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2	New theropod dinosaur teeth from the Middle Jurassic of the Isle of Skye, Scotland
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6	
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14	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	(μCT) 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 35 Middle Jurassic remains a largely mysterious time for not only dinosaurs, but also terrestrial 36 ecosystems in general. This is because very few Middle Jurassic localities preserve vertebrate 37 fossils (e.g., Weishampel et al. 2004). One of these rare places is the Isle of Skye in Scotland, 38 where deltaic and lagoonal sedimentary rocks of the Great Estuarine Group (Bathonian, ca. 39 168-166 million years old; Harris & Hudson 1980; Hudson 1993) are exposed. These yield 40 41 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; 42 Barrett 2006; Wills et al. 2014; Brusatte & Clark 2015; Brusatte et al., 2015; Clark and Gavin, 43 44 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; 45 Anquetin et al. 2009; Wills et al. 2014; Young et al. 2016; Panciroli et al. 2017a, b, 2018; Yi et 46 al. 2017). 47

Among the rarest dinosaur fossils from Skye are those of theropods, members of the 48 mostly carnivorous group that includes iconic species like Tyrannosaurus rex and 49 Velociraptor. Most Skye theropod fossils are footprints, made by small-to-mid-sized animals 50 that probably stood about 1.0-2.5 metres tall at the hip. These have been described from several 51 52 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 53 limited information on the identity of the trackmakers. Bones of these animals are much less 54 55 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 56 fragmentary theropod tooth described by Wills et al. (2014). A handful of teeth that have been 57

alluded to in the literature or in specimen lists are not yet described (e.g., Evans & Waldman1996).

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

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Anatomical Abbreviations

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

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

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- 86

Institutional Abbreviations

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

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Materials and Methods

Computed microtomography scanning

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The two teeth are catalogued at National Museums Scotland: the large Lealt specimen as NMS 112 G.2018.17.1 and the small Valtos specimen as NMS G.2018.17.2. We subjected both teeth to 113 X-ray computed microtomography (μ CT) scanning at the School of GeoSciences, University 114 of Edinburgh. Data for NMS G.2018.17.1 and NMS G.2018.17.2 were acquired at peak 115 116 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 v8.9 117 software (Vlassenbroek et al. 2010) to yield tomographic slices with a geometric resolution of 118 119 68 µm for NMS G.2018.17.1 and 20µm for NMS G.2018.17.2. We used the µCT slices to 120 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, 121 and assessed other details of the morphology, by examining the teeth under a binocular 122 microscope. 123

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Comparative methodology and terminology

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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,

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

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Cladistic analysis

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

158	analyses using TNT 1.1 (Goloboff <i>et al.</i> 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	Tyrannosauroidea; 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
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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	Hendrickx et al.'s (2015b) dataset initially included 11 measurements (i.e., CBL, CBW,
181	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

