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1   Osteological redescription of the Late Triassic sauropodomorph dinosaur *Thecodontosaurus*

2   *antiquus* based on new material from Tytherington, southwestern England

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ABSTRACT—*Thecodontosaurus antiquus* is a basal sauropodomorph from the Rhaetian locality of Durdham Down in Bristol, U.K. Sauropodomorph material putatively assigned to this species was found in the nearby site of Tytherington. Here, we describe the osteology of the Tytherington specimens, comparing them to *T. antiquus* and other Late Triassic sauropodomorphs from Britain. We find that this material can be assigned to *T. antiquus* based on multiple shared morphological traits, and we provide a revised diagnosis of this taxon. The new anatomical information from the Tytherington specimens enriches the osteology of the species, particularly of previously unknown parts of the skeleton such as the skull. We find poor anatomical support to distinguish the contemporary *Pantydraco caducus* from *T. antiquus*, which might represent a juvenile of the latter. We also discuss the questionable validity of *Asylosaurus yalensis*. *Thecodontosaurus* is one of the most basal sauropodomorphs that shows craniodental traits related to herbivory, while retaining a plesiomorphic limb morphology and posture. This taxon was an important component of Rhaetian insular ecosystems of southwestern Britain.

INTRODUCTION

Dinosaurs are a clade of avemetatarsalian archosaurs that originated in Gondwana in the Middle–Late Triassic (Marsola et al., 2019), splitting early in their history into three main lineages (Baron et al., 2017; Langer et al., 2017) and rising to ecological dominance by the Early Jurassic (Brusatte et al., 2008a; 2008b). One of these lineages, Sauropodomorpha, rapidly radiated to give rise to a diverse assemblage of Carnian taxa in South Gondwana (Langer et al., 1999; Martínez and Alcober, 2009; Ezcurra, 2010; Cabreira et al., 2011, 2016; Sereno et al., 2013). After this early diversification, sauropodomorphs, as well as other dinosaurs, migrated

34 also to northern latitudes; and by the Norian and Rhaetian, Laurasia was inhabited by several

35 early members of this clade of dinosaurs (Marsola et al., 2019). One of these Late Triassic

36 sauropodomorphs was *Thecodontosaurus antiquus*, which lived in the region that today forms

37 the British Isles (Benton et al., 2000) and occupies a basal phylogenetic position as a non-

38 plateosaurian (sensu Yates, 2007) sauropodomorph (Benton et al., 2000; Otero and Pol, 2013;

39 Langer et al., 2019).

40   *Thecodontosaurus* was named and described by Riley and Stutchbury (1836; 1840) from

41 dinosaurian material found in the fissure fill deposit of Durdham Down in Bristol, U.K. The

42 collection was curated in the BRSMG, although many of the *Thecodontosaurus* specimens were

43 destroyed during the Second World War (Benton, 2012). Benton et al. (2000) formally described

44 the remaining specimens and assigned them to *Thecodontosaurus antiquus*. A new specimen

45 found in the south Wales locality of Pant-y-Ffynnon (Whiteside et al., 2016; Keeble et al., 2018)

46 that was first interpreted as a juvenile *T. antiquus* (Kermack, 1984; Benton et al., 2000) was later

47 assigned to a new species, *T. caducus* (Yates, 2003a) and finally to a different genus, *Pantydraco*

48 *caducus* (Galton et al., 2007), based on morphological differences in the cervical vertebrae and

49 humerus from the Durdham Down material. Additionally, an articulated pectoral girdle and

50 forelimb (YPM 2195) from Bristol (Benton et al., 2000) was later named *Asylosaurus yalensis*,

51 on the basis that it exhibited distinctive humeral traits (Galton, 2007). In 1975, sauropodomorph

52 material was found in Tytherington, southwest England (Whiteside and Marshall, 2008;

53 Whiteside et al., 2016) and since then, it has been housed and prepared at the BRSUG. The new

54 Tytherington material was later identified as *T. antiquus* (Whiteside, 1983; Galton et al., 2007)

55 but never formally described. These interpretations and findings complicate the taxonomic status

56 of *Thecodontosaurus* and apparently increase the number of sauropodomorph taxa that lived in

57 southwestern Britain during the Late Triassic.

58   As it currently stands, *Thecodontosaurus* was found in two geographically close fissure

59 localities, Durdham Down and Tytherington (Benton et al., 2000; Whiteside and Marshall, 2008;

60 Foffa et al., 2014; Whiteside et al., 2016), which were traditionally thought to be Carnian in age.

61 However, recent analyses of the geology and palynology of the numerous Late Triassic fissure

62 fill deposits of southwestern Britain suggests the age of these two localities, as well as Pant-y-

63 Ffynnon, was Rhaetian (205 Ma) instead (Whiteside et al., 2016). Their paleoenvironment has

64 been reconstructed as small islands in a shallow sea that housed a diverse herpetofauna

65 composed of rhynchocephalians, "sphenosuchian" crocodylomorphs and coelophysoid dinosaurs

66 (Whiteside and Marshall, 2008; Foffa et al., 2014; Whiteside et al., 2016; Mussini et al., 2019).

67 *Thecodontosaurus* was thus part of a peculiar insular ecosystem of the Late Triassic.

68   Here, we provide the first detailed descriptive account of the sauropodomorph material

69 found in Tytherington and assign it to *Thecodontosaurus antiquus*. The abundant and well-

70 preserved BRSUG collection provides new information on the osteology of the species,

71 especially of elements of the skull that were unknown. Based on its anatomy, we discuss aspects

72 of its paleobiology and paleoecology, including feeding and posture, and comment on the

73 taxonomic status of Late Triassic British sauropodomorphs.

74   **Institutional Abbreviations**—**BRSMG**, Bristol City Museum and Art Gallery, Bristol,

75 United Kingdom; **BRSUG**, University of Bristol Geology Department, Bristol, United Kingdom;

76 **NHMUK**, Natural History Museum, London, United Kingdom; **PULR**, Paleontología,

77 Universidad Nacional de La Rioja, La Rioja, Argentina; **YPM**, Yale Peabody Museum, New

78 Haven, United States of America.

79

80   MATERIAL

81

82   The *Thecodontosaurus* material from the Tytherington locality comprises over a thousand

83   specimens housed at BRSUG. These include isolated bones or bone fragments of very disparate

84   sizes extracted from fissure fill deposits, similar to the previously described *Thecodontosaurus*

85   material from Durdham Down (Benton et al., 2000). Therefore, the term "specimen" is here used

86   to indicate an item within the BRSUG collection, as opposed to an "individual animal". The

87   disarticulation of the *Thecodontosaurus* fossils from Tytherington renders the assignment of

88   specimens to the same individual very difficult or impossible. Thus, ratios and proportions

89   between skeletal elements are not provided in the description, despite their taxonomic

90   importance. The anatomical description is based on the most complete specimens representing

91   known skeletal elements and that can be confidently identified.

92

93   SYSTEMATIC PALEONTOLOGY

94

95   DINOSAURIA Owen, 1842

96   SAURISCHIA Seeley, 1887

97   SAUROPODOMORPHA Huene, 1932

98   *THECODONTOSAURUS* Riley and Stutchbury, 1936

99   *THECODONTOSAURUS ANTIQUUS* Morris, 1843

100   **Diagnosis**—A sauropodomorph dinosaur distinguished from other basal

101   sauropodomorphs by the following combination of characters (autapomorphies indicated with an

102 asterisk): absence of a postorbital flange; maxillary and dentary tooth crowns not recurved and

103 with coarse serrations; extensive muscle scar for the origin of M. triceps brachii caput scapulare

104 on the lateral side of the glenoid lip of the scapula*; elaborate humeral cuboid fossa with a

105 bilobate proximal outline and extensively pitted surface*; reduced brevis fossa and shelf;

106 incompletely perforated acetabulum; absence of a femoral trochanteric shelf; posterolateral

107 descending process of the tibia anteroposteriorly wide and mediolaterally narrow, not reaching

108 the lateral extent of the anterolateral process* (convergent with *Anchisaurus*, *Eucnemesaurus*

109 *entaxonis, Aardonyx* and Sauropoda).

110   **Holotype**—BRSMG Ca7465, right dentary, destroyed in 1940 (Benton et al., 2000).

111   **Neotype**— BRSMG C4529, left dentary, designated by Galton (1985).

112   **Referred Specimens**—In addition to the sauropodomorph material from Durdham Down

113 referred to *T. antiquus* by Benton et al. (2000), over 1000 specimens from Tytherington fissure 2

114 housed at BRSUG are here referred to this species: BRSUG 23606–23972, 26585–26660,

115 28121–28404 and 29372-2805–29372-3812.

116   **Locality and Horizon**—Late Triassic, Rhaetian localities of Durdham Down and

117 Tytherington fissure 2, southwestern England, Europe (Benton et al., 2000; Whiteside and

118 Marshall, 2008; Whiteside et al., 2016; Mussini et al., 2019).

119

120   DESCRIPTION

121

122 **Skull**

123   **Maxilla**—A posterior portion of a left maxilla was found in Tytherington (Fig. 1A, B). The

124 lateral surface preserves the two posteriormost lateral foramina. The posterior maxillary foramen

125   is the most notable in size and is placed at the anterior end of an anteroposteriorly elongated

126   groove, as seen in *Saturnalia* (Bronzati et al., 2019). The ventral surface bears a series of seven

127   posterior alveoli that are small, circular and closely packed, with very thin interalveolar walls.

128   The ventral surface of the maxilla medial to the toothrow presents numerous minute pits. Only

129   one tooth, attached to the anteriormost alveolus, is preserved (Fig. 1C). It has a small, lanceolate

130   crown with coarse serrations (five per mm) oblique to the carina and the apicobasal axis of the

131   tooth. The crown is labiolingually compressed and not curved. The crowns are basally

132   constricted. The root is deep and straight. Tooth morphology is very similar to that of the dentary

133   teeth of the *T. antiquus* neotype (Benton et al., 2000) and *Pantydraco* (Galton and Kermack,

134   2010), but differs from more basal taxa such as *Buriolestes* (Müller et al., 2018a), *Saturnalia*

135   (Bronzati et al., 2019) and *Eoraptor* (Sereno et al., 2013), which have curved and finely serrated

136   teeth.

137   **Squamosal**—Tytherington yielded a right squamosal that is missing the anterior portion

138   (Fig. 1D, E). The medial surface is marked by a semispherical quadrate cotyle for reception of

139   the quadrate head. The quadrate cotyle is dorsally roofed by the squamosal main body, which

140   presents a medial concave and anteroposteriorly elongated surface, laterally bounded by a ridge,

141   which represents the parietal articular surface. The quadrate ramus is straight and directed

142   anteroventrally, tapers ventrally and bears a medial groove. The medial ramus is directed

143   posteromedially, it is short and acute, and with a triangular cross section.

144   **Frontal**—A complete right frontal (Fig. 1F, G) and incomplete right frontal are preserved.

145   The bone is dorsoventrally flat, and its dorsal and ventral surfaces are smooth. The frontal is

146   longer than wide and has a similar mediolateral width throughout its length unlike other

147   sauropodomorphs such as *Saturnalia* (Bronzati et al., 2019) and *Panphagia* (Martínez et al.,

148   2012), in which the bone notably increases in width posteriorly. In dorsal view (Fig. 1F), the

149   frontal presents a deep, anterolateral V-shaped fossa, with the apex directed posteriorly, which

150   corresponds to the prefrontal articular surface. Anteromedial to the prefrontal articular surface,

151   representing the anterior end of the bone, a concavity marks the nasal articular surface. The

152   lateral margin of the bone posterior to the prefrontal articular surface is concave and represents

153   the orbital rim. The medial margin of the bone is slightly projected dorsally forming the frontal

154   medial crest along the suture with the left counterpart. Contribution of the frontal to the

155   supratemporal fossa, lost in sauropods (Wilson, 2002), cannot be confirmed because the

156   posterolateral corner of the bone is obscured by matrix. A laterally concave, ventrally projecting

157   ridge is present on the ventral surface of the frontal (Fig. 1G). This is the orbital margin and the

158   surface lateral to it forms the orbital roof and slopes dorsally in a lateral direction. Medial to the

159   orbital margin, the ventral surface is depressed. The posterior part of the ventral surface shows

160   an anteroposteriorly elongated oval fossa that corresponds to the cerebral cavity. The cerebral

161   cavity depression is continued anteriorly by a laterally narrow olfactory tract depression that

162   dorsally bounded the olfactory tract. As in *Massospondylus* (Chapelle and Choiniere, 2018), this

163   is the shallowest part of the depression. This continues with the anterior portion of the medial

164   depression, represented by the olfactory bulb depression. Unlike in *Macrocollum* (Müller, 2019),

165   this depression is not medially bounded by a crest. In lateral view, the orbital margin is almost

166   straight, unlike in other sauropodomorphs in which it is dorsally convex like *Pantydraco* (Galton

167   and Kermack, 2010) and *Massospondylus* (Chapelle and Choiniere, 2018).

168   **Jugal**—A single specimen representing a right jugal is known (Fig. 1H). The jugal is

169   triradiate and forms the posteroventral and ventral margins of the orbit, the infraorbital bar and

170   the anterior portion of the infratemporal bar. The jugal is not straight in anterior view, as the

171   postorbital ramus curves laterally with respect to the jugal main body. The postorbital ramus is

172   relatively short and posterodorsally oriented. Its dorsal end articulates with the jugal ramus of the

173   postorbital by a larger anterior fossa ventrally delimited by a mediolaterally oriented ridge, and a

174   smaller posteromedial fossa. The orbital margin of the jugal laterally bounds a flat

175   anteromedially oriented surface which represents the anterodorsal surface of the bone and the

176   postorbital articular surface.

