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Revision of Erpetosuchus (Archosauria: Pseudosuchia) and new erpetosuchid material from the Late Triassic 'Elgin Reptile' fauna based on µCT scanning techniques

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1 **Revision of *Erpetosuchus* (Archosauria: Pseudosuchia) and new erpetosuchid material**

2 **from the Late Triassic 'Elgin Reptile' fauna based on μCT scanning techniques**

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4 Davide Foffa[1,*], Richard J. Butler[2], Sterling J. Nesbitt[3], Stig Walsh[1,4], Paul M. Barrett[5],
5 Stephen L. Brusatte[4,1] and Nicholas C. Fraser[1,4]

6

7 [1] Department of Natural Sciences, National Museums Scotland, Chambers Street, Edinburgh
8 EH1 1JF, United Kingdom

9 [2] School of Geography, Earth and Environmental Sciences, University of Birmingham,
10 Edgbaston, Birmingham B15 2TT, United Kingdom

11 [3] Department of Geosciences, Virginia Tech, 4044 Derring Hall (MC0420) 926 West Campus
12 Drive, Blacksburg 24061, Virginia, USA

13 [4] School of GeoSciences, University of Edinburgh, Grant Institute, Hutton Road, Edinburgh
14 EH9 3FE, United Kingdom

15 [5] Department of Earth Sciences, Natural History Museum, Cromwell Road, London SW7
16 5BD, United Kingdom

17

18 * Corresponding author

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21   ABSTRACT: The Late Triassic fauna of the Lossiemouth Sandstone Formation (LSF) from

22   the Elgin area, Scotland, has been pivotal in expanding our understanding of Triassic

23   terrestrial tetrapods. Frustratingly, due to their odd preservation, interpretations of the Elgin

24   Triassic specimens have relied on destructive moulding techniques, which only provide

25   incomplete, and potentially distorted, information. Here, we show that micro-computed

26   tomography (μCT) could revitalise the study of this important assemblage. We describe a

27   long-neglected specimen that was originally identified as a pseudosuchian archosaur,

28   *Ornithosuchus woodwardi*. μCT scans revealed dozens of bones belonging to at least two

29   taxa: a small-bodied pseudosuchian and a specimen of the procolophonid *Leptopleuron*

30   *lacertinum*. The pseudosuchian skeleton possesses a combination of characters that are

31   unique to the clade Erpetosuchidae. As a basis for investigating the phylogenetic

32   relationships of this new specimen, we reviewed the anatomy, taxonomy and systematics of

33   other erpetosuchid specimens from the LSF (all previously referred to *Erpetosuchus*).

34   Unfortunately, due to the differing representation of the skeleton in the available

35   *Erpetosuchus* specimens, we cannot determine whether the erpetosuchid specimen we

36   describe here belongs to *E. granti* (to which we show it is closely related) or if it represents a

37   distinct new taxon. Nevertheless, our results shed light on rarely preserved details of

38   erpetosuchid anatomy. Finally, the unanticipated new information extracted from both

39   previously studied and neglected specimens suggests that fossil remains may be much more

40   widely distributed in the Elgin quarries than previously recognized, and that the richness of

41   the LSF might have been underestimated.

42

43   KEY WORDS: anatomy, *Erpetosuchus granti*, Erpetosuchidae, *Leptopleuron*, systematics

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45   The fossil reptiles of the Upper Triassic Lossiemouth Sandstone Formation (LSF), from

46   Elgin, Scotland, have been central in revealing the early evolution of modern groups of

47   terrestrial vertebrates (Benton & Walker 1985, 2002, 2011). Unfortunately, studying these

48   specimens, most of which were collected in the 19th century, is exceedingly difficult because

49   of their preservation as voids (or crumbled bones) in hard sandstone matrix (Benton &

50   Walker 1985). Historically the 'Elgin reptiles' have been studied using plaster or latex

51   (Walker 1964; Benton & Walker 1985, 2002; Bennett 2020). These traditional techniques

52   often permanently damaged the sandstone blocks containing the fossil and involved

53   deliberate removal of the fragmentary bones to obtain better casts. Furthermore, each new

54   cast changed the morphology of delicate features and has led to ongoing debates about

55   morphology and relationships (Bennett 2020). However, a small number of specimens

56   collected decades ago were left unprepared and their capacity for revealing new information

57   has never been assessed. This unstudied material has the potential to reveal important new

58   information on the anatomy, ecology, relationships and composition of the LSF reptile fauna.