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

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

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

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

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
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2.0	
247	The cladistic analysis of the dentition-based data matrix (Supplementary Appendix 2) with
247 248	The cladistic analysis of the dentition-based data matrix (Supplementary Appendix 2) with NMS G.2018.17.1 as the floating OTU yielded twelve most parsimonious trees (MPTs) when
247 248 249	The cladistic analysis of the dentition-based data matrix (Supplementary Appendix 2) with NMS G.2018.17.1 as the floating OTU yielded twelve most parsimonious trees (MPTs) when scored as a mesial tooth (Consistency Index (CI) = 0.212 ; Retention Index (RI) = 0.461 ; Length
247 248 249 250	The cladistic analysis of the dentition-based data matrix (Supplementary Appendix 2) with NMS G.2018.17.1 as the floating OTU yielded twelve most parsimonious trees (MPTs) when scored as a mesial tooth (Consistency Index (CI) = 0.212 ; Retention Index (RI) = 0.461 ; Length = 1211) and five most parsimonious trees when scored as a lateral tooth (CI = 0.212 ; RI =
247 248 249 250 251	The cladistic analysis of the dentition-based data matrix (Supplementary Appendix 2) with NMS G.2018.17.1 as the floating OTU yielded twelve most parsimonious trees (MPTs) when scored as a mesial tooth (Consistency Index (CI) = 0.212 ; Retention Index (RI) = 0.461 ; Length = 1211) and five most parsimonious trees when scored as a lateral tooth (CI = 0.212 ; RI = 0.461 ; Length = 1211). Scored as a mesial crown, NMS G.2018.17.1 occupied various
247 248 249 250 251 252	The cladistic analysis of the dentition-based data matrix (Supplementary Appendix 2) with NMS G.2018.17.1 as the floating OTU yielded twelve most parsimonious trees (MPTs) when scored as a mesial tooth (Consistency Index (CI) = 0.212 ; Retention Index (RI) = 0.461 ; Length = 1211) and five most parsimonious trees when scored as a lateral tooth (CI = 0.212 ; RI = 0.461 ; Length = 1211). Scored as a mesial crown, NMS G.2018.17.1 occupied various positions among non-abelisauroid Ceratosauria and Megalosauridae, or as the basal-most
247 248 249 250 251 252 253	The cladistic analysis of the dentition-based data matrix (Supplementary Appendix 2) with NMS G.2018.17.1 as the floating OTU yielded twelve most parsimonious trees (MPTs) when scored as a mesial tooth (Consistency Index (CI) = 0.212 ; Retention Index (RI) = 0.461 ; Length = 1211) and five most parsimonious trees when scored as a lateral tooth (CI = 0.212 ; RI = 0.461 ; Length = 1211). Scored as a mesial crown, NMS G.2018.17.1 occupied various positions among non-abelisauroid Ceratosauria and Megalosauridae, or as the basal-most Tetanurae, Megalosauroidea or Avetheropoda. Scored as a lateral tooth, it was placed among
247 248 249 250 251 252 253 254	The cladistic analysis of the dentition-based data matrix (Supplementary Appendix 2) with NMS G.2018.17.1 as the floating OTU yielded twelve most parsimonious trees (MPTs) when scored as a mesial tooth (Consistency Index (CI) = 0.212 ; Retention Index (RI) = 0.461 ; Length = 1211) and five most parsimonious trees when scored as a lateral tooth (CI = 0.212 ; RI = 0.461 ; Length = 1211). Scored as a mesial crown, NMS G.2018.17.1 occupied various positions among non-abelisauroid Ceratosauria and Megalosauridae, or as the basal-most Tetanurae, Megalosauroidea or Avetheropoda. Scored as a lateral tooth, it was placed among Ceratosauria, as the basal-most taxon of the clades <i>Berberosaurus</i> + Ceratosauridae or
247 248 249 250 251 252 253 254 255	The cladistic analysis of the dentition-based data matrix (Supplementary Appendix 2) with NMS G.2018.17.1 as the floating OTU yielded twelve most parsimonious trees (MPTs) when scored as a mesial tooth (Consistency Index (CI) = 0.212 ; Retention Index (RI) = 0.461 ; Length = 1211) and five most parsimonious trees when scored as a lateral tooth (CI = 0.212 ; RI = 0.461 ; Length = 1211). Scored as a mesial crown, NMS G.2018.17.1 occupied various positions among non-abelisauroid Ceratosauria and Megalosauridae, or as the basal-most Tetanurae, Megalosauroidea or Avetheropoda. Scored as a lateral tooth, it was placed among Ceratosauria, as the basal-most taxon of the clades <i>Berberosaurus</i> + Ceratosauridae or Abelisauroidea, among Megalosauroidea, closely related to <i>Monolophosaurus</i> or <i>Sciurumimus</i> ,

270	Discriminant analysis
269	
268	sister taxon of Megaraptor among Megaraptora as a mesial crown.
267	of Tsaagan among Dromaeosauridae (Figure 2), whereas the specimen was recovered as the
266	= 0.461; Length $= 1213$). In the latter analysis, GLAHM 125390a was placed as the sister taxon
265	coded as a mesial (CI = 0.212 ; RI = 0.462 ; Length = 1212) and a lateral tooth (CI = 0.212 ; RI
264	The analysis with GLAHM 125390a as the floating taxon yielded a single MPT when
263	Limusaurus among Noasauridae.
262	more basal than Daemonosaurus among non-theropod Saurischia or as the sister taxon of
261	other hand, when scored as a mesial crown, NMS G.2018.17.2 was recovered either as a taxon
260	G.2018.17.2 was found as the sister taxon of Velociraptor among Dromaeosauridae. On the
259	RI = 0.461; Length = 1212) when scored as a lateral tooth. As a lateral crown, NMS
258	scored as a mesial tooth (CI = 0.212 ; RI = 0.462 ; Length = 1211) and a single MPT (CI = 0.212 ;
257	The analysis with NMS G.2018.17.2 as the floating OTU yielded three MPTs when

271

Results of the various DFAs, summarized in Table 1 and detailed in Supplementary 272 Appendix 4, show no consistent placement of either NMS G.2018.17.1 or GLAHM 125390a, 273 at the group level or the taxon level. The two isolated teeth are recovered outside the 274 morphospace occupied by other theropods in the DFA performed on the whole dataset 275 (Appendix 4), whereas GLAHM 125390a was retrieved within the morphospace occupation 276 of non-abelisaurid ceratosaurs and non-spinosaurid megalosauroids in the analysis performed 277 using our personal dataset (Figure 3). Both teeth are assigned to distantly related clades or 278 taxa such as Dilophosaurus, Ceratosauridae, non-abelisauroid Ceratosauria, Torvosaurus, 279 Suchomimus, Metriacanthosauridae, Neovenatoridae, Carcharodontosauridae, and 280