177   **Postorbital**—A left postorbital is known, which has its three rami tips broken (Fig. 1I). The

178   bone is triradiate and forms the posterior margin of the orbit. The anterior surface is flat,

179   separated from the lateral and medial surfaces of the bone by two marked rims, making the jugal

180   ramus triangular in cross-section. The postorbital lacks an orbital flange, unlike other basal

181   sauropodomorphs (Galton and Kermack, 2010; Yates et al., 2011; Sereno et al., 2013; Müller et

182   al., 2018a; Bronzati et al., 2019; Langer et al., 2019; Müller, 2019). This flange is reduced or

183   absent in other – particularly more derived – sauropodomorphs such as *Plateosaurus* (Prieto-

184   Márquez and Norell, 2011), *Massospondylus* (Chapelle and Choiniere, 2018) and

185   *Adeopapposaurus* (Martínez, 2009). The frontal ramus is robust but anteromedially compressed.

186   Its lateral surface presents multiple pits and grooves. The squamosal ramus forms the anterior

187   portion of the supratemporal bar. It is mediolaterally compressed and its anteroventral surface,

188   dorsal to the posterodorsal end of the jugal ramus, presents a small fossa bounded by a lateral

189   ridge.

190   **Quadrate**—Only a left quadrate is known from Tytherington, which exhibits the typical

191   columnar, dorsoventrally elongated morphology of early dinosaurs (Fig. 1J–L). The main body

192   of the quadrate has a gentle sigmoidal shape in lateral view (Fig. 1L), but less curved than in

193   *Macrocollum* (Müller, 2019). The quadrate head is ellipsoid in dorsal view, with a mediolateral

9

194   long axis. Both the quadratojugal and pterygoid flanges have their anterior tips broken. Thus, the

195   presence of a quadrate foramen cannot be determined. The medial pterygoid flange projects

196   anteromedially and the quadratojugal flange, anterolaterally. Both are laminar and delimit a

197   dorsoventrally elongated anterior groove. The pterygoid flange is taller, reaching a more dorsal

198   position. The lateral surface of the quadratojugal ramus is concave and posteriorly bounded by a

199   marked quadrate ridge that runs along the posterior surface of the bone. The ventral end bears the

200   quadrate condyles, of which the medial condyle projects more ventrally. In ventral view, the

201   medial condyle is more anteroposteriorly elongated, while the lateral one is rounded and dome-

202   shaped. The two quadrate condyles are separated by an anteromedially oriented groove.

203   **Basioccipital**—The basioccipital forms the ventral margin of the foramen magnum and the

204   posterior floor of the endocranial cavity (Fig. 1M, N). The dorsal surface is marked by an

205   anteroposterior groove running along the parasagittal plane from the foramen magnum, which

206   represents the neural or medullar groove. The neural groove is bounded on both sides by pitted

207   and rugose surfaces, the left and right otoccipital articular surfaces. A median ridge splits the

208   neural groove into two at the anterior third of the bone, as seen in YPM 2192 and in other early

209   dinosaurs such as *Pantydraco* (Galton and Kermack, 2010) and *Lesothosaurus* (Porro et al.,

210   2015). The metotic fissure is preserved on the left side of the dorsal surface of the bone,

211   branching perpendicular to the neural groove. The metotic fissure is similarly laterally elongated

212   and anteroposteriorly narrower to that of YPM 2192 and *Pantydraco* (Galton and Kermack,

213   2010). The basal tubera are prominent and anterolaterally oriented ridges with knob-like medial

214   ends. The lateral portion of the basal tubera is less robust than in *Macrocollum* (Müller, 2019). A

215   mediolaterally oriented ridge connects the paired basal tubera. A deep basisphenoid recess is

216   present anterior to the basal tubera and posterior to the basioccipital-basisphenoid suture, as in

10

217 *Efraasia* (Bronzati and Rauhut, 2018), *Unaysaurus* (McPhee et al., 2019) and *Massospondylus*

218 (Chapelle and Choiniere, 2018), among others. The occipital condyle is knob-shaped and its

219 ventral projection is not notably marked due to weathering. In ventral view (Fig. 1N), the

220 occipital condyle is anteroposteriorly longer than those of *Saturnalia* (Bronzati et al., 2019),

221 *Efraasia* (Bronzati and Rauhut, 2018) and *Adeopapposaurus* (Martínez, 2009), but similar to

222 YPM 2192 (Benton et al., 2000). The occipital condyle and the basal tubera are connected by the

223 biconcave basioccipital neck.

224   **Otoccipital**—The otoccipital exhibits the usual triradiate morphology, with a lateral

225 paraoccipital process, a ventral pyramidal projection (sensu Bronzati and Rauhut, 2018) and an

226 anteroventral crista interfenestralis (Fig. 1O, P). The paraoccipital process is elongated and

227 posterolaterally directed as seen in *Pantydraco* (Galton and Kermack, 2010) and

228 *Adeopapposaurus* (Martínez, 2009), and in the braincase (YPM 2192) of the Durdham Down *T.*

229 *antiquus* (Benton et al., 2000). It is dorsoventrally widest at its mediolateral midpoint and its

230 lateral end has a rounded outline in anterior view. The posterior surface of the paraoccipital

231 process is marked by an oblique, ventrolaterally oriented, dorsolaterally curved ridge. This

232 delimits ventrally a concave surface where neck muscles would have attached. The anterior

233 surface of the paraoccipital process is marked by a proximal semicircular area with multiple

234 mediolaterally oriented ridges that represent the prootic articular surface. The dorsal surface of

235 the paraoccipital process shows a notch which might represent the posterior border of the post-

236 temporal foramen, a derived trait present in *Pantydraco* (Galton and Kermack, 2010),

237 *Macrocollum* and more derived sauropodomorphs (Müller, 2019). On the lateral side of the bone

238 (Fig. 1P), ventral to the paraoccipital process, two posterior foramina representing the openings

239 for cranial nerve XII (hypoglossal) are present. The posteriormost of the two is the largest, oval-

240   shaped and more dorsally positioned. Both openings have their medial counterparts on the

241   posteroventromedial surface of the otoccipital. Anterodorsal to the CN XII foramina, there is a

242   large, dorsoventrally elongated opening infilled with matrix that probably represents the metotic

243   fissure. This opening is the exit for cranial nerves IX, X and XI and is not subdivided as in YPM

244   2192 (Benton et al., 2000), *Plateosaurus* (Prieto-Márquez and Norell, 2011) and

245   *Massospondylus* (Chapelle and Choiniere, 2018) but unlike most basal sauropodomorphs

246   (Bronzati and Rauhut, 2018). The metotic fissure is anteriorly bounded by a tall, posterodorsally

247   inclined crista interfenestralis (= metotic crest). This ramus separates the metotic fissure from the

248   foramen ovale. The metotic fissure seems to be posteriorly bounded by a crista tuberalis,

249   although this part of the bone is abraded. The posteroventral end of the pyramidal projection

250   forms the dorsolateral portion of the occipital condyle. The posterodorsal surface of the

251   otoccipital is rugose and pitted and represents the supraoccipital articular surface.

252

253   **Mandible**

254   **Surangular**—The incomplete left surangular is missing its anterior portion (Fig. 1Q–S). The

255   surangular is mediolaterally flat and dorsally convex in lateral view. The dorsal shelf is

256   dorsolaterally flattened, lacking a coronoid process. Its dorsal surface is smooth and medially

257   bounded by a medial ridge, representing the insertion site of the M. adductor mandibulae

258   externus complex (Holliday, 2009). Posterolaterally to the muscle attachment area, a lateral ridge

259   extends to the posterior end of the shelf. Posterior to the dorsal shelf, the surangular decreases in

260   dorsoventral depth, forming a dorsally concave margin that continues posteriorly with the broken

261   posterodorsally oriented retroarticular process. The medial portion of the bone houses the

262   adductor fossa, insertion site for M. adductor mandibulae profundus and M. pseudotemporalis

263   complexes (Holliday, 2009), which are laterally bounded by the lateral lamina, dorsally by the

264   dorsal shelf and posteriorly by the medial flange. It is open medially through the internal

265   mandibular fenestra. The medial flange is a medial protrusion of the surangular with a triradiate

266   shape in medial view. Its anteroventral extension, which forms the posterior wall of the adductor

267   fossa, would articulate medially with the prearticular. Its posterior ramus presents a

268   medioventrally facing articular surface for the articular. The dorsal portion of the medial flange

269   is dorsomedially concave and forms the anterior part of the mandibular glenoid.

270

271   **Axial Skeleton**

272   **Atlas**—A right atlantal neurapophysis is known from Tytherington (Fig. 2A, B), which has a

273   similar morphology to those of other basal sauropodomorphs like *Adeopapposaurus* (Martínez,

274   2009) and *Leyesaurus* (Apaldetti et al., 2011). The anteriormost feature is the pedicel, which is

275   ventromedially oriented and has a reniform end, the dorsal portion of which represents the

276   occipital condyle articular surface, and the ventral, the atlantal intercentrum articular surface.

277   The prezygapophysis is anteromedially directed and is formed by a thick lamina. The broken

278   postzygapophysis is placed posterior to it and is thinner than the anterior zygapophysis. A

279   shallow dorsal depression is present on the lateral wall of the postzygapophysis and of the

280   posterior portion of the prezygapophysis. This depression is ventrally bounded by a keel that

281   extends posteriorly to form the posteriorly directed, spear-shaped epipophysis.

282   **Cervical Vertebrae**—Few postaxial cervical vertebrae have been found at Tytherington,

283   none of them in articulation. Anterior cervical vertebrae are elongated, dorsoventrally short and

284   mediolaterally narrow (Fig. 2C). The neural spine is dorsoventrally short and mediolaterally thin.

285   The zygapophyses are horizontal and extend anterior and posterior to the neural arch and the

286   centrum. The prezygapophyses are dorsomedially oriented and are separated by a deep,

287   anteroposteriorly elongated spinoprezygapohyseal fossa (sensu Wilson et al., 2011). The

288   postzygapophyses face ventrolaterally and are separated by a deep spinopostzygapohyseal fossa

289   that seems to penetrate superficially below the neural spine (Fig. 2D). The epipophyses are

290   abraded in almost all specimens, but the left epipophysis in BRSUG 29372-2842 is plate-like and

291   reaches the posterior end of the postzygapohysis. The position and morphology of the

292   diapophyses vary between cervical vertebrae. In more anterior cervical vertebrae, the

293   diapophyses are anteriorly positioned, elongated and slightly projected laterally. In more

294   posterior cervicals (Fig. 2E–H), the diapophyses are placed more towards the vertebral midlength

295   and are aliform and project laterally. This variation is seen in other sauropodomorphs such as

296   *Adeopapposaurus* (Martínez, 2009) and *Leonerasaurus* (Pol et al., 2011). The anterior and

297   posterior openings of the neural canal are elliptical, wider than tall. The zygodiapophyseal table

298   is separated from the centrum by a dorsally convex keel. The centra are amphicoelous and

299   constricted dorsoventrally and mediolaterally at midlength; they are approximately three times

300   longer than tall. In ventral view (Fig. 2G), the anterior end of the centrum is mediolaterally wider

301   than the posterior because of the circular parapophyses. There is an anteroposteriorly oriented

302   ventral keel, most developed towards the anterior end, as well as anteroposterior striations on the

303   ventral centrum. The neural spine in the posteriormost cervical vertebrae is anteroposteriorly

304   shorter than in anterior and mid cervicals. The prezygapophyeses are relatively shorter, not

305   extending much anterior to the centrum, and the postzygapophyses are not horizontal, but project

306   posterodorsally. The diapophyses are more elongated and aliform, projecting ventrolaterally.

307   **Dorsal Vertebrae**—Vertebral elements of the trunk (Fig. 2I–N) belong to middle or

308   posterior dorsals, which are not preserved in articulation. Neural spines are broken in most

14

309   specimens except for a posterior dorsal (Fig. 2N), in which this structure is subrectangular in

310   lateral view and subequal in dorsoventral height to the rest of the neural arch. The shapes of the

311   neural canal anterior and posterior openings differ, the former being subcircular in outline, and

312   the latter being dorsoventrally tall and slot-shaped (Fig. 2J, K). The diapophyses are directed

313   laterally, as in other basal sauropodomorphs, with a slight dorsal component in some specimens

314   (Fig. 2L). The prezygapophyses are short, hardly extending anterior to their respective centrum

315   in posterior dorsals (Fig. 2I, N). Their articular facets are oval and directed mediodorsally. The

316   spinoprezygapohyseal fossa is reduced to a small ellipsoid depression (Fig. 2J). The

317   postzygapophyses project posteriorly, extending beyond the posterior margin of the centrum

318   unlike the prezygapophyses. A narrow, dorsoventrally high spinopostzygapophyseal fossa is

319   present in between. The zygapophyses bear hyposphene-hypantrum articulations (Fig. 2I–K, N).