59   One of these specimens is BGS GSM 91072–81, 91085–6. Walker (1964) referred to

60   a partial skeleton visible on the surface of this specimen as a small/juvenile *Ornithosuchus*

61   based on *"the presence of paired dorsal scutes associated with hollow femora"* (Walker

62   1964, p. 55) and the paired row of osteoderms emerging from the matrix. BGS GSM 91072–

63   81, 91085–6 did not receive further attention until Von Baczko & Ezcurra (2016) revised the

64   taxonomy of *Ornithosuchus* and mentioned it among the specimens referred to this genus.

65   This referral was presumably done following Walker (1964), because BGS GSM 91072–81,

66   91085–6 was not amongst the materials that were studied first-hand by the authors (Von

67   Baczko & Ezcurra 2016, p. 200). Walker (1964) and Von Baczko & Ezcurra (2016),

68   however, had access to only the limited portion of the specimen that is exposed on the

69   surfaces of the blocks, and it has never been clear if other bones were preserved inside. Here,

70   we re-study this specimen using μCT scanning techniques (Cunningham *et al.* 2014), which

71   reveal a wealth of new bones inside the blocks, including at least two skeletons belonging to

72   different reptiles, neither of which is *Ornithosuchus*. One of these is an erpetosuchid, a clade

73   of archosaurs that belongs within the pseudosuchian lineage that also includes extant

74   crocodylians. In addition to providing key new anatomical information on the rare

75   erpetosuchids, our scans demonstrate that μCT can provide an unprecedented level of

76   anatomical information on the hitherto problematic 'Elgin reptiles'. Along with recent

77   successful CT scans of the Elgin pseudosuchian *Stagonolepis* (Keeble & Benton 2020), this

78 indicates that previously used destructive techniques will no longer be necessary to study
79 these critically important fossils.

80   To identify the erpetosuchid specimen contained in the BGS GSM 91072–81, 91085–
81 6 blocks, and conduct an appropriate comparative study, we first needed to revise the
82 diagnosis of the co-occurring pseudosuchian archosaur *Erpetosuchus granti*. Until recently,
83 *E. granti* was the only recognised member of the eponymous family Erpetosuchidae (see
84 Watson 1917; Olsen *et al.* 2001; Benton & Walker 2002; Nesbitt & Butler 2013; Lacerda *et*
85 *al.* 2018). However, in the last decade, re-evaluation of historical specimens as well as new
86 discoveries from the Middle and Late Triassic of South America and Africa have shown that
87 several features once thought to be unique to *Erpetosuchus* are, in fact, diagnostic of a more
88 speciose erpetosuchid clade (Nesbitt & Butler 2013; Ezcurra *et al.* 2017; Lacerda *et al.* 2018;
89 Nesbitt *et al.* 2018). Unfortunately, the diagnosis of *E. granti* has not been reassessed, and it
90 is unclear how this species can be diagnosed. This issue was initially noticed by Nesbitt &
91 Butler (2013), and has become more problematic with the description of new erpetosuchids,
92 and with our increased understanding of pseudosuchian taxonomy and systematics (Maisch &
93 Matzke 2013; Ezcurra *et al.* 2017; Lacerda *et al.* 2018; Nesbitt *et al.* 2018; Müller *et al.*
94 2020). Here we address this problem by revising the diagnosis of *E. granti* based on the
95 available literature (see Ezcurra *et al.* 2017, Supplementary Information) and newly obtained
96 µCT data from referred specimens.

