two main arguments against the three teeth belonging to the same species:
583 differences in carina denticulation and differences in size. NMS G.2018.17.2 lacks denticles
584 on the mesial carina, whereas NMS G.2018.17.1 and GLAHM 125390a both have a
585 denticulated mesial carina. However, some theropods such as *Coelophysis* (Buckley & Currie
586 2014) and *Ornitholestes* (AMNH 619) have some mesial teeth devoid of a mesial carina,
587 whereas mesial denticles are present in at least some lateral teeth. Thus, this difference alone
588 does not indicate species-level separation.

589 Even more striking, however, is the enormous size difference between the tiny tooth
590 NMS G.2018.17.2 and the other two Skye teeth. It is doubtful that these teeth could belong to
591 individuals of the same general body size, although it is possible that NMS G.2018.17.2 is from
592 an extremely young juvenile and NMS G.2018.17.1 and GLAHM 125390a from more mature
593 individuals. This seems implausible, however, as the adult would be a medium-to-large-bodied
594 theropod, and the vast majority of such species (with teeth longer than 6 cm in adults) exhibit
595 mesial denticles in both mesial and lateral teeth (C. H. pers. obs.). There is only one known
596 exception: tyrannosaurids, in which juveniles of some species lack denticles before acquiring
597 them in adulthood (Carr & Williamson 2004). We cannot completely rule out a single Skye
598 theropod species that underwent a tyrannosaurid-like ontogenetic change in denticle
599 development, but consider it unlikely. The Skye teeth are much older, and from theropods only
600 very distantly related to, the Late Cretaceous tyrannosaurids, which (uniquely among known
601 theropods) underwent extreme ontogenetic changes as they grew from svelte hatchlings into

602 colossal, robust, deep-skulled, incrassate-tooth-bearing, bone-crunching adults (Carr 1999;
603 Brusatte *et al.* 2010).

604 Although we cannot discount the idea that the three Skye teeth belong to the same
605 species, if this were so then this species would have displayed highly unusual ontogenetic
606 variation that is otherwise known in only one clade of highly specialized theropods living ca.
607 100 million years later (tyrannosaurids). The teeth therefore probably reflect at least two
608 species: a smaller taxon represented by NMS G.2018.17.2 and one or more larger taxa
609 represented by NMS G.2018.17.1 and GLAHM 125390a.

610

611

Discussion

612

613 The new teeth described here help to clarify the diversity of theropod dinosaurs on the Isle of
614 Skye. Although these specimens are extremely limited and difficult to assign to theropod
615 groups, at a minimum they support the presence of two different types of theropods inhabiting
616 the deltaic and lagoonal environments of Middle Jurassic Skye.

617 Both new specimens, NMS G.2018.17.1 and NMS G.2018.17.2, can be assigned to
618 neotheropods, based on their size, distal curvature, ziphodont morphology, and serrated edges
619 (along with the previously described GLAHM 125390a). Classifying them into particular
620 theropod groups is more difficult. The cladistic and morphometric (DFA) analyses provide
621 conflicting results, which are perhaps not surprising given that the teeth are incompletely
622 preserved, can be assessed for only a small proportion of the measurements or characters in the
623 analyses, and cannot even be identified with confidence as mesial or lateral teeth. That being
624 so, by considering the cladistic and DFA results alongside a survey of key qualitative
625 characteristics of the teeth, we can narrow down the most likely classifications for each tooth
626 among Neotheropoda.

627 For NMS G.2018.17.2, we conclude that it belonged to a small-bodied individual (i.e.,
628 a small-sized species or a juvenile of a larger taxon) and was probably a member of one of a
629 few major clades (i.e., coelophysoid, ceratosaur, piatnitzkysaurid, allosauroid, tyrannosauroid).
630 NMS G.2018.17.1, on the other hand, belonged to a larger animal that is probably either a non-
631 abelisauroid ceratosaur, a megalosauroid, or an allosauroid. Our reanalysis of GLAHM
632 125390a suggests that this specimen most likely belonged to a non-maniraptoriform theropod,
633 possibly a megalosauroid or an allosauroid, and possibly even the same species as NMS
634 G.2018.17.1 (and, although unlikely, the same species as NMS G.2018.17.2).

635 The teeth from Skye are small clues that fit into a growing understanding of dinosaur
636 evolution during the Middle Jurassic. This was a critical time in theropod history, as the more
637 uniform faunas of the Late Triassic and Early Jurassic gave way to new species of different
638 sizes, morphologies, and behaviours. These included apex predator megalosauroids and
639 allosauroids that grew to over a ton in body mass, primitive human-sized tyrannosauroids that
640 established the lineage that would eventually produce *T. rex*, and derived maniraptorans that
641 shrank in size, developed wings, and evolved into birds (reviews in: Brusatte 2012; Hendrickx
642 et al. 2015c; Benson 2018). At present, it is difficult to assign the Skye teeth to any of these
643 groups, although the teeth and footprints from Skye hint at a tantalizing diversity of theropods,
644 ranging from small to large size, that filled various niches in the Middle Jurassic food chain,
645 probably both on land and in the lagoons. Further discoveries of more complete skeletal
646 remains on Skye may reveal more about the identities, behaviours, appearances, and
647 evolutionary importance of these animals, which will have huge potential for understanding
648 keystone events in dinosaur evolution.

649

650

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651

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666

667

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955

Figures

956

957

958

959 **Fig. 1.** Map of the Isle of Skye (Scotland), with a box denoting Brothers' Point (Rubha nam
960 Brathairean), where the two theropod teeth described here (NMS G.2018.17.1 and NMS
961 G.2018.17.2) were discovered. Close up map of Brother's Point, with major geological units
962 indicated (B).