320   The hypantrum is present as an anteroposterior groove on the ventromedial side of the

321   prezygapophysis. The hyposphene results from a ventral projection of the postzygapophysis, and

322   its dorsoventral height is less than that of the neural canal, as is common in basal

323   sauropodomorphs. The postzygapophysis and the hyposphene delimit a laterally concave fossa

324   that serves for reception of the prezygapophysis of the vertebra immediately behind. This fossa is

325   anteroventrally separated from the posterior infradiapophyseal fossa (sensu Yates et al., 2012) by

326   an accessory lamina. The centrodiapophyseal fossa is triangular in lateral view and located

327   ventral to the diapophysis. This fossa is posteriorly bounded by the posterior centrodiapophyseal

328   lamina and, in posterior dorsal vertebrae, anteriorly delimited by the parapophysis and a short

329   paradiapophyseal lamina. The well-developed postzygodiapophyseal and posterior

330   centrodiapophyseal laminae dorsally and anteriorly bound the deep posterior infradiapophyseal

331   fossa, respectively. The parapophyses are fully located on the neural arch in all specimens, well

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332   separated from the centrum by anterior centroparapophyseal laminae (sensu Wilson et al., 2011).

333   The articular surface of the parapophyses is subcircular in outline and concave (Fig. 2L). The

334   neurocentral sutures are visible in all specimens. The relative length of the centrum varies among

335   dorsal vertebrae, from 1.1 to 1.6 times the centrum height. Dorsal centra are amphicoelous to

336   amphiplatyan and bear an anteroposteriorly elongated lateral depression. In lateral view, the

337   ventral margin of the centrum is strongly concave, with anterior and posterior ends extending

338   further ventrally than at the center.

339   **Sacral Vertebrae**—Two sacral vertebrae have been found at Tytherington: a relatively

340   complete second primordial (Fig. 3A–D) and a very fragmentary centrum. The centrum

341   morphology of the second primordial in anterior and posterior views is an isosceles trapezoid

342   with a convex ventral side. The length of the second sacral centrum is 1.7 times its dorsoventral

343   height and equal to its transverse width. The anterior articular surface of the centrum is wider

344   and taller than the posterior one. The second sacral rib has a ventrally positioned anterior iliac

345   contact that curves dorsally in a posterior direction to contact the transverse process, forming an

346   anterodorsally concave outline. The anterior portion of the sacral rib contacts the sacral centrum,

347   while the posterior one articulates with the transverse process of the neural arch, which is

348   broken. This condition supports the identification of this element as a second primordial sacral.

349   In dorsal view (Fig. 3A), the distal portion of the sacral rib expands anterioposteriorly to contact

350   the ilium and its anterior end is notably robust. The neural spine and most of the neural arch is

351   not preserved. The neural canal is wide, contributed by a sulcus on the dorsal surface of the

352   centrum, which left space for a lumbar enlargement of the spinal cord. No articulated sacrum is

353   preserved, but the sacral rib articular surface of the ilium (Fig. 9B) suggests the presence of two

354 primordial sacral vertebrae. Evidence for additional sacral vertebrae is unclear (see Ilium

355 section).

356 **Caudal Vertebrae**—Multiple isolated caudals from different positions in the tail were found

357 at Tytherington (Fig. 3E–K). The caudal centra become progressively more elongated and

358 dorsoventrally shorter posteriorly along the tail, from a length to height ratio of 1.4 in proximal

359 elements to 3.4 in posterior ones. The transverse processes are lenticular in proximal cross

360 section (Fig. 3E, G). The only well-preserved transverse process corresponds to a mid-anterior

361 vertebra (Fig. 3H). This process is plate-like, horizontal and posterolaterally oriented. The neural

362 spines are not completely preserved and are located on the posterior half of the neural arch.

363 Anteriorly, the neural spine turns into a dorsal ridge that bifurcates to meet both

364 prezygapophyses (Fig. 3F). The laterally projecting prezygapophyses are anterodorsally oriented

365 and slightly exceed the anterior end of the centrum, while the postzygapophyses project

366 posterodorsally beyond the posterior end of the centrum. This condition is similar to

367 *Adeopapposaurus* (Martínez, 2009), but different from *Pampadromaeus*, in which it is the

368 prezygapohyses that surpass the end the centra (Langer et al., 2019). As in most basal

369 sauropodomorphs, the postzygapophyses are located on both sides of the posterior portion of the

370 base of the neural spine. The articular surfaces of the pre- and postzygapophyses face

371 dorsomedially and ventrolaterally, respectively. In anterior to mid caudals, the space between the

372 prezygapophyses delimits a V-shaped spinoprezygapophyseal fossa which terminates posteriorly

373 in a subcircular hole (Fig. 3F). The spinopostzygapophyseal fossa is a dorsoventrally oriented slit

374 located posteroventrally to the base of the neural spine. The neural canal is cylindrical along the

375 caudal series, becoming slightly dorsoventrally compressed in the posteriormost caudals. The

376 articular surfaces of the centra are amphicoelous. The ventral surface of the centrum presents a

reduced anteroposterior groove that extends from end to end and is bounded laterally by ridges

(Fig. 3H). The posterior ends of the centra bear two ventral condyles on both sides of the

longitudinal sulcus that articulate with the chevrons. The posterior caudals have rod-like centra

and lack transverse processes (Fig. 3J, K). The neural spine is reduced to a posterior ridge on the

neural arch, or absent in the posteriormost elements. The articular surfaces of the

prezygapophyses face medially and those of the postzygapophyses are directed laterally.

Dorsal Ribs—Dorsal ribs are slender elements of which only proximal fragments are

preserved (Fig. 4A, B). The shaft presents a gentle curvature, with a greater medial inflection

immediately distal to the tuberculum-capitulum junction. The capitulum and the tuberculum

delimit a U-shaped medial margin of the rib head. The capitulum is twice the length of the

tuberculum, and it is mediolaterally broader. It is slightly constricted at the base and expands

medially to form a hemispherical head. The shaft of the dorsal ribs is ovoid in cross section, as in

Pampadromaeus (Langer et al., 2019), anteroposteriorly flattened and with a sharp lateral edge.

The posterior surface of the shaft bears a lateral groove that runs distally from the tuberculum-

capitulum junction.

Chevrons—Three complete chevrons are preserved, which vary in length from 2.4 to 6.5

cm. Chevrons present the usual Y-shaped morphology (Fig. 4C–E). The proximal articulations

for the caudal centra contact at the midsagittal plane, with no signs of dorsal opening of the

hemal canal. The proximal articular facets delimit a concave surface in anterior view, with lateral

flanks that extend dorsally contacting the ventral and ventrolateral margins of the centrum ends.

The hemal canal openings differ, the anterior being proximodistally shorter than the posterior.

The anterior opening is a mediolaterally narrow slit, and the posterior one is triangular,

proximodistally elongated and mediolaterally narrow, both being proximally broader and

400   tapering distally. One-third along their length, the chevrons curve from a ventral to

401   posteroventral orientation. The distal portion of the chevron is mediolaterally flattened and of

402   similar anteroposterior width, without a distal expansion.

403

404   **Appendicular Skeleton**

405   **Scapula**—Several scapulae have been found at Tytherington, most of them fragmentary but

406   well-preserved, and only one being essentially complete (Fig. 5C, D). The scapular blade is

407   narrow and elongated, with parallel dorsal and ventral margins. It is arched laterally and does not

408   expand significantly at its posterior end, differing from other basal members of

409   Sauropodomorpha such as *Saturnalia* (Langer et al., 2007) and *Panphagia* (Martínez and

410   Alcober, 2009). The body of the scapula is dorsoventrally tall compared to the blade. The dorsal

411   and ventral margins expand gradually from the neck, unlike in *Eoraptor* (Sereno et al., 2013),

412   *Saturnalia* (Langer et al., 2007) and *Panphagia* (Martínez and Alcober, 2009), in which they

413   form almost right angles. The acromial (dorsal) half of the body is mediolaterally narrow and

414   plate-like, with a sharp edge, compared to the robust glenoid (ventral) half. The scapular lateral

415   fossa is large and shallow, and it is bounded by a low acromial ridge. This fossa represents the

416   scapular origin of M. supracoracoideus (Otero, 2018). The lateral surface of the glenoid lip bears

417   a muscle scar in the form of a rugose oval buttress (Fig. 5A) that indicates the origin of M.

418   triceps brachii caput scapulare (Otero, 2018). Such an extensive scar is not present in any other

419   basal sauropodomorph (Langer et al., 2007, 2019; Martínez and Alcober, 2009). The lateral

420   surface of the acromion posterior to the lateral fossa exhibits numerous deep and wide pits that

421   are a muscle scar left by the origin of M. deltoideus clavicularis. The medial surface of the

422   scapular blade shows a ventromedial ridge extending posteriorly from the glenoid lip (Fig. 5B).

423   The surface between this ridge and the sharp ventral border of the blade is grooved and served as

424   the origin of M. scapulohumeralis posterior. Dorsal to the ventromedial ridge, the medial

425   longitudinal fossa with surface pitting marks the origin of M. subscapularis (Otero, 2018).

426   **Coracoid**—Only one coracoid specimen was found, which represents the posteroventral part

427   of a right coracoid, including the glenoid and the coracoid foramen (Fig. 5E–G). The coracoid

428   has a concave medial surface and a convex lateral surface. The coracoidal glenoid surface is

429   abraded but this part of the bone is very robust, as with the scapular glenoid compared to the rest

430   of the bone, which is plate-like. In ventral view, the glenoid surface has a subrectangular shape,

431   with its posterior end mediolaterally wider than the anterior. The coracoid foramen is large and

432   perforates the bone in a posteromedial direction (Fig. 5E, F). The lateral opening of the foramen

433   is wider than the medial one. An oval fossa bounded by a dorsal ridge is present on the lateral

434   surface of the coracoid, anterior to the glenoid, and this probably served as the insertion of M.

435   coracobrachialis (Otero, 2018). The lateral surface of the coracoid posterodorsal to the coracoidal

436   foramen is pitted (Fig. 5E), which might represent the ventral portion of the origin site of M.

437   supracoracoideus. Only the ventral portion of the scapular articular surface is preserved, which is

438   concave. The medial surface of the coracoid anterior to the scapular articulation (Fig. 5F) bears

439   deep striations corresponding to the scapulocoracoid synchondrosis, as in *Saturnalia* (Langer et

440   al., 2007).

441   **Humerus**—The humerus is sigmoid in lateral view, with the proximal half curving

442   posteriorly and the distal half curving anteriorly (Fig. 6). The proximal end is rotated

443   approximately 45 degrees with respect to the distal end, unlike in *Saturnalia*, in which both ends

444   are in the same plane (Langer et al., 2007). Nonetheless, this rotation might be affected by

445   taphonomic distortion. The proximal and distal ends are mediolaterally expanded compared to

20

446   the slender shaft. The proximal part of the bone is anteroposteriorly flat and plate-like. The

447   humeral head is ellipsoid and is anteroposteriorly expanded with respect to the rest of the

448   proximal end (Fig. 6B). The medial side of the proximal humerus mediodistal to the head

449   presents a medial tuberosity (Fig. 6D), which is bulbous and posteriorly prominent and has a

450   grooved surface, but its medial tip is abraded in all specimens.

451   The well-developed deltopectoral crest forms an approximate right angle with the rest of the

452   proximal humerus. The deltopectoral crest extends for approximately 43 percent of the length of

453   the humerus, similar to most basal sauropodomorphs (Galton, 1973; Langer, 2003; Pol et al.,

454   2011; Sereno et al., 2013; McPhee et al., 2019), including the Durdham Down *T. antiquus* and

455   YPM 2195 (Benton et al., 2000; Galton et al., 2007). Galton (2007) noted that the deltopectoral

456   crest of YPM 2195 had a rounded apex at 25 percent of the humeral length, proposing it as an

457   autapomorphy of *Asylosaurus* that distinguished it from the rest of the Durdham Down humeri,

458   although this crest is incomplete in these specimens. Similarly, in all Tytherington specimens,

459   the top of the deltopectoral crest is weathered so its exact shape cannot be determined nor the

460   insertion of the M. supracoracoideus identified. The anterior surface of the proximal humerus

461   medial to the deltopectoral crest is characterized by a proximodistally elongated depression that

462   tapers distally (Fig. 6A), which represents the biceps gutter (Langer et al., 2007). A faint ridge

463   that runs along the lateral side of the humerus, from the base of the deltopectoral crest to the

464   shaft, might represent an intermuscular line that delimits the origin of the M. triceps brachii

465   caput medialis (Langer et al., 2007; Burch, 2014; Otero, 2018). The lateral side of the base of the

466   deltopectoral crest exhibits a proximodistally elongated rugose surface for the insertion of M.

467   latissimus dorsi, which resembles the crest seen in *Buriolestes* (Cabreira et al., 2016) and

468   *Unaysaurus* (Leal et al., 2004). Distal to this rugosity there is a small subcircular fossa where the

469   M. humeroradialis originated (Fig. 6B, C), a trait shared with *Saturnalia* (Langer et al., 2007)

470   and *Unaysaurus* (Leal et al., 2004). The posterior surface of the proximal humerus exhibits two

471   large and shallow fossae separated by an oblique ridge.