97   **Institutional abbreviations:** AMNH, American Museum of Natural History, New
98 York, USA; BGS GSM, British Geological Survey, Keyworth, UK; MCZ, The Louis Agassiz
99 Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA;
100 NHMUK, Natural History Museum, London, UK; NMS, National Museums Scotland,
101 Edinburgh, UK; NMT, National Museum of Tanzania, Dar es Salaam, Tanzania; SMNS,
102 Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany.
103

1. Materials and methods

105 The LSF sandstones are composed of white, yellow to pink well-rounded, well-sorted (0.2–
106 0.5 mm) grains of quartz and feldspar with rare clasts of chert and quartzite (Peacock *et al.*
107 1968; Benton & Walker 1985). Frostick *et al.* (1988) described the LSF deposits as an
108 intercalated sequence of large-scale cross-bedded aeolian dunes and parallel-bedded,
109 bioturbated lake-shore medium to fine sands. Benton & Walker (1985) recorded that, at

110   Spynie Quarry, the reptiles were recovered stratigraphically low in the quarry, from a layer of

111   friable sandstone near the base of the aeolian dunes, just above a water-laid sands and silts

112   layer. This layer is reported to sit near the base of the LSF in all of the quarries in the Elgin

113   area (Gordon 1859; Murchison 1859; Martin 1860; Benton & Walker 1985: Fig. 1).

114   BGS GSM 91072–81, 91085–6 is a collection of 11 small blocks (from ~5–15 cm in

115   maximum length) of yellow to mustard coloured sandstones from Spynie Quarry (Elgin,

116   Moray), one of many sandstone quarries in the Elgin area (Figs 1–2). They were *"purchased*

117   *by Mr Howell (of the Geological Survey) on 14th March 1893"* (Walker 1964, p. 56). Little

118   information is available on the state of these blocks at the time of purchase, but it is implied

119   that the blocks were already separated when Walker (1964) studied them. Walker (1964)

120   noted that several of these pieces fitted together (Figs 1–2) and were linked by the *"peculiar*

121   *preservation of the matrix"* (Walker 1964, pp. 55–56) confirming that they belonged

122   together. One of us (DF) verified that the blocks fit together in two groups: BGS GSM

123   91080–1, 91085–6 and, on the other side, BGS GSM 91072–79, 91086 (Figs 1–2). The fit

124   between these two groups is less certain, other blocks from this sequence (presumably

125   including blocks with the missing numbers BGS GSM 91083–84) probably linked the two

126   groups originally. Unfortunately, we were unable to locate these additional blocks – it is

127   likely that they went missing before Walker studied these materials as they were not

128   mentioned in his description (*"GSM 91072–78, 91081–82, 91085–86"*: Walker 1964, p. 55).

129   Some blocks have been glued together, so it is possible that BGS GSM 91083–84 are

130   currently stuck to others (DF, pers. obs.). It is also possible that the fit between the two

131   groups of blocks has been rendered imperfect by the mechanical preparation evident from

132   some of the blocks' surfaces. Nevertheless, the internal content of the blocks, as revealed by

133   µCT scanning, corroborates the conclusion that they all belong together. Focusing on the two

134   most complete skeletons preserved within the blocks, we notice that there is no duplication of

135   bone elements (i.e. no element is represented more than once) between the two groups and

136   that comparable elements (e.g. osteoderms) are identical in size and morphology in the

137   separate blocks (Fig. 2). Indeed, the presumed cervical-dorsal vertebrae and distal tail of this

138   individual is in BGS GSM 91072–79, 91086, whereas the posterior dorsal, sacral and

139   anterior–middle caudal vertebrae and hindlimbs are all in BGS GSM 91080–1, 91085. The

140   arch-like orientation of the dorsal to caudal vertebral series hints at the original relationship

141   of the blocks to one another, as depicted in Figures 1–2, which matches the tentative

142   arrangement based on the broken sandstone surface.