963

964 **Fig. 2.** Isolated neotheropod teeth from the Middle Jurassic of the Isle of Skye, Scotland. (A-
965 J), Crown of NMS G.2018.17.1 from the Lealt Shale Formation in A, E lingual; B, linguodistal;
966 F, labial; G, mesial; H, distal; I, apical; and basal views; with close up on C, the apical portion
967 of the mesial carina in mesial view; and D, the distoapical denticles in linguodistal view. (K-
968 R), Crown apex of NMS G.2018.17.2 from the Valtos Sandstone Formation in K, M, labial; N,
969 lingual; O, distal; P, mesial, Q, apical; and R, basal views; with L, close up on distoapical
970 denticles in labial view. A-D, K-L are photographs; E-J, M-R are CT scan renderings.
971 Abbreviations: dca, distal carina; mca, mesial carina. All scale bars equal 1 cm; top scale bars
972 for A-J (except C,D); bottom scale bar for K-R (except L).

973

974 **Fig. 3.** Classification of NMS G.2018.17.1, NMS G.2018.17.2 and GLAHM 125390a coded
975 as lateral crowns and analysed separately in the cladistic analysis performed with the
976 datamatrix of 145 dental characters using TNT 1.1 and a constrained tree (ci = 0.21; ri = 0.46).
977 For details of the constraint, please see the main text. For silhouette acknowledgements, see
978 Appendix 5.

979

980 **Fig. 4.** Results of the discriminant function analysis (DFA) performed at the group-level on our
981 personal datasets of 550 teeth belonging to 71 taxa gathered into 20 groupings along the first

982 two canonical axes of maximum discrimination in the dataset (Eigenvalue of Axis 1 = 14.113,
983 which accounts for 59.27% of the total variation; Eigenvalue of Axis 2 = 4.794, which accounts
984 for 20% of the total variation). 59.27% of the theropod specimens were correctly classified in
985 their respective groups, with NMS G.2018.17.2 and GLAHM 125390a being classified as non-
986 abelisauroid Ceratosauria and Troodontidae, respectively. The absence of mesial and distal
987 denticles was considered as inapplicable in this analysis. For silhouette acknowledgements, see
988 Appendix 5.

Datasets	NMS G.2018.17.1		GLAHM 125390a	
	Clade level	Taxon level	Clade level	Taxon level
Whole dataset	Neovenatoridae	<i>Rugops</i>	Troodontidae	<i>Rugops</i>
Whole dataset (no denticles = ?)	Troodontidae	<i>Rugops</i>	Troodontidae	<i>Majungasaurus</i>
Personal dataset	Neovenatoridae	<i>Megaraptor</i>	Troodontidae	<i>Megaraptor</i>
Personal dataset (no denticles = ?)	Non-abelisauroid Ceratosauria	<i>Arcovenator</i>	Troodontidae	<i>Majungasaurus</i>
Whole dataset with large teeth	Non-abelisauroid Ceratosauria	<i>Torvosaurus</i>		
Whole dataset with large teeth (no denticles = ?)	Non-abelisauroid Ceratosauria	<i>Arcovenator</i>		
Personal dataset with large teeth	Non-abelisauroid Ceratosauria	<i>Torvosaurus</i>		
Personal dataset with large teeth (no denticles = ?)	Non-abelisauroid Ceratosauria	<i>Arcovenator</i>		
Smith and Lamanna's (2006) dataset (No ratios, with CA2, DAVG2)	Carcharodontosauridae	<i>Dilophosaurus</i>	Ceratosauridae	<i>Ceratosaurus</i>
Smith and Lamanna's (2006) dataset (No ratios and no CA2, DAVG2)	Ceratosauridae	<i>Carcharodontosaurus</i>	Carcharodontosauridae	<i>Suchomimus</i>
Gerke and Wings' (2016) dataset (with CHR but not CBL)	Ceratosauridae	<i>Carcharodontosaurus</i>	Neovenatoridae	<i>Neovenator</i>
Gerke and Wings' (2016) dataset (with CBL, no ratios)	Metriacanthosauridae	<i>Carcharodontosaurus</i>	Neovenatoridae	<i>Neovenator</i>
Datasets	Reclassification Rate (RR)		Clade level	
	Clade level (%)	Taxon level (%)	Axis 1 (%)	Axis 2 (%)
Whole dataset	62.66	62.2	51.51	19.72
Whole dataset (no denticles = ?)	63.44	60.65	50.31	19.14
My dataset	60.91	60.91	61.03	19.59
My dataset (no denticles = ?)	59.27	61.82	58.85	20.02
Whole dataset with large teeth	60.71	58	38.38	30.53
Whole dataset with large teeth (no denticles = ?)	63.43	58.57	39.2	30.84
Personal dataset with large teeth	59.47	61.47	48.3	27.66
Personal dataset with large teeth (no denticles = ?)	62.13	61.87	56.52	24.31
Smith and Lamanna's (2006) dataset (No ratios, with CA2, DAVG2)	78.49	84.3	55.77	33.54
Smith and Lamanna's (2006) dataset (No ratios and no CA2, DAVG2)	78.2	84.88	56.29	33.99
Gerke and Wings' (2016) dataset (with CHR but not CBL)	73.73	86.57	51.46	38.12
Gerke and Wings' (2016) dataset (with CBL, no ratios)	74.33	85.97	51.26	38.01

992 **Table 1.** Group and taxon-level identifications of NMS G.2018.17.1 and GLAHM 125390a
993 from the various discriminant function analyses (DFAs) conducted on different datasets, with
994 reclassification rate and percentage of variance for the two principal axes for each analysis.