472   The humeral shaft has an oval cross-section at its midpoint, with an almost flat posterior

473   margin. The shaft is relatively short compared to the expanded ends. The distal end is robust,

474   with a transverse width ca. 33 percent of the proximodistal length of the bone, similar to

475   *Saturnalia* (Langer et al., 2007) and *Unaysaurus* (McPhee et al., 2019). In anterior view, the

476   distal end is asymmetrical, with the medial condyle more prominent than the lateral. On the

477   anterior surface (Fig. 6E), the cuboid fossa is a wide and deep depression located between the

478   two distal condyles, which is morphologically elaborate, presenting an irregular outline with a

479   bilobate proximal margin and a strongly pitted surface. The cuboid fossa is also well developed

480   in *Saturnalia* (Langer et al., 2007) and other basal sauropodomorphs, unlike the absent or poorly

481   developed fossa of basal saurischians such a *Herrerasaurus* (Sereno, 1994) and *Tawa* (Burch,

482   2014). There is no evident fossa olecrani on the posterior surface of the distal humerus between

483   the condyles, a feature seen in other sauropodomorphs like *Saturnalia* (Langer et al., 2007) and

484   *Sarahsaurus* (Marsh and Rowe, 2018). Both the entepicondyle and the ectepicondyle present

485   striations on their posterolateral surfaces, possibly associated with the origin of digital flexors

486   and extensors, respectively (Fig. 6F, G, H).

487   **Ulna**—The ulna presents the plesiomorphic morphology of early sauropodomorphs, with a

488   developed olecranon process and a bowed shaft (Fig. 7A–C). It is posteriorly convex in lateral

489   view and slightly laterally convex in anterior view. The proximal end is twice as

490   anteroposteriorly wide as the distal end. The proximal end is triangular in proximal view, the

491   vertices of which are the anteromedial process anteriorly, the lateral process laterally and the

492   olecranon process posteriorly. The medial surface of the proximal ulna is slightly concave. The

493   radial fossa (Fig. 7A), the lateral depression for the reception of the radius that separates the

494   anteromedial and lateral processes, is shallow. A low subcircular tubercle is present on this fossa.

495   Proximodistally oriented long striae on the posterior surface of the proximal ulna, including the

496   olecranon, extend distally up to 25 percent of the length of the ulna (Fig. 7A, B), and represent

497   the insertion of M. triceps brachii. The apex of the olecranon process is abraded in most of the

498   specimens, but in those that preserve it, it is less prominent than in *Saturnalia* (Langer et al.,

499   2007) and *Chromogisaurus* (Ezcurra, 2010), and some early saurischians such as *Eodromaeus*

500   (Martínez et al., 2011) and *Gnathovorax* (Pacheco et al., 2019).

501   The shaft is elliptical in cross-section with an anteroposterior long axis. A posterolateral

502   ridge starts from the posterior edge of the shaft and extends anterodistally on the lateral surface

503   of the bone (Fig. 7A, B). This ridge probably represents an intermuscular line. The distal end of

504   the ulna has an elliptical outline in distal view, with its longest axis oriented anterolaterally with

505   respect to the proximal end. The anteromedial surface of the distal end is grooved and represents

506   the articular surface for the distal radius.

507   **Radius**—Only two radii are known from Tytherington, of which the most complete has a

508   strongly abraded surface, and only a few features can be identified and described. The radius is a

509   slender element, with proximal and distal ends subequal in size (Fig. 7D–F). The shaft presents a

510   laterally convex curvature. The distal end is mediolaterally compressed. A sculptured rugosity is

511   present on its posterolateral side, from which a posterolateral ridge extends distally forming an

512   acute angle between the posteromedial and posterolateral surfaces of the proximal radius. At the

513   midpoint of the shaft, an anteromedial protuberance appears to be present (Fig. 7F), although it

514   could be the result of taphonomic distortion. Nonetheless, the biceps tubercle is present more

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515 proximally on the anteromedial portion of the radius of *Herrerasaurus* (Sereno, 1994). The ulnar

516 articular surface is smooth and medially concave. The distal end is subtriangular in lateral view.

517 **Manus**—Known manual elements from Tytherington are disarticulated and comprise

518 metacarpals I to III of both sides, a proximal manual phalanx and two unguals (Fig. 8).

519 Numerous phalanges are also present in the collection, but due to the disarticulation and size

520 disparity, they are very difficult to assign to the manus or the pes and therefore are excluded

521 from the present descriptive account.

522 Metacarpal (MC) I is the most robust metapodial element of the manus, being shorter and

523 broader than the other metacarpals (Fig. 8A, B). The mediolateral width of the proximal end is

524 55 percent the proximodistal length of the bone, relatively broader than the MC I of

525 *Macrocollum* (Müller et al., 2018b), but narrower than those of *Eoraptor* (Sereno et al., 2013)

526 and more derived sauropodomorphs like *Unaysaurus* (McPhee et al., 2019), *Adeopapposaurus*

527 (Martínez, 2009), *Sarahsaurus* (Marsh and Rowe, 2018) or *Mussaurus* (Otero and Pol, 2013).

528 Since manual elements are isolated, the proximal inset of MC I into the carpus, characteristic of

529 basal sauropodomorphs (Sereno, 2007; Martínez, 2009; Otero and Pol, 2013; Sereno et al.,

530 2013), cannot be determined. The proximal end is quadrangular in shape, with the lateral side

531 being longer than the medial, and the dorsal longer than the palmar. The medial side is rounded

532 in proximal view, and the lateral side is straight to slightly concave. The dorsal surface of the

533 proximal end is pitted and rugose (Fig. 8A), and was the origin of M. extensor digitorum

534 profundus (mEDP) on MC I. The palmar surface of the proximal end is marked by a scarred

535 shallow concavity located on the lateral side (Fig. 8B), which represents the origin of M. flexor

536 digitorum profundus (mFDP) on MC I (Otero, 2018). The lateral side of the proximal portion is

537 straight to concave and directed lateropalmarly, being the articular surface for metacarpal II. The

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538 shaft is short, subequal in length to the proximal and distal ends, and dorsopalmarly compressed.

539 A lateral depression is present immediately proximal to the lateral condyle on the dorsal surface

540 of the shaft. The distal end is strongly asymmetric, and hourglass-shaped in distal view,

541 represented by two condyles separated by a deep groove. The lateral condyle is more prominent

542 laterodistally than the medial, and is more dorsopalmarly deep, particularly projecting in a dorsal

543 direction. The medial condyle is less prominent. The lateral collateral pit is proximodistally

544 elongated while the medial pit is circular. The distal condyles are twisted approximately 15

545 degrees relative to the transverse axis of the proximal end, similar to *Eoraptor* (Sereno et al.,

546 2013), but less than in more derived sauropodomorphs such as *Mussaurus* (Otero and Pol, 2013).

547   Metacarpal II (Fig. 8C, D) is longer and narrower than MC I, but more robust than MC III.

548 The proximal end is laterally wider than the distal end and quadrangular in proximal view. The

549 lateral side of the proximal part of MC II is dorsolaterally oriented and concave, representing the

550 articular surface for MC III (Fig. 8C). The medial side of the proximal portion is mediopalmarly

551 oriented, with a shallow, heavily grooved concave surface that articulates with MC I (Fig. 8D).

552 The palmar surfaces of the proximal portion are heavily pitted, representing the muscle scar for

553 the origin of mFDP on MC II (Otero, 2018). The dorsomedial edge of the proximal portion

554 presents a distally elongated rugosity extending up to the beginning of the shaft, which might

555 represent the origin of mEDP on MC II, as well as the flat dorsal surface of the proximal end,

556 lateral to the ridge. The shaft is straight and wider mediolaterally than dorsopalmarly, with an

557 ellipsoid cross section. The distal end presents dorsally a deep, subcircular extensor depression

558 that extends up to the sides and is delimited by marked ridges on both sides. The distal end is

559 subrectangular in distal view. The distal condyles are subequal in size and are not distally

560 separated by an intercondylar groove. Instead, the distal surface of MC II, which articulates with

25

561 the proximal phalanx of digit II, is smooth and cylindrical. The medial collateral pit is very

562 shallow in contrast with the deep and ovoid lateral collateral pit.

563   Metacarpal III (Fig. 8E, F) is more slender than the two more medial metacarpals. The

564 proximal end is notably laterally wider than the distal end. The proximal end is relatively flat and

565 subtriangular in proximal view, with a straight palmar side, like in *Unaysaurus* (McPhee et al.,

566 2019). The dorsolateral side of the proximal end is slightly concave and heavily scarred,

567 representing the articulation surface for MC IV (Fig. 8E). The palmar side of the proximal end is

568 marked by a lateral rugose surface that represent the origin of the mFDP (Fig. 8F). The shaft is

569 relatively longer with respect to the ends than in MC II, and it is subcylindrical. The dorsal

570 extensor depression is shallower than in MC II, semicircular in shape due to the dorsal extension

571 of the cylindrical phalangeal articular surface. The distal condyles are subequal in size and not

572 separated by an intercondylar groove.

573   The proximal phalanx of manual digit I has an expanded proximal end and a relatively

574 narrower distal end (Fig. 8G, H). The proximal articulation for MC I is concave and

575 asymmetrical, divided into two facets for the distal condyles of MC I, with the lateral facet being

576 larger than the medial one. In lateral view, the palmar margin of the proximal end extends further

577 proximally than the dorsal margin. The shaft is circular in cross section and subequal in length to

578 the ends. The distal end lacks an extensor depression and presents a deep and narrow

579 proximopalmar intercondylar groove. The distal condyles are twisted with respect to the

580 proximal end, as seen in other basal sauropodomorphs (Martínez, 2009; Otero and Pol, 2013;

581 Sereno et al., 2013; McPhee et al., 2019). The two well-developed circular collateral pits face

582 mediodorsally and laterodorsally.

583   A number of unguals are known from Tytherington, some of them robust and dorsoventrally

584   deep, representing manual digit I unguals (Fig. 8I). Manual ungual I is slightly mediolaterally

585   compressed (width to height ratio of the proximal end of 64 percent), and relatively wider than in

586   many basal sauropodomorphs (Martínez, 2009; Otero and Pol, 2013; McPhee et al., 2019). The

587   articular surface is concave in lateral view, with a central dorsopalmar ridge that fitted to the

588   intercondylar groove of the distal condyles of the proximal phalanx of digit I. The dorsal edge

589   projects proximally and exhibits pits and grooves that mark the insertion of M. extensores

590   digitorum profundus et superficialis (Otero, 2018). The palmar portion of the proximal end

591   presents a prominent flexor tubercle with a strongly grooved surface that represents the insertion

592   of M. flexor digitorum longus (Otero, 2018). Manual ungual I is notably curved distally and

593   presents deep collateral grooves, the proximal portions of which curve palmarly. Other ungual

594   elements are more slender and straighter (Fig. 8J). The proximal end is dorsoventrally shorter

595   and the flexor tubercle is less prominent. These unguals probably belong to digits II or III, or the

596   pes.

597   **Ilium**—Tytherington has yielded a number of *Thecodontosaurus* ilia, three of which are

598   almost complete, enabling the accurate reconstruction of this element (Fig. 9). The ilium is

599   anteroposteriorly longer than dorsoventrally tall, with a height to length (from the anterior end of

600   the pubic peduncle to the posterior end of the postacetabular process) ratio of 54 percent, similar

601   to *Panphagia* (52%, Martínez and Alcober, 2009) and proportionally more elongated than those

602   of *Chromogisaurus* (61%, Ezcurra, 2010), *Saturnalia* (62%, Langer, 2003) and particularly

603   *Buriolestes* (67%, Cabreira et al., 2016) and *Pantydraco* (68%, Galton et al., 2007; Galton and

604   Kermack, 2010). The dorsal outline, complete in BRSUG 28121, is almost straight in lateral

605   view.

606   The preacetabular process is short, with a rounded anterior outline, and is slightly curved

607   laterally, as in the Durdham Down *T. antiquus* (NHMUK PV R1539, Benton et al., 2000). The

608   ventral deflection of this process, used to differentiate *T. antiquuus* from *Pantydraco* (Yates,

609   2003a), is absent in all the Tytherington specimens and in the specimen NHMUK PV R1539

610   from Durdham Down (Benton et al., 2000). In anterior view, the preacetabular process is

611   dorsolaterally convex. The anterodorsal border of the preacetabular process shows a pitted and

612   grooved surface (Fig. 9A) and corresponds to the insertion of M. iliotibialis 1 (Hutchinson,

613   2001a). The anterior margin of the ilium between the preacetabular process and the base of the

614   pubic peduncle is anteriorly concave and U-shaped in lateral view. In this part of the bone the

615   preacetabular fossa is present and separated from the main lateral body of the ilium by the

616   preacetabular ridge (Fig. 9A). This fossa has a pitted surface that represents the origin of the M.

617   iliofemoralis internus (Hutchinson, 2001a). The medial side of the preacetabular process exhibits

618   a faintly scarred surface, similar to *Pampadromaeus* (Langer et al., 2019), which could indicate

619   the incorporation of a dorsal vertebra into the sacrum, as seen in *Eoraptor* (Sereno et al., 2013)

620   and sauropodomorphs more derived than *Thecodontosaurus* (Yates, 2003b).