143   It is convenient at this point to simplify the nomenclature of BGS GSM 91072–82,

144   91085–6. BGS assigned an individual register number to each sandstone block, but this

145   nomenclature cannot be used easily herein because the μCT scans show that the skeletons of

146   at least two individuals of distinct species are embedded within them. The first of these

147   belongs to a pseudosuchian archosaur – the specimen that is currently referred to

148   *Ornithosuchus woodwardi* (Walker 1964; Von Baczko & Ezcurra 2016) – and is partially

149   exposed on the surfaces of the blocks; the second is a previously undocumented partial

150   skeleton of the procolophonid *Leptopleuron lacertinum* (also known from the LSF fauna)

151   (Benton & Walker 1985; Säilä 2010). For example, BGS GSM 91075 contains both cranial

152   material of the archosaur and the *Leptopleuron lacertinum* remains. Thus, for simplicity we

153   will use 'BGS GSM Elgin A' ('A' standing for 'archosaur') to refer to the archosaur skeleton

154   in BGS GSM 91072–82, 91085–6, which is the focus of this manuscript. The second skeleton

155   in the same blocks will be referred as to 'BGS GSM Elgin P' (for 'procolophonid') and is

156   separately described along with additional unidentified bones. We use specific BGS register

157   numbers to reference individual sandstone blocks, in order to specify where each bone is

158   preserved.

159

160   **1.1. μCT-scanning methods**

161   BGS GSM 91072–81, 91085–6 (Figs 1–2) were scanned with the assistance of Dr Tom G.

162   Davis and Dr Elizabeth Martin-Silverstone using a Nikon XT H 225 μCT scanner at the

163   Palaeobiology Lab of the University of Bristol. To increase resolution by reducing the field

164   of view, the 10 blocks of BGS GSM 91072–81, 91085–6 were scanned separately in six

165   groups (Figs 1D, E, 2, Table 1) (Supporting Information, Table S1). During the scanning

166   some of the blocks were held together with rubber bands to maintain their original association

167   (some bones, such as the quadrate, are split between blocks). Given the limited dimensions of

168   the samples, this procedure did not significantly affect the resolution of the scans, which vary

169   from 0.023–0.073 mm (isometric voxel size) depending on the size of each block (see

170   Supplementary Information, Table S1 for individual scan parameters).

171   Blocks containing a referred specimen of *Erpetosuchus granti* (NMS G.1992.37.1)

172   (Figs 3–4) were scanned for comparative purposes with the assistance of Dr Alice Macente

173   and SW. The scanning took place at the μCT facility (Nikon XT H 225 μCT) hosted in the

174   Advanced Materials Research Laboratory of the Civil & Environmental Engineering

175 Department at the University of Strathclyde and shared with the School of Earth &

176 Geographical Science of the University of Glasgow. The resolution of these datasets varies

177 from 0.0624–0.0678 mm (isometric voxel size) (Table 1) (see Supplementary Information,

178 Table S1 for individual scan parameters).

179   The CT dataset of *Erpetosuchus* sp. (AMNH 29300) (Fig. 5) was acquired by one of

180 the authors (SLB) in Autumn 2012 at the Microscopy and Imaging Facility at AMNH with

181 the assistance of Morgan Hill (Table 1) (see Supplementary Information, Table S1 for

182 individual scan parameters).

183   All the μCT datasets were segmented using Mimics 21.0

184 (www.materialise.com/mimics). The 3D models and μCT datasets were uploaded to

185 Morphosource (https://www.morphosource.org/) and can be accessed at [MORPHOSOURCE

186 link to be added here upon acceptance], following the recommendations on sharing digital

187 data proposed by Davies *et al.* (2017). The small size of the bones in the BGS specimens may

188 raise questions about over the confidence with which we are presenting interpretations of our

189 data. We were able to segment extremely small structures thanks to the reduced physical size

190 of the samples (approximately 10 x 10 x 4 cm for the largest block), small voxel size and the

191 strong contrast between the bones/cavities and the sandstone in the Elgin (BGS and NMS)

192 specimens (Supplementary Information, Fig. S1). This combination made it possible to

193 segment the specimens with great accuracy and allowed interpretation of details, in some

194 cases, even without post-processing (e.g. smoothing) the segmented models. This is

195 important because we were able to avoid possible post-processing artefacts that could affect

196 our interpretation of the anatomy and, consequently, the information coded in the

197 phylogenetic analyses.