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

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

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

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

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

Broad interdenticular spaces like those in NMS G.2018.17.2 are also seen in nonaverostran theropods (e.g., *Herrerasaurus, Dracoraptor*; PVSJ 407; BP/1/5243), non355 abelisauroid ceratosaurs (e.g., Ceratosaurus, Genyodectes; UMNH VP 5278; MLP 26-39), non-megalosaurian megalosauroid (e.g., Marshosaurus, Monolophosaurus; DMNH 3718; 356 IVPP 84019), allosauroids (e.g., Sinraptor, Allosaurus, Acrocanthosaurus; IVPP V10600; 357 USNM 8335; UMNH VP 6499; NCSM 14345), tyrannosauroids (e.g., Guanlong, 358 Gorgosaurus; IVPP V14531; RTMP 1991.36.500) and some dromaeosaurids such as 359 Bambiraptor (AMNH 30556) and Deinonychus (YPM 5232). However, this space is narrow 360 in Abelisauroidea and Spinosauridae, and we consider it unlikely that NMS G.2018.17.2 361 belongs to one of these clades. 362

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

Finally, the unserrated mesial carina, combined with a denticulated distal carina, is a condition restricted to the mesial and/or lateral dentition of non-neotheropod theropods (e.g., *Herrerasaurus, Ischisaurus*; PVSJ 407, PVSJ 605), noasaurids (e.g., *Masiakasaurus*; FMNH PR 2476), the juvenile megalosaurid *Sciurumimus* (Rauhut et al. 2012), megaraptorans (e.g., *Megaraptor*; Porfiri et al. 2014), some basal tyrannosauroids (e.g., *Dilong*; IVPP V14242) compsognathids (e.g., Currie & Chen 2001; Peyer 2006; Dal Sasso & Maganuco 2011), basal maniraptoriforms (e.g., *Aorun, Ornitholestes, Haplocheirus*; AMNH 619; Choiniere et al. 2014*b*, *b*), and many dromaeosaurids (e.g., Currie et al. 1990; Norell et al. 2006; Godefroit et
al. 2008) and troodontids (e.g., Currie 1987; Currie and Dong 2001; Norell et al. 2009). These
are therefore all candidate clades for NMS G.2018.17.2.

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

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

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

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

Gen. and sp. indet.

- 411
- 412 Averostra Paul 2002
- 413
- 414 (Fig. 2)
- 415

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

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).

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

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

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

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

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

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

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

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

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

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Revision of GLAHM 125390a

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

We included GLAHM 125390a within our larger datasets and conducted a series of new DFAs and cladistic analyses. The DFAs on our whole dataset, our dataset of personal measurements, and the datasets of Smith & Lamanna (2006) and Gerke & Wings (2016) classify GLAHM 125390a as either a troodontid, ceratosaurid, neovenatorid or a carcharodontosaurid at the group level. At the taxon level, GLAHM 125390a was assigned to the abelisaurids *Rugops* and *Majungasaurus*, as well as *Ceratosaurus*, *Suchomimus*, *Neovenator* and *Megaraptor*. In the cladistic analysis, GLAHM 125390a is positioned as a dromaeosaurid closely related to *Tsaagan* or as the sister taxon of *Megaraptor* within
Megaraptora (when coded as a mesial and lateral tooth, respectively).

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

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

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

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

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Theropod Diversity on Skye

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

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

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

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

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

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

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Discussion

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

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

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

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

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Acknowledgements

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Figures

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

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

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

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

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

Table

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Deterate	NMS G.2018.17.1		GLAHM 125390a	
Datasets	Clade level	Taxon level	Clade level	Taxon level
Whole dataset	Neovenatoridae	Rugops	Troodontidae	Rugops
Whole dataset (no denticles = ?)	Troodontidae	Rugops	Troodontidae	Majungasauru s
Personal dataset	Neovenatoridae	Megaraptor	Troodontidae	Megaraptor
Personal dataset (no denticles = ?)	Non-abelisauroid Ceratosauria	Arcovenator	Troodontidae	Majungasauru s
Whole dataset with large teeth	Non-abelisauroid Ceratosauria	Torvosaurus		
Whole dataset with large teeth (no denticles = ?)	Non-abelisauroid Ceratosauria	Arcovenator		
Personal dataset with large teeth	Non-abelisauroid Ceratosauria	Torvosaurus		
Personal dataset with large teeth (no denticles = ?)	Non-abelisauroid Ceratosauria	Arcovenator		
Smith and Lamanna's (2006) dataset (No ratios, with CA2, DAVG2)	Carcharodonto- sauridae	Dilophosaurus	Ceratosauridae	Ceratosaurus
Smith and Lamanna's (2006) dataset (No ratios and no CA2, DAVG2)	Ceratosauridae	Carcharodon- tosaurus	Carcharodonto- sauridae	Suchomimus
Gerke and Wings' (2016) dataset (with CHR but not CBL)	Ceratosauridae	Carcharodon- tosaurus	Neovenatoridae	Neovenator
Gerke and Wings' (2016) dataset (with CBL, no ratios)	Metriacanthos- auridae	Carcharodon- tosaurus	Neovenatoridae	Neovenator
	Reclassification Rate (RR)		Clade level	
Datasets	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

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- **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.