621   The ilium bears a laterally prominent, dorsally convex supracetabular crest that almost

622   reaches the ventral end of the pubic peduncle (Fig. 9A). This crest is similarly expanded in other

623   basal sauropodomorphs (Langer, 2003; Martínez and Alcober, 2009; Ezcurra, 2010; Cabreira et

624   al., 2016; Sereno et al., 2013, Langer et al., 2019), becomes less prominent in plateosaurians

625   (Martínez, 2009; Otero and Pol, 2013; Apaldetti et al., 2013; McPhee et al., 2015; Marsh and

626   Rowe, 2018, Tsai et al., 2018) and greatly reduced in *Lessemsaurus* and eusauropods (Pol and

627   Powell, 2007). The pubic peduncle is longer that the ischial peduncle, and projects

628   anteroventrally. The ischial peduncle is oriented ventrally and presents a slightly convex

629 antitrochanter on its anterolateral surface, within the acetabulum. Both peduncles are

630 subtriangular in cross-section defined by the laterally projecting supracetabular crest and a

631 straight medial side. The acetabulum is not fully perforated, with a medial wall that extends

632 ventrally to the level of the pubic and ischial peduncles, the plesiomorphic condition also seen in

633 other basal sauropodomorphs (Langer, 2003; Ezcurra, 2010; Galton and Kermack, 2010; Müller

634 et al., 2018a; Langer et al., 2019; Pretto et al., 2019), and differing from the fully perforated

635 acetabulum of *Efraasia* and more derived sauropodomorphs (Yates, 2007; Martínez, 2009; Otero

636 and Pol, 2013; McPhee et al., 2014, Tsai et al., 2018). The medial side of the ilium bears a

637 sinusoidal scar that related to the sacral rib articulations (Fig. 9B). The articular facet for the first

638 sacral rib is subhorizontal, while the second sacral rib articulation is posterodorsally oriented.

639   The postacetabular process is more prominent than the preacetabular one, extending well

640 posteriorly behind the ischial peduncle. It becomes mediolaterally broader posteriorly, with a

641 robust posterior end. The process is oriented posteriorly similar to those of *Saturnalia* (Langer,

642 2003), *Pampadromaeus* (Langer et al., 2019) and *Macrocollum* (Müller et al., 2018b), and unlike

643 the posterodorsally projecting process of *Buriolestes* (Müller et al., 2018a), *Bagualosaurus*

644 (Pretto et al., 2019) and *Pantydraco* (Yates, 2003a; Galton and Kermack, 2010). The

645 postacetabular process presents a well-developed dorsal ridge that delimits an anteroposteriorly

646 elongated dorsal concavity with a grooved surface (Fig. 9A) that marks the origin of M.

647 iliotibialis 3. The posterolateral surface of the postacetabular process, ventral to the dorsal ridge,

648 bears an extensive muscle scar for the origin of M. flexor tibialis externus, also present in

649 *Saturnalia* (Langer, 2003), *Chromogisaurus* (Ezcurra, 2010) and *Buriolestes* (Müller et al.,

650 2018a), and previously considered an apomorphy of Saturnaliinae (Garcia et al., 2019). On the

651 posterior part of the ilium, ventral to the postacetabular process, a shallow brevis fossa is present,

652   anterodorsally bounded by a faintly defined the brevis shelf in lateral view (Fig. 9A). This

653   reduced brevis fossa is similar to that of *Pantydraco* (Yates, 2003; Galton and Kermack, 2010)

654   and more derived sauropodomorphs (McPhee et al., 2015; McPhee and Choiniere, 2016), and

655   differs from the well-developed fossae of other basal sauropodomorphs (Galton, 1973; Langer,

656   2003; Martínez and Alcober, 2009; Ezcurra, 2010; Cabreira et al., 2016; Sereno et al., 2013). The

657   brevis shelf is also more conspicuous in other taxa such as *Buriolestes* (Cabreira et al., 2016),

658   *Chromogisaurus* (Ezcurra, 2010), *Pampadromaeus* (Langer et al., 2019), and *Efraasia* (Galton,

659   1973). The brevis fossa has a pitted surface with a different texture from the rest of the bone,

660   marking the origin of the M. caudofemoralis brevis. In medial view (Fig. 9B), the brevis fossa is

661   anterodorsally separated from the sacral rib articular surface by the posteromedial shelf, a feature

662   that is also present in *Pampadromaeus* (Langer et al., 2019). Dorsal to this shelf, a dorsomedial

663   ridge bounds a dorsomedial pitted concavity.

664   **Ischium**—Only two fragmentary ischia have been recovered from Tytherington. The distal

665   end, the anterior edge of the shaft and the medioventral lamina are missing in the two specimens,

666   providing an incomplete idea of this element. The ischial shaft is subrectangular in cross-section,

667   flat and is slightly laterally convex (Fig. 9C). The posterodorsal surface of the ischial shaft

668   ventral to the iliac peduncle bears a groove delimited by a marked ridge on both sides that

669   represents the origin site for M. adductor femoris 2 (Hutchinson, 2001a).

670   **Femur**—Several femora attributable to *Thecodontosaurus* were found at Tytherington, some

671   of them almost complete (Fig. 10). There is a remarkable variation in size among Tytherington

672   femora, with the complete specimens ranging from 12 to 22 cm in length (Fig. S2).

673   The femur is sigmoid in anterior view, with an anteromedially projecting head and a

674   posterior end that is curved in a posterolateral direction (Fig. 10). In dorsal view, the main axes

675   of the femoral head and the distal end form an angle greater than 90 degrees. The proximal end

676   of the femur is abraded in most specimens, and consequently the morphology of the greater

677   trochanter cannot be determined. The femoral head has a semicircular shape, with flat anterior

678   and posterior sides. Its medial orientation delimits a medially concave ventral emargination distal

679   to it. Distal to this emargination, a large oval foramen for the femoral nutrient artery is present on

680   the medial surface of the bone (Fig. 10D). The proximal end of the femur has a reduced

681   anterolateral tuber that is connected to the proximal tip of the lesser trochanter by an oblique

682   anteromedial crest, as seen in other basal sauropodomorphs (Langer, 2003; Müller et al., 2018a,

683   2018b; Langer et al., 2019). A faint posteromedial tuber is also present at the proximal end,

684   shared by other basal taxa (Langer, 2003; Müller et al., 2018a; Langer et al., 2019) and less

685   developed than in *Macrocollum* (Müller et al., 2018b).

686   A synapomorphic feature of the proximal femur of *Thecodontosaurus* is the absence of a

687   trochanteric shelf (Fig. 10A). This structure evolved in Dinosauriformes (Novas, 1996) and is

688   retained by other basal sauropodomorphs such as *Buriolestes* (Müller et al., 2018a),

689   *Pampadromaeus* (Langer et al., 2019) and *Bagualosaurus* (Pretto et al., 2019), but lost in more

690   derived sauropodomorphs (Galton, 1973; Martínez, 2009; Müller et al., 2018b; Barrett et al.,

691   2019). This character seems to be affected by ontogeny in *Pampadromaeus*, as juvenile

692   specimens lack a trochanteric shelf which is seen in adults (Müller et al., 2019), although this is

693   probably not the case in *Thecodontosaurus* as this structure is absent in juvenile to adult femora

694   (Fig. S2). This indicates that *Thecodontosaurus* is among the most basal taxa to lose the

695   trochanteric shelf. The lesser (anterior) trochanter is proximodistally elongated and located on

696   the anterolateral surface of the proximal femur. The proximal tip of the lesser trochanter is

697   completely attached to the shaft as in *Pampadromaeus* (Müller et al., 2015; Langer et al., 2019)

698 and unlike *Saturnalia*, in which it is separated by a cleft (Langer and Ferigolo, 2013). A shallow

699 fossa proximolaterally bounds the lesser trochanter and in turn is laterally delimited by the

700 rugose dorsolateral trochanter (Fig. 10A, B). Both the lesser trochanter and the fossa present a

701 pitted and grooved surface that represent the muscle scar for the insertion of M. iliofemoralis

702 (Hutchinson, 2001b). A dorsolateral trochanter located on the anterolateral proximal femur

703 laterally delimits this fossa and would have been continuous with the greater trochanter. On the

704 posterolateral surface of the proximal femur a similar rugose and pitted feature, the posterolateral

705 proximal tuberosity, is present (Fig. 10C).

706 In BRSUG 23615, the shaft has a diameter of 2.1 cm at its midpoint, with a diameter to

707 length ratio of 10 percent. The shaft is subtriangular in cross section due to the presence of three

708 intermuscular lines. The anterior intermuscular line runs from the distal end of the lesser

709 trochanter to the anterior surface of the lateral distal condyle (Fig. 10A). The posteromedial

710 intermuscular line is continuous with the distal end of the fourth trochanter and ends at the

711 medial condyle (Fig. 10C). The third intermuscular line, the posterolateral one, has its origin

712 distal to the greater trochanter and reaches the posterior surface of the lateral condyle (Fig. 10B).

713 The anterior and posteromedial intermuscular lines delimit the origin site of M. femorotibialis

714 medialis, and the anterior and posterolateral lines bound that of M. femorotibialis lateralis

715 (Hutchinson, 2001b).

716 The fourth trochanter is subrectangular and placed on the posterior part of the femur, with its

717 distal tip located approximately 40 percent along the bone in BRSUG 23615. The fourth

718 trochanter is also located in the proximal half of the femur in other basal sauropodomorphs

719 (Galton, 1973; Otero and Pol, 2013; Cabreira et al., 2016; Müller et al., 2018b) and becomes

720 more distally positioned in *Melanorosaurus*, *Anchisaurus*, *Aardonyx* and more derived

721 sauropodiforms (Yates and Kitching, 2003; Galton et al., 2005; Yates et al., 2010). The medial

722 surface of the trochanter bears a clear concave muscle scar with a highly pitted surface which

723 represents the insertion of M. caudofemoralis longus (Fig 10C, D). The proximolateral portion of

724 the fourth trochanter exhibits a tear-drop-shaped pitted surface and was the insertion of M.

725 caudofemoralis brevis (Fig. 10C). Variation in fourth trochanter morphology and position

726 associated with size can be described among the different *Thecodontosaurus* femora from

727 Tytherington (Fig. S2). This structure seems to experience negative allometry throughout

728 ontogeny, as its proximodistal length is relatively greater (20% of total femoral length) in

729 BRSUG 26602, a possible infant specimen of 12 cm in length, compared to larger femora (16%

730 in BRSUG 23615, of 22 cm). Additionally, the relative position of the fourth trochanter seems to

731 shift proximally with size: the distal end of the trochanter is located at 44% of the femoral length

732 in BRSUG 26602 and at 40% in BRSUG 23615. These changes possibly had implications for

733 locomotion throughout ontogeny, particularly affecting the orientation and moment arms of the

734 caudofemoralis musculature.

735   The distal condyles are slightly asymmetrical, with the lateral (fibular) condyle being more

736 prominent as a result of the slight lateral curvature of the distal end of the femur (Fig. 10C). In

737 posterior view, the condyles are laterally pinched and separated by the popliteal fossa, a marked

738 concavity with extensive pitting, bounded by the distal segments of the posteromedial and

739 posterolateral intermuscular lines (Fig. 10C). In some specimens (e.g. BRSUG 29372-2882), a

740 muscle scar is seen on the lateral surface of the distal femur, anteroproximal to the fibular

741 condyle. This scar might be homologous to the anteromedial distal crest of other dinosaurs

742 (Hutchinson, 2001b), an osteological correlate for the attachment of the distal head of M.

743 femorotibialis lateralis. Further evidence of muscle scarring is found on the anterolateral surface

744   of the distal end of the femur, proximal to the lateral condyle, probably representing the femoral

745   origin of the digital extensors. The distal surface of the femur is abraded in all specimens,

746   making the interpretation of features on the zeugopod articular surface complicated.

747   **Tibia**—Tibial morphology is reconstructed based on several specimens of different sizes,

748   bracketed between the smallest (13.3 cm), possibly a juvenile, and the largest (19.7 cm). The

749   tibia is a straight bone with anteroposteriorly expanded ends, the proximal end being twice as

750   anteroposteriorly wide as the distal (Fig. 11A, B). The proximal end is subtriangular in proximal

751   view, with the three edges represented by the anterior cnemial crest and the medial and lateral

752   condyles (Fig. 11C). The cnemial crest is anteroproximally projected and extends about a fourth

753   of the length of the tibia. The surface of the crest is pitted, marking the insertion scar of the

754   muscles that form the triceps femoris group. The cnemial crest and the lateral condyle are

755   separated by a shallow anterolateral notch, the incisura tibialis (Fig. 11A). Anterodistal to the

756   lateral condyle an oval rugosity with a pitted surface is present in some specimens, such as

757   BRSUG 26656. This structure is also present in *Saturnalia* (Langer, 2003) and is homologous to

758   the fibular crest of *Eoraptor* and some theropods (Sereno et al., 2013). Such a rugosity serves for

759   articulation with the fibula and the insertion of the tibiofibularis ligament (Langer, 2003). The

760   lateral condyle does not extend posteriorly as far as the medial one, being placed at the middle of

761   the proximal tibia in lateral view. The medial and posterior surfaces of the medial condyle

762   present a pitted and grooved pattern indicative of muscle attachment (Fig. 11B), possibly for the

763   insertion of M. flexor tibialis internus and M. flexor tibialis externus, components of the flexor

764   cruris group.