198

1.2. Phylogenetic analysis

200 To test the phylogenetic relationships of BGS GSM Elgin A we updated the dataset of Müller

201 *et al.* (2020), which incorporates the most recent iterations made to the original dataset of

202 Ezcurra (2016), including modifications implemented in Ezcurra *et al.* (2017). This dataset

203 was selected because it contains the most complete sampling of erpetosuchid species. Before

204 conducting our analysis, we modified the taxon/character matrix by adding four terminal taxa

205 and updated the scores of two others (see Supplementary Information). Specifically, in

206 addition to BGS GSM Elgin A, we scored the two most complete specimens of *Parringtonia*

207 *gracilis* (NMT RB426, NMT RB460: Nesbitt *et al.* 2018) (see Supplementary information,

208 Fig. S2). We also updated the scores of *Erpetosuchus granti* based on direct examination of

209 multiple generations of casts of the holotype specimen (NHMUK PV R3139), and newly

210 acquired μCT scans of a referred specimen (NMS G.1992.37.1). This resulted in the

211 rescoring of 52 character states, including new information on the cervical-dorsal vertebral

212 series, osteoderms, pectoral girdle and forelimbs for *E. granti* (see Supplementary

213 Information). Finally, we updated the scores for *Erpetosuchus* sp. (AMNH 393000), also

214 based on CT scans (see Supplementary Information). The inclusion of new information from

215 *Erpetosuchus granti* and the addition of better preserved *Parringtonia gracilis* specimens

216 increases knowledge of the osteology (particularly postcranial) of the group, which is still

217 poorly understood due to the scarcity of complete specimens (Nesbitt & Butler 2013; Lacerda

218 *et al.* 2018).

219   The final version of the matrix includes 676 characters and 113 terminal taxa. Ten

220 taxa, *Eorasaurus olsoni, Archosaurus rossicus, Vonhuenia fredericki, Chasmatosuchus*

221 *rossicus, Chasmatosuchus magnus, 'Chasmatosuchus' vjushkovi, Kalisuchus rewanensis,*

222 *Shansisuchus kuyeheensis, Uralosaurus magnus* and *Koilamasuchus gonzalezdiazi*, were

223 excluded *a priori* (see Ezcurra 2016 for justifications for the exclusions of these taxa). The

224 following characters were treated as additive (1, 2, 7, 10, 17, 19, 20, 21, 28, 29, 36, 40, 42,

225 50, 54, 66, 71, 75, 76, 122, 127, 146, 153, 156, 157, 71, 176, 177, 187, 202, 221, 227, 263,

226 266, 279, 283, 324, 327, 331, 337, 345, 351, 352, 354, 361, 365, 370, 377, 379, 398, 410,

227 424, 430, 435, 446, 448, 454, 458, 460, 463, 472, 478, 482, 483, 489, 490, 504, 510, 516,

228 529, 537, 546, 552, 556, 557, 567, 569, 571, 574, 581, 582, 588, 648, 652 and 662). The

229 analysis was performed in TNT v. 1.5 (Goloboff *et al.* 2008) using equally weighted

230 parsimony. The tree space was generated and searches for the most parsimonious trees

231 (MPTs) were conducted using the following protocol: 'New Technology Search' (Sectorial

232 Search, Ratchet, Drift and Tree fusing) with 1000 random-addition replicates (RAS). Each

233 method was run for 100 replicates/cycles/iterations. A final round of tree bisection

234 reconnection (TBR) branch swapping was performed after the New Technology search, with

235 a 50% collapsing rule. This procedure retrieved the same results as the protocol followed by

236 Müller *et al.* (2020) that relies instead on 'Traditional search' (RAS+TBR) with 1000

237 replicates of Wagner trees (random seed = 0), and TBR and branch swapping (with 10 trees

238 saved per replicate). As in previous analyses, *Petrolacosaurus kansensis* was used to root the

239 MPTs.

240

2. Systematic palaeontology

Archosauria Cope, 1869, *sensu* Gauthier & Padian 1985

Pseudosuchia Zittel, 1887–1890, *sensu* Sereno *et al.* 2005

Suchia Krebs, 1974, *sensu* Nesbitt 2011

Erpetosuchidae Watson, 1917, *sensu* Nesbitt & Butler 2013

Erpetosuchus granti Newton, 1894

Type specimen. NHMUK PV R3139, consisting of the natural mould of a complete skull and mandible, articulated series of cervical and anterior dorsal vertebrae, and the shoulder girdle and forelimbs. Associated with this specimen are different generations of casts: Newton's original gutta percha casts are BGS GSM 91029–91051; the PVC and Vinagel casts made by Walker are located with NHMUK PV R3139 (see Benton & Walker 2002).

Referred material. NMS G.1992.37.1 articulated series of cervical and anterior dorsal vertebrae, associated with paramedian and lateral osteoderms, ribs, and the shoulder girdle and forelimbs (complete right forelimb, only missing its distal phalanges, and incomplete left humerus); NMS G.1966.43.4, partial dorsal vertebral region, with associated paramedian and lateral osteoderms and ribs.

Locality and horizon. The type specimen of *Erpetosuchus granti* was collected from the breakwater at Lossiemouth, near Elgin (Moray, Scotland, United Kingdom) and it originated from either Spynie or the Lossiemouth quarries. NMS G.1992.37.1 was found in a block on the beach near Lossiemouth old rail station, likely from the material discarded by the Lossiemouth quarries. NMS G.1966.43.4 is part of the Stollery Collection at the NMS, obtained from Mr E. Stollery of Sandend (Cullen); its precise provenance is unknown. All of the specimens come from aeolian sandstones of the Lossiemouth Sandstone Formation (Upper Triassic; ~upper Carnian/lower Norian: but see Benton & Walker 2011).

269   **Other potentially referable material.** NHMUK PV R4807 is a series of 16

270 articulated vertebrae from Lossiemouth, but this specimen cannot be referred to *Erpetosuchus*

271 unambiguously (see Benton & Walker 2002). AMNH 29300 is a partial skull from the New

272 Haven Formation of Connecticut (Hartford Basin, Newark Supergroup) (Upper Triassic:

273 ~upper Carnian/lower Norian; but see Olsen *et al.* 2001). This specimen is referred to

274 *Erpetosuchus* sp. and is re-described separately (see below).

275   **Emended diagnosis.** *Erpetosuchus granti* differs from all other erpetosuchids in (*

276 indicates local autapomorphies): having a snout that tapers anteriorly in lateral view; obtuse

277 angle (~105°) between the alveolar and anterior margins of the premaxilla* (unique within

278 Erpetosuchidae); 4–5 maxillary teeth; teeth without carinae; posterior process of the

279 quadratojugal is thin and strongly elongated (anteroposterior length / vertical depth at the

280 base > 4; shared with *Erpetosuchus* sp. [AMNH 29300]); strongly elongated scapula (total

281 length / minimum anteroposterior width of the scapular blade > 13)* (unique within

282 Pseudosuchia); well-developed trapezoidal hypapophyses on the middle–posterior cervical

283 and anterior dorsal vertebrae (based on NMS G.1992.37.1); spine tables (and pit) present on

284 the dorsal surface of the neural spine on the cervical and anterior dorsal vertebrae and absent

285 from the middle dorsals (based on NMS G.1992.37.1); paramedian and lateral osteoderms

286 longer than wide and with a distinct keel (shared with *Parringtonia gracilis*); paramedian

287 osteoderms with unornamented anterior articular lamina (shared with *Archeopelta arborensis*

288 and *Parringtonia gracilis*).