765   The shaft is straight and subrectangular in cross section, with flattened medial and lateral

766   sides and an anteroposterior axis slightly longer than the mediolateral axis. On the lateral surface

767 of the proximal fourth of the tibia a large, oval nutrient foramen for the passage of the tibialis

768 cranialis artery is present in BRSUG 26656, as seen in *Saturnalia* (Langer, 2003). The distal end

769 of the tibia in *Thecodontosaurus* exhibits a highly derived morphology, being slightly wider

770 mediolaterally than anteroposteriorly and with an almost squared outline in distal view. The

771 anterior portion of the distal end consists of an anterolateral process that distally bears a concave

772 facet for the astragalar ascending process (Fig. 11D). This facet is posteriorly bounded by a

773 convex posterolateral descending process, anteroposteriorly wider than in other basal

774 sauropodomorphs such as *Eoraptor* (Sereno et al., 2013), *Saturnalia* (Langer, 2003), *Panphagia*

775 (Martínez and Alcober, 2009), *Adeopapposaurus* (Martínez, 2009), *Coloradisaurus* (Apaldetti et

776 al., 2013) and *Mussaurus* (Otero and Pol, 2013). However, the posterolateral process is

777 mediolaterally compressed and does not extend as far laterally as the anterolateral process, which

778 is a proposed synapomophy of Sauropoda (Yates, 2004; Pol and Powell, 2007; Yates and

779 Kitching, 2010; Ezcurra and Apaldetti, 2012; McPhee et al., 2014), also present in *Anchisaurus*

780 *polyzelus* (Yates, 2004), *Eucnemesaurus entaxonis* (McPhee et al., 2015) and *Aardonyx* (Yates et

781 al., 2010). A proximodistally oriented notch runs along the lateral surface of the distal end of the

782 tibia and separates the anterolateral and posterolateral processes. This notch is remarkably

783 reduced compared to other basal sauropodomorphs (Langer, 2003; Martínez, 2009; Martínez and

784 Alcober, 2009; Apaldetti et al., 2013; Otero and Pol, 2013; Sereno et al., 2013), and resembles

785 that of PULR 136 and *Antetonitrus* (Yates and Kitching, 2010; Ezcurra and Apaldetti, 2012;

786 McPhee et al., 2014). Unlike *Riojasaurus* and PULR 136, a notch is absent from the

787 posteromedial corner of the distal end of the tibia (Ezcurra and Apaldetti, 2012).

788   **Fibula**—No complete fibula is preserved but some partial specimens have been found at

789 Tytherington. The fibula is a slender and straight bone. The proximal end is rounded in lateral

790   view and anteroposteriorly elongated and mediolaterally compressed, with an oval-shaped

791   proximal head in proximal view. The head is heavily scarred indicating it was covered by a

792   cartilaginous sheath (Fig. 11F). Within the proximal part of the bone there is a proximodistally

793   elongated anterolateral tubercle that bears scarring and was the insertion of M. iliofibularis (Fig.

794   11E). On the medial side and slightly distal to this scar, a medial pitted ridge is present (Fig.

795   11F), which is less pronounced and proximodistally elongated than that of *Buriolestes* (Müller et

796   al., 2018a) and *Gnathovorax* (Pacheco et al., 2019). The distal end of the fibula is

797   anteroposteriorly expanded and oval in distal view. The distal surface is proximomedially

798   oriented and anterodistally inclined. The medial surface of the distal end is slightly expanded and

799   presents an ornamented articular facet for the astragalus.

800   **Pes**—Disarticulated elements of the pes have been found at Tytherington, including

801   metatarsals I to IV of both sides and some proximal and possible distal pedal phalanges (Fig. 12).

802   The orientation of metatarsal (MT) I differs from the other elements of the metatarsus, as

803   indicated by the articular surface for MT II, facing more medially than the other pedal

804   metapodials. The shape of MT I (Fig. 12A–D) indicates that it was appressed to MT II, with its

805   distal end not notably separated from the latter. The proximal and distal ends are subequal in size

806   (Fig. 12A–D), and they are not rotated relative to each other, unlike in other sauropodomorphs

807   such as *Pampadromaeus* (Langer et al., 2019) or *Adeopapposaurus* (Martínez, 2009). The

808   proximal end and the shaft are mediolaterally compressed. The elliptical proximal end presents a

809   rugose lateroplantar side that articulates with MT II (Fig. 12B). The maximum width of the

810   proximal end is 34 percent the proximodistal length of the bone, being proportionally more

811   robust than in Carnian sauropodomorphs (Sereno et al., 2013; Langer et al., 2019; Pretto et al.,

812   2019), but within the range of most post-Carnian basal sauropodomorphs such as

813   *Adeopapposaurus* (Martínez, 2009), *Coloradisaurus* (Apaldetti et al., 2013), *Leonerasaurus* (Pol

814   et al., 2011), *Sarahsaurus* (Marsh and Rowe, 2018) and *Mussaurus* (Otero and Pol, 2013). The

815   minimum transverse width of the shaft is 19 percent of the MT I proximodistal length, which is

816   slightly lower than in most post-Carnian basal sauropodomorphs (McPhee et al., 2014, 2019),

817   but higher than that of Carnian sauropodomorphs (Sereno et al., 2013; Langer et al., 2019; Pretto

818   et al., 2019). The orientation of MT I results in the extensor depression facing dorsomedially and

819   the collateral pits, dorsal and plantarly. The extensor depression is deep and subcircular in

820   outline, and it is distally bounded by a prominent ventromedially facing phalangeal articular

821   surface that lacks an intercondylar groove (Fig. 12B). The distal condyles differ in size, with the

822   dorsolateral one being bigger and more prominent. No clear muscle scars are present in MT I,

823   similar to *Saturnalia* (Langer, 2003) and unlike *Herrerasaurus* (Novas, 1994).

824   Metatarsal II (Fig. 12E–H) is long and one of the weightbearing elements of the metatarsus,

825   unlike MT I. The proximal end is flat and rectangular in proximal view, dorsoplantarly expanded

826   and mediolaterally compressed, similar to that of *Saturnalia* (Langer, 2003) and *Herrerasaurus*

827   (Novas, 1994), and unlike the hourglass-shape of more derived sauropodomorphs (Martínez,

828   2009; Otero and Pol, 2013). The dorsal (anterior) surface of the proximal end is concave and

829   grooved (Fig. 12E), probably indicating the insertion of M. tibialis anterior (Carrano and

830   Hutchinson, 2002), as in other metatarsals. Its mediodorsal side is concave and contacted the

831   proximal end of MT I, while the lateroplantar side is flat and contacted MT III (Fig. 12F). The

832   long axis of the proximal end is rotated approximately 60 degrees with respect to the transverse

833   axis of the distal end (Fig. 12G, H), similar to *Mussaurus* (Otero and Pol, 2013). The shaft is

834   long and straight, with a subcircular cross section. The distal end is slightly medially curved,

835   with distal condyles that are subequal in size and separated by a shallow intercondylar groove

37

836 that continues posteriorly. The dorsal extensor depression is shallow and semicircular in shape.

837 The lateral collateral pit is deep while the medial one is absent.

838   Metatarsal III (Fig. 12I–L) is a long, slender and weightbearing element. In proximal view,

839 the proximal end is subtriangular with a rounded plantar border. The dorsomedial surface of the

840 proximal MT III is flat and contacts MT II (Fig. 12I). The lateroplantar side of the proximal end

841 is concave and houses the medial projection of proximal MT IV (Fig. 12J). The long axes of both

842 ends are twisted approximately 45 degrees from one another (Fig. 12K, L). On the dorsolateral

843 edge of the proximal shaft, a pitted proximodistally elongated scar is present. The shaft is long,

844 and its cross section is wider mediolaterally than dorsoplantarly, with a straight dorsal margin.

845 The distal end is medially curved as in MT II, and presents a deep lateral collateral pit and a

846 shallow medial collateral depression. The dorsal extensor depression is shallow and semicircular.

847   Metatarsal IV (Fig. 12M–P) is the third weightbearing element of the metatarsus. It is

848 proportionately more robust than MT III. The proximal end is remarkably wide mediolaterally

849 and flattened dorsoplantarly. The outline of the proximal end is subtriangular, with a straight

850 plantar side and an obtuse angle formed by the dorsal and dorsomedial sides. The proximal

851 surface of MT IV is concave, with a marked depression at the center, probably for the reception

852 of distal tarsal IV. The dorsomedial side of proximal MT IV projects medially to contact MT III

853 plantarly (Fig. 12M). A proximodistally elongated crest is present on the dorsal surface distal to

854 the MT III articular surface. The plantar surface of proximal MT IV shows an oval medial

855 rugosity and a reduced articular surface for MT V on the lateral corner (Fig. 12N). The shaft is

856 mediolaterally wider than dorsoplantarly, and is slightly sigmoid in lateral view. Unlike in other

857 metatarsals, the distal end presents similar dorsoplantar and mediolateral lengths, while in

858 *Saturnalia* it is not subequal (Langer, 2003). The distal condyles are not separated by an

859   intercondylar groove. There is no medial collateral pit and the lateral collateral pit is wide, deep

860   and subtriangular.

861   Two phalanges can be identified as proximal pedal phalanges and probably belonging to

862   either digits II, III or IV. One is more elongated and has a more slender shaft, probably belonging

863   to digit III (Fig. 12Q, R), while the other is shorter and more robust, and thus could be assigned

864   to digit IV (Fig. 12S, T). They are hourglass-shaped in dorsal view, with proximal and distal

865   ends of almost equal mediolateral widths. The proximal end is concave and semicircular in

866   outline, with a straight plantar side and a proximally projecting dorsal margin. The proximal end

867   is wider mediolaterally than dorsoplantarly. The collateral pits are deep and the extensor fossa is

868   shallow. The distal condyles are equal in size and separated by a shallow and wide intercondylar

869   depression. Some phalanges of small size, short and robust are likely distal pedal phalanges (Fig.

870   12U, V) but difficult to assign to specific digits.

871

872   DISCUSSION

873

874   **The Taxonomic Status of *Thecodontosaurus***

875   The sauropodomorph material from Tytherington shares characters that support its

876   assignment to *Thecodontosaurus antiquus*. From the original diagnosis of the species (Benton et

877   al., 2000), the only apomorphy that can be assessed, a subquadratic posterior end of the

878   postacetabular process of the ilium, is matched by Tytherington ilia. This character was later

879   identified as a plesiomorphy (Yates, 2003a), although recent sauropodomorph discoveries show

880   its variability and continuous variation (e.g., Langer, 2003; Cabreira et al., 2016; Pretto et al.,

881   2019), making it a poor diagnostic trait. Yates (2003) proposed an emended diagnosis of the

882 genus *Thecodontosaurus*, of which two characters – (1) extreme posterior position of the neural

883 spines in anterior and mid-caudal vertebrae and (2) reduced ventral groove in anterior caudals

884 and absent in mid and posterior caudals – are clearly identified in the Tytherington vertebrae

885 (Fig. 3E–K), although a reduced ventral groove is present in Tytherington posterior caudals (Fig.

886 3K). However, these two traits have poor diagnostic power: the first one fails to discriminate

887 *Thecodontosaurus* from other basal sauropodomorphs, such as *Chromogisaurus* (Ezcurra, 2010),

888 *Bagualosaurus* (Pretto et al., 2019) or *Efraasia* (Galton, 1973); and the second character is

889 equivocal for being highly variable at both intra- and interspecific levels (Yates, 2004; Martínez,

890 2009; Ezcurra, 2010; Marsh and Rowe, 2018; Langer et al., 2019). A third *Thecodontosaurus*

891 apomorphy, anterior cervical epipophyses plate-like and overhanging the postzygapophyses

892 posteriorly, was later considered diagnostic of *Pantydraco caducus* instead by Galton and

893 Kermack (2010), who argued that the Durdham Down cervicals formed raised ridges. However,

894 the Tytherington cervicals have plate-like epipophyses (Fig. 2D) that do not overhang the

895 posterior margin of the postzygapophyses, a condition that we also identify in the Durdham

896 Down material.

897   Yates (2003) noted two additional characters of *T. antiquus* that differed from *T.* (now

898 *Pantydraco*) *caducus*: a strongly projecting medial tuberosity of the humerus and a ventrally

899 oriented preacetabular process of the ilium. The first of these two characters is problematic, as

900 the tip of the humeral medial tuberosity is highly abraded in most of the *Thecodontosaurus* and

901 *Pantydraco* specimens (Benton et al., 2000; Galton et al., 2007; Galton and Kermack, 2010),

902 including the Tytherington humeri (Fig. 6). Only YPM 2195 seems to preserve a complete

903 medial tuberosity, which projects strongly in a medial direction (Benton et al., 2000; Galton,

904 2007). Thus, this character is not valid to establish differences between *Thecodontosaurus*,

905   *Pantydraco* and the problematic *Asylosaurus*. Similarly, all Tytherington ilia have an anteriorly

906   oriented preacetabular process as in *Pantydraco* and unlike the interpretation of the Durdham

907   Down ilia (Yates, 2003a; Galton and Kermack, 2010). The orientation of this process, as well as

908   a few other iliac traits, have been reported to be affected by taphonomic deformation in other

909   basal sauropodomorphs because of its fragility (Müller et al., 2018c). Although the morphology

910   of the preacetabular process, as well as other iliac characters, is different in *T. antiquus* and *P.*

911   *caducus*, its orientation results in confusion when used to diagnose taxa. Therefore, we consider

912   these two characters ineffective in distinguishing *T. antiquus* from *P. caducus*.

913   The diagnosis of *Pantydraco caducus* included the presence of pleurocoel-like openings

914   on the neurocentral suture of the sixth to eight cervicals as an autapomorphy (Yates, 2003a;

915   Galton and Kermack, 2010). This is the remaining character, together with the position of the

916   anterior cervical epipophyses, that distinguished *Pantydraco* from *T. antiquus*, and it is also

917   absent in the Tytherington cervicals. Nonetheless, this character is problematic and is affected by

918   ontogeny, as these openings commonly occur in juvenile sauropods (Wedel, 2003; 2007). When

919   first described, *Pantydraco* was identified as a juvenile *T. antiquus* (Kermack, 1984; Benton et

920   al., 2000), and the differences between the two were attributed to morphological variation in

921   ontogenetic states of the same taxon. In cladistic analyses, *Pantydraco* is consistently recovered

922   as either the sister taxon to *Thecodontosaurus* (Bronzati et al., 2019; Langer et al., 2019; Pretto et

923   al., 2019), or to the clade including *Thecodontosaurus* and more derived sauropodomorphs

924   (Otero and Pol, 2013; McPhee et al., 2015), indicating that it might belong to the same taxon or

925   that the more basal position of *Pantydraco* is because it retains some plesiomorphic character

926   states due to its early ontogenetic stage. In conclusion, anatomical, phylogenetic and

927 biochronological evidence render the validity of *Pantydraco caducus* uncertain and opens the

928 possibility that it represents an immature individual of *T. antiquus*.

929   Three autapomorphies were originally proposed for *Asylosaurus yalensis* (Galton, 2007):

930 deltopectoral crest with a round apex at 25 percent of the humeral length, manus with phalangeal

931 lateral reduction (phalangeal formula 2-3-4-2-?1), and ischia distally separated by a medial cleft

932 with an "inverted V" shape in dorsal view. As discussed above, the first character is problematic

933 in establishing differences with *Thecodontosaurus*, as the deltopectoral crest is not intact in any

934 of the Durdham Down or Tytherington humeri (Benton et al., 2000; Galton et al., 2007).

935 Additionally, the morphology of the tip of the deltopectoral crest is susceptible to taphonomic

936 distortion (Yates, 2003; Langer et al., 2007), so the presence of the apex in YPM 2195 could be

937 partly caused by these processes. Second, the phalangeal formula is unknown in

938 *Thecodontosaurus*, as a complete, articulated manus has not been found, making the second

939 character ineffective in distinguishing YPM 2195 as a separate taxon. Additionally, lateral

940 reduction of the manual phalangeal count is a phenomenon that also occurs in other basal

941 sauropodomorphs such as *Eoraptor* (Sereno et al., 2013) and *Sarahsaurus* (Marsh and Rowe,

942 2018). The third character is based on ischium fragments that were tentatively referred to

943 *Asylosaurus*, without any evidence (Galton, 2007). Thus, none of the three synapomorphies of

944 *Asylosaurus* proposed by Galton (2007) provides solid diagnostic evidence for the validity of this

945 genus. The taxonomic status of *Asylosaurus* has not been further examined as it has not been

946 included in phylogenetic analyses as an independent taxon – but as *Thecodontosaurus* in Sertich

947 and Loewen (2010). However, Galton and Kermack (2010) suggested that *Asylosaurus* would

948 probably occupy a position close to *Thecodontosaurus* and *Pantydraco*. Based on the lack of

949   diagnostic traits to distinguish it from *Thecodontosaurus*, we consider *Asylosaurus yalensis* a

950   taxon of highly questionable validity.

951

952   **Paleobiology and Ecology of *Thecodontosaurus***

953   *Thecodontosaurus* is the basalmost sauropodomorph, excluding *Pantydraco*, that lived in

954   the Northern Hemisphere (Otero and Pol, 2013; McPhee et al., 2015; Langer et al., 2019; Pretto

955   et al., 2019) and thus has great importance in documenting the ecological evolution of

956   sauropodomorphs. The first sauropodomorphs from the Carnian of South America exhibited

957   notable variation in craniodental morphology (Bronzati et al., 2019; Müller and Garcia, 2019)

958   soon after the origin of the clade. The basalmost sauropodomorph *Buriolestes* (Cabreira et al.,

959   2016; Müller et al., 2018a) exhibits spaced, posteriorly curved tooth crowns with fine serrations

960   that indicate a faunivorous diet (Cabreira et al., 2016; Bronzati et al., 2019; Müller and Garcia,

961   2019). Other contemporary taxa like *Eoraptor* and *Saturnalia* have some ambiguous craniodental

962   traits, but which are consistent with predominantly carnivorous habits (Sereno et al., 2013;

963   Bronzati et al., 2017; 2019; Müller and Garcia, 2019). Three species of Carnian

964   sauropodomorphs (*Panphagia*, *Pampadromaeus* and *Bagualosaurus*) exhibit some dental traits

965   associated with herbivory, suggesting a shift from the plesiomorphic carnivorous condition to an

966   omnivorous diet (Bronzati et al., 2019; Müller and Garcia, 2019). In *Bagualosaurus*, this change

967   in dietary habits was coupled with the acquisition of larger body size compared to other Carnian

968   sauropodomorphs (Pretto et al., 2019). *Bagualosaurus* has a femoral length of approximately

969   21.5 cm (Pretto et al., 2019), indicating it was about the same body size as *Thecodontosaurus*.

970   This increase in body size could have promoted niche partitioning between *Bagualosaurus* and

971   coeval sauropodomorphs (Bronzati et al., 2019; Müller and Garcia, 2019; Pretto et al.,2019). In

972 this context, *Thecodontosaurus* is the basalmost sauropodomorph that exhibits dental traits

973 related to herbivory, with straight, spear-like crowns and coarse, oblique serrations, as seen in

974 more derived sauropodomorphs like *Plateosaurus* (Prieto-Márquez and Norell, 2011) or

975 *Unaysaurus* (Leal et al., 2004; McPhee et al., 2019). However, this typically herbivorous tooth

976 morphology in *Plateosaurus* was accompanied by a cranial configuration that permitted

977 facultative faunivorous habits (Button et al., 2016), a condition that seems to have been common

978 among post-Carnian taxa (Barrett, 2000; Müller et al., 2018b). Therefore, *Thecodontosaurus* is

979 one of the earliest sauropodomorphs that shifted to a predominantly herbivorous diet while

980 probably maintaining occasional faunivorous habits.

981   Despite its larger body size compared to most Carnian sauropodomorphs,

982 *Thecodontosaurus* shows a pelvic and hindlimb morphology that indicates the retention of

983 plesiomorphic locomotory traits. Its sigmoidal femoral shape resembles that of more basal

984 sauropodomorphs (Cabreira et al., 2016; Müller et al., 2018a; Langer et al., 2019; Pretto et al.,

985 2019) and contrasts with the straighter femur of more derived post-Carnian taxa, a shape change

986 that has been interpreted as indicating a gradual loss of cursoriality in the clade (Yates et al.,

987 2010; Kubo and Kubo, 2012; Müller et al., 2018b). In addition, the ilium retains a plesiomorphic

988 morphology, with an incompletely perforated acetabulum and an expanded supracetabular crest,

989 indicating a lack of modifications in pelvic soft tissues associated with graviportalism and

990 eventually quadrupedality that evolved in more derived sauropodomorphs (Tsai and Holliday,

991 2015; McPhee and Choiniere, 2016; Tsai et al., 2018). *Thecodontosaurus* is also the basalmost

992 sauropodomorph to lack a trochanteric shelf, a dinosauriform apomorphy (Novas, 1996) that is

993 absent in post-Carnian taxa (Müller et al., 2018b; McPhee et al., 2019) but is plesiomorphically

994 retained by Carnian taxa, including *Bagualosaurus* (Cabreira et al., 2016; Müller et al., 2018a;

995   Langer et al., 2019; Pretto et al., 2019), although the functional implications of this loss are not

996   well understood apart from a possible reduction of M. iliofemoralis externus (Hutchinson,

997   2001b). In any case, pelvic and hindlimb morphology in *Thecodontosaurus* indicates it was an

998   agile biped that retained plesiomorphic cursorial habits.

999   *Thecodontosaurus* was a key component of the Rhaetian fissure faunas of southwestern

1000   Britain. As a medium-sized, predominantly herbivorous biped, it was the main primary consumer

1001   of small island ecosystems (Whiteside et al., 2016) that were also inhabited by carnivorous

1002   coelophysoid dinosaurs (Whiteside and Marshall, 2008; Foffa et al., 2014; Keeble et al., 2018)

1003   that could have preyed on the former, as well as "sphenosuchian" crocodylomorphs, diverse

1004   rhynchocephalians and other lepidosaurs. These Late Triassic islands housed faunas that might

1005   have been similar to those of some modern reptile-dominated sub-tropical islands (Whiteside and

1006   Marshall, 2008). Additionally, the insular habitat of *Thecodontosaurus*, as well as its basal

1007   phylogenetic position, might explain the retention of a relatively small size compared to younger

1008   Norian taxa like *Plateosaurus*. The stratigraphically late occurrence of such a phylogenetically

1009   plesiomorphic sauropodomorph as *Thecodontosaurus* might be explained by the fact it was an

1010   island-living dinosaur (Whiteside et al., 2016; Skinner et al., in press); dwarfing and retention of

1011   primitive characters are commonly seen in island mammals and, for example, in the island

1012   dinosaurs of the Late Cretaceous of Romania (Benton et al., 2010). Further work is required to

1013   better understand the complexity of these fissure faunas and the ecological relevance of

1014   *Thecodontosaurus* within them.

1015

1016   CONCLUSIONS

1017

1018   The early evolution and diversity of sauropodomorphs is increasingly understood thanks

1019   to recent discoveries of Late Triassic species. The first sauropodomorph to be named,

1020   *Thecodontosaurus antiquus*, is one of the most basal members of the clade and an important

1021   taxon for the characterization of the morphological and functional modifications that occurred

1022   early in their evolution. The Tytherington sauropodomorph shares osteological features that

1023   support its assignment to *Thecodontosaurus antiquus*, and provides new information on

1024   previously unknown skeletal elements, notably within the skull. These findings cast doubt on the

1025   validity of *Pantydraco caducus* and *Asylosaurus yalensis*, and the former might represent a

1026   juvenile *T. antiquus* as originally proposed. *Thecodontosaurus*, together with findings from

1027   South America, documents an early shift towards a predominantly herbivorous diet in

1028   Sauropodomorpha, while maintaining a plesiomorphic posture, and was a key component of the

1029   Rhaetian fissure faunas of southwestern Britain.

1030

1031   ACKNOWLEDGMENTS

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1317   FIGURE 1. *Thecodontosaurus antiquus*, skull bones. **A–C**, left maxilla (BRSUG 28221) in **A**,

1318   lateral, and **B**, ventral views, and **C**, close-up of the maxillary tooth. **D–E**, left squamosal

1319   (BRSUG 28223) in **D**, medial, and **E**, lateral views. **F–G**, left frontal (BRSUG 29372-2855) in

1320   **F**, dorsal, and **G**, ventral views. **H**, left jugal (BRSUG 28224) in lateral view. **I**, left postorbital

1321   (BRSUG 26660) in lateral view. **J–L**, left quadrate (BRSUG 26596) in **J**, anterior, **K**, posterior,

1322   and **L**, lateral views. **M–N**, basioccipital (BRSUG 28230) in **M**, dorsal and **N**, ventral views. **O–**

1323   **P**, right otoccipital (BRSUG 28234) in **O**, posterior and **P**, lateral views. **Q–S**, left surangular

1324   (BRSUG 28201) in **Q**, lateral, **R**, medial, and **S**, dorsal views. **Abbreviations**: **alv**, alveoli; **aras**,

1325   articular articular surface; **bmr**, basioccipital median ridge; **bn**, basioccipital neck; **boas**,

1326   basioccipital articular surface; **br**, basioccipital recess; **bt**, basal tubera; **ci**, crista interfenestralis;

1327   **ct**, crista tuberalis; **dcc**, dorsal roof of cerebral cavity; **ds**, dorsal shelf; **fm**, foramen magnum;

1328   **frr**, frontal ramus; **itm**, margin of the infratemporal fenestra; **jur**, jugal ramus; **ll**, lateral lamina;

1329   **mame**, M. adductor mandibulae externus (mAME) insertion; **maf**, mandibular adductor fossa;

1330   **mf**, medial flange; **mfi**, metotic fissure; **mfo**, maxillary foramina; **mg**, mandibular glenoid; **mt**,

1331   maxillary tooth; **mxr**, maxillary ramus; **nas**, nasal articular surface; **ng**, neural groove; **obd**,

1332   olfactory bulb depression; **oc**, occipital condyle; **om**, orbital margin; **ooas**, otoccipital articular

1333   surface; **or**, orbital roof; **otd**, olfactory tract depression; **paas**, prearticular articular surface; **pas**,

1334   parietal articular surface; **pfas**, prefrontal articular surface; **poas**, prootic articular surface; **por**,

1335   postorbital ramus; **pp**, paraoccipital process; **ppdn**, dorsal notch; **ppr**, paraoccipital process

1336   ridge; **psas**, parabasisphenoid articular surface; **ptf**, pterygoid flange of quadrate; **qag**, quadrate

1337   anterior groove; **qc**, quadrate cotyle; **qh**, quadrate head; **qjf**, quadratojugal flange of quadrate;

1338   **qjr**, quadratojugal ramus; **qlc**, quadrate lateral condyle; **qmc**, quadrate medial condyle; **qr**,

1339   quadrate ridge; **rap**, retroarticular process; **salr**, surangular lateral ridge; **samr**, surangular

1340 medial ridge; **sar**, squamosal anterior ramus; **smg**, squamosal medial groove; **smr**, squamosal

1341 medial ramus; **soas**, supraoccipital articular surface; **sqr**, squamosal quadrate ramus, **XII**, cranial

1342 nerve XII (hypoglossal) foramina. Scale bars equal 1 cm (**A–B**, **D–S**) and 5 mm (**C**). [planned

1343 for page width]

1344

1345 FIGURE 2. *Thecodontosaurus antiquus*, cervical and dorsal vertebrae. **A–B**, right atlantal

1346 neurapophysis (BRSUG 28198) in **A**, medial and **B**, lateral views. **C**, mid cervical vertebra

1347 (BRSUG 28124) in lateral view. **D**, mid cervical neural arch (BRSUG 29372-2842) in dorsal

1348 view. **E–H**, posterior cervical vertebra (BRSUG 26629) in **E**, left lateral, **F**, dorsal, **G**, ventral

1349 and **H**, posterior views. **I–K**, posterior dorsal vertebra (BRSUG 29372-3811) in **I**, left lateral, **J**,

1350 anterior and **K**, posterior views. **L–M**, mid dorsal vertebra (BRSUG 29372-2806) in **L**, left

1351 lateral, and **M**, dorsal views. **N**, posterior dorsal vertebra (BRSUG 29372-2848) in left lateral

1352 view. **Abbreviations**: **cdf**, centrodiapophyseal fossa; **pcdl**, posterior centrodiapophyseal lamina;

1353 **cpl**, centroparapophyseal lamina; **di**, diapophysis; **epi**, epipophysis; **hypa**, hypantrum; **hypo**,

1354 hyposphene; **ias**, intercentrum articular surface; **ld**, lateral depression; **ncs**, neurocentral suture;

1355 **nc**, neural canal; **ns**, neural spine; **ped**, pedicel; **ocas**, occipital articular surface; **pa**,

1356 parapophysis; **pif**, posterior infradiapophyseal fossa; **poz**, postzygapophysis; **pozl**,

1357 postzygodiapophyseal lamina; **prz**, prezygapophysis; **spozf**, spinopostygapophyseal fossa; **sprzf**,

1358 spinoprezygapophyseal fossa; **vk**, ventral keel. Scale bars equal 1 cm (**A–B**) and 2 cm (**C–N**).

1359 [planned for page width]

1360

1361 FIGURE 3. *Thecodontosaurus antiquus*, sacral and caudal vertebrae. **A–D**, second sacral

1362 vertebra (BRSUG 28130) in **A**, dorsal, **B**, ventral, **C**, anterior, and **D**, right lateral views. **E–F**,

1363 mid-anterior caudal vertebra (BRSUG 29372-2843) in **E**, left lateral and **F**, dorsal views. **G–H**,

1364 mid caudal vertebra (BRSUG 29372-2830) in **G**, right lateral and **H**, ventral views. **I**, two

1365 articulated mid caudal vertebrae (BRSUG 26614) in left lateral view. **J–K**, mid-posterior caudal

1366 vertebra (BRSUG 29372-2812) in **J**, left lateral, and **K**, ventral views. **Abbreviations**: **nc**, neural

1367 canal; **ns**, neural spine; **poz**, postzygapophysis; **prz**, prezygapophysis; **sprzf**,

1368 spinoprezygapophyseal fossa; **sr**, sacral rib; **tp**, transverse process; **vg**, ventral groove. Scale bars

1369 equal 2 cm. [planned for page width]

1370

1371 FIGURE 4. *Thecodontosaurus antiquus*, dorsal ribs and chevron. **A**, proximal portion of left

1372 dorsal rib (BRSUG 29372-3595) in anterior view. **B**, head of right dorsal rib (BRSUG 29372-

1373 3592) in ventral view. **C–E**, chevron (BRSUG 29372-3285) in **C**, anterior, **D**, posterior and **E**,

1374 left lateral views. **Abbreviations**: **cap**, capitulum; **hc**, haemal canal; **paf**, proximal articular

1375 facets; **pg**, posterior groove; **tub**, tuberculum. Scale bar equals 1 cm. [planned for column width]

1376

1377 FIGURE 5. *Thecodontosaurus antiquus*, pectoral girdle. **A–B**, anterior end of right scapula

1378 (BRSUG 28126) in **A**, lateral and **B**, medial views. **C–D**, left scapula (BRSUG 29372-3349) in

1379 **C**, lateral and **D**, lateroventral views. **E–F**, right coracoid (BRSUG 26612) in **E**, lateral and **F**,

1380 medial views. G, reconstruction of a right scapulocoracoid complex in lateral view, based on

1381 several specimens. **Abbreviations**: **acr**, acromion; **als**, acromial lateral scar; **ar**, acromial ridge;

1382 **cbf**, M. coracobrachialis (mCB) fossa; **cf**, coracoid foramen; **CO**, coracoid; **gl**, glenoid; **mlf**,

1383 medial longitudinal fossa; **sas**, scapular articular surface; **sb**, scapular blade; **sbso**, M.

1384 subscapularis (mSBS) origin; **SC**, scapula; **ss**, synchondrosis strations; **suco**, M.

1385 supracoracoideus (mSUC) origin; **slf**, scapular lateral fossa; **tbsr**, M. triceps brachii caput

1386 scapulare (mTBS) rugosity; **vmr**, ventromedial ridge. Scale bars equal 2 cm. [planned for page

1387 width]

1388

1389 FIGURE 6. *Thecodontosaurus antiquus*, humeri. **A–D**, proximal portion of right humerus

1390 (BRSUG 23608) in **A**, anterior, **B**, lateral, **C**, posterior and **D**, medial views. **E–H**, distal portion

1391 of left humerus (BRSUG 28151) in **E**, anterior, **F**, lateral, **G**, posterior and **H**, medial views.

1392 Photographs in **B–D** were edited to digitally remove annotations on the fossil; see Figure S1 for

1393 the original photographs. **Abbreviations**: **bg**, biceps gutter; **cf**, cuboid fossa; **deo**, digital

1394 extensors origin; **dfo**, digital flexors origin; **dpc**, deltopectoral crest; **ec**, ectepocondyle; **en**,

1395 entepicondyle; **hh**, humeral head; **hrf**, M. humeroradialis (mHR) fossa; **ldi**, M. latissimus dorsi

1396 (mLD) insertion; **mt**, medial tuber; **pmf**, posteromedial fossa; **plf**, posterolateral fossa; **plr**,

1397 posterolateral ridge; **rc**, radial condyle; **uc**, ulnar condyle. Scale bar equals 2 cm. [planned for

1398 page width]

1399

1400 FIGURE 7. *Thecodontosaurus antiquus*, fore zeugopodium. **A–C**, left ulna (BRSUG 26598) in

1401 **A**, lateral, **B**, posterior and **C**, medial views. **D–F**, right radius (BRSUG 26594) in **D**, lateral, **E**,

1402 posterior and **F**, medial views. **Abbreviations**: **amp**, anteromedial process; **lc**, lateral condyle;

1403 **ol**, olecranon process; **plru**, posterolateral rugosity; **rdas**, distal articular surface for the radius;

1404 **rf**, radial fossa; **rplr**, posterolateral ridge of the radius; **tbi**, M. triceps brachii (mTB) insertion;

1405 **tn**, trochlear notch; **udas**, distal articular surface for the ulna; **upas**, proximal articular surface for

1406 the ulna; **uplr**, posterolateral ridge of ulna. Scale bars equal 2 cm. [planned for page width]

1407

1408   FIGURE 8. *Thecodontosaurus antiquus*, manus. **A–B**, left metacarpal I (BRSUG 28161) in **A**,

1409   dorsal and **B**, palmar views. **C–D**, right metacarpal II (BRSUG 26585) in **C**, dorsal and **D**,

1410   palmar views. **E–F**, right metacarpal III (BRSUG 29372-2828) in **E**, dorsal and **F**, palmar views.

1411   **G–H**, proximal phalanx of manual digit I (BRSUG 29372-2832) in **G**, dorsal and **H**, palmar

1412   views. **I**, ungual phalanx of manual digit I (BRSUG 26639) in lateral view. **J**, ungual phalanx of

1413   manual digit II or III (BRSUG 23646) in lateral view. **Abbreviations**: **1as**, metacarpal I articular

1414   surface; **2as**, metacarpal II articular surface; **3as**, metacarpal III articular surface; **4as**, metacarpal

1415   IV articular surface; **cp**, collateral pit; **edi**, digital extensors insertion; **edpo**, M. extensor

1416   digitorum profundus (mEDP) origin; **exd**, extensor depression; **fdi**, digital flexors insertion;

1417   **fdpo**, M. flexor digitorum profundus (mFDP) origin; **ft**, flexor tubercle; **icg**, intercondylar

1418   groove; **lc**, lateral condyle; **ld**, lateral depression; **lg**, lateral groove; **mc**, medial condyle; **vlru**,

1419   ventrolateral rugosity. Scale bar equals 1 cm. [planned for column width]

1420

1421   FIGURE 9. *Thecodontosaurus antiquus*, pelvic girdle. **A–B**, left ilium (BRSUG 23613) in **A**,

1422   lateral and **B**, medial views. **C–D**, left ischium (BRSUG 29372-3338) in **C**, lateral and **D**,

1423   posterodorsal views. **Abbreviations**: **ac**, acetabulum; **at**, antitrochanter; **bf**, brevis fossa; **bs**,

1424   brevis shelf; **fteo**, M. flexor tibialis externus (mFTE) origin; **gr**, groove; **ifio**, M. iliofemoralis

1425   internus (mIFI) origin; **ilp**, iliac peduncle; **ip**, ischiadic plate; **is**, ischiadic shaft; **isp**, ischiadic

1426   peduncle; **it1o**, M. iliotibialis 1 (mIT1) origin; **it3o**, M. iliotibialis 3 (mIT3) origin; **pms**,

1427   posteromedial shelf; **pomr**, postacetabular medial ridge; **pop**, postacetabular process; **prf**,

1428   preacetabular fossa; **prms**, preacetabular medial scar; **prp**, preacetabular process; **prr**,

1429   preacetabular ridge; **pup**, pubic peduncle; **sac**, supracetabular crest; **sr1**, first sacral rib articular

1430   surface; **sr2**, second sacral rib articular surface. Scale bars equal 2 cm. [planned for page width]

1431

1432   FIGURE 10. *Thecodontosaurus antiquus*, left femur (BRSUG 23615) in **A**, anterior, **B**, lateral,

1433   **C**, posterior and **D**, medial views. **Abbreviations**: **4t**, fourth trochanter; **ail**, cranial intermuscular

1434   line; **alt**, anterolateral tuber; **amc**, anteromedial crest; **apf**, anterior proximal fossa; **cfbi**, M.

1435   caudofemoralis brevis (mCFB) insertion; **cfli**, M. caudofemoralis longus (mCFL) insertion; **dlt**,

1436   dorsolateral trochanter; **gt**, greater trochanter; **fh**, femoral head; **lc**, lateral condyle; **lt**, lesser

1437   trochanter; **mc**, medial condyle; **naf**, nutrient artery foramen; **plil**, caudolateral intermuscular

1438   line; **plpt**, posterolateral proximal tuberosity; **pmil**, caudomedial intermuscular line; **pmt**,

1439   posteromedial tuber; **popf**, popliteal fossa; **ve**, ventral emargination. Scale bar equals 2 cm.

1440   [planned for 2/3 page width]

1441

1442   FIGURE 11. *Thecodontosaurus antiquus*, hind zeugopodium. **A–C**, left tibia (BRSUG 23621) in

1443   **A**, lateral, **B**, medial and **C**, proximal views. **D**, left tibia (BRSUG 23647) in distal view. **E–F**,

1444   proximal portion of left fibula (BRSUG 26634) in **E**, lateral and **F**, medial views.

1445   **Abbreviations**: **alp**, anterolateral process; **cc**, cnemial crest; **faap**, articular facet for the

1446   astragalar ascending process; **ilfr**, M. iliofibularis (mILFB) rugosity; **it**, incisura tibialis; **lc**,

1447   lateral condyle; **ln**, lateral notch; **mc**, medial condyle; **mr**, medial ridge; **tas**, tibial articular

1448   surface; **pldp**, posterolateral descending process. Scale bars equal 2 cm. [planned for page width]

1449

1450   FIGURE 12. *Thecodontosaurus antiquus*, pes. **A–D**, left metatarsal I (BRSUG 26606) in **A**,

1451   dorsal, **B**, plantar, **C**, proximal and **D**, distal views. **E–H**, right metatarsal II (BRSUG 26627) in

1452   **E**, dorsal, **F**, plantar, **G**, proximal and **H**, distal views. **I–L**, left metatarsal III (BRSUG 23627) in

1453   **I**, dorsal, **J**, plantar, **K**, proximal and **L**, distal views. **M–P**, right metatarsal IV (BRSUG 29372-

1454 3812) in **M**, dorsal, **N**, plantar, **O**, proximal and **P**, distal views. **Q–R**, proximal phalanx of pedal

1455 digit III (BRSUG 28218) in **Q**, dorsal and **R**, plantar views. **S–T**, proximal phalanx of pedal digit

1456 IV (BRSUG 29372-2851) in **S**, dorsal and **T**, plantar views. **U**, distal pedal phalanx (BRSUG

1457 29372-2839) in dorsal view. **V**, distal pedal phalanx (BRSUG 29372-2840) in dorsal view. **C**, **G**,

1458 **K**, **O**, dorsal towards the bottom. **D**, **H**, **L**, **P**, dorsal towards the top. **Abbreviations**: **1as**,

1459 metatarsal I articular surface; **2as**, metatarsal II articular surface; **3as**, metatarsal III articular

1460 surface; **4as**, metatarsal IV articular surface; **5as**, metatarsal V articular surface; **cp**, collateral pit;

1461 **dls**, dorsolateral scar; **exd**, extensor depression; **lc**, lateral condyle; **mc**, medial condyle; **mdru**,

1462 mediodorsal rugosity; **mpru**, medioplantar rugosity; **tai**, M. tibialis anterior (mTA) insertion.

1463 Scale bar equals 1 cm. [planned for page width]

1464