289   **Comments.** Six autapomorphies were used by Benton & Walker (2002) to diagnose

290 *Erpetosuchus granti*: (1) reduced maxillary dentition restricted to the anterior maxilla; (2)

291 large antorbital fenestra, in a deep antorbital fossa delimited by sharp margins; (3) sharp ridge

292 on the lateral surface of the jugal; (4) 'otic notch' below an overhanging squamosal; (5)

293 angular and surangular marked by a strong ridge extending from the ventral margin of the

294 mandibular fenestra; (6) teeth with oval cross-section without carinae. Nesbitt & Butler

295 (2013) used three of these (1, 3, 6) to revise the diagnosis of Erpetosuchidae, while others

296 (except perhaps 6), have shown some of these characters to be common among other

297 erpetosuchids (Nesbitt & Butler 2013; Ezcurra *et al.* 2017; Lacerda *et al.* 2018; Nesbitt *et al.*

298 2018), and/or shared with other groups (e.g. character 5 is present in Erpetosuchidae +

299 Ornithosuchidae) (Von Baczko & Desojo 2016; Ezcurra *et al.* 2017; Lacerda *et al.* 2018;

300 Müller *et al.* 2020). For this reason, we here provide a revised diagnosis of *E. granti*.

301

2.1. New information on *Erpetosuchus granti* (NMS G.1992.37.1)

Erpetosuchus granti was originally described by Newton (1894) and was last redescribed by Benton & Walker (2002). Minor anatomical reinterpretations were added by Ezcurra *et al.* (2017), based largely on NMS G.1992.37.1. We agree with these descriptions, except where stated explicitly herein. In this section, we expand upon these descriptions by updating the osteology of *Erpetosuchus granti*, based on the first μCT scans of the taxon (referred specimen: NMS G.1992.37.1). This specimen was previously studied based only on moulds and the six visible cervical (C) vertebrae (C3–C8) (Benton & Walker 2002; see Ezcurra *et al.* 2017, Supplementary Information). Our μCT scans revealed previously unseen elements including: six additional vertebrae from the cervico-dorsal transition, associated osteoderms and ribs, two complete scapulae and other parts of the shoulder girdle, and an almost complete forelimb (missing the distal phalanges) (Fig. 3). The μCT scans also showed a previously unnoticed pathology in the right hand (digit I) of this individual (red arrows in Fig. 3). Based on our new diagnosis, NMS G.1992.37.1 belongs to *Erpetosuchus granti* on the basis of: markedly elongated scapula; keeled osteoderms; paramedian osteoderms that are longer than wide with unornamented anterior lamina; and identical vertebral and forelimb morphology to other specimens of the species.

   2.1.1. Vertebrae. A total of six cervical and six dorsal vertebrae are preserved in life position within NMS G.1992.37.1. Of these, the cervicals are partially visible in lateral view in the previously prepared cast. Ezcurra *et al.* (2017) noticed that the posterior cervical vertebrae have well-developed trapezoidal hypapophyses projecting ventrally from the surfaces of the centra (Figs 3–4). We confirm the presence of these prominent hypapophyses and note that they decrease in size and thickness posteriorly, disappearing a few vertebrae posterior to the cervical-dorsal transition (Fig. 4). Dorsal (D) vertebrae D1 and D2 possess anteroventrally projecting hypapophyses. In D3 and D4 the hypapophyses are replaced by a single thin central keel, but from D5 onward (in the posterior direction) the ventral surface of the centrum is smooth and transversely convex (Fig. 4).

   The centra of all preserved vertebrae are rectangular in lateral view (anterior and posterior articular faces are placed at the same level), being anteroposteriorly longer than dorsoventrally tall. The ratio between the length and height of the most posterior completely preserved dorsal centrum (D5) is ~1.91 (7.0 mm / 3.6 mm) (Fig. 4). The transverse width

333 across the transverse processes is greater than the centrum length in all preserved dorsal
334 vertebrae (Fig. 4).

335   The neural spines are well preserved in all vertebrae (Figs 3–4). They are rectangular
336 in lateral view and therefore more similar to those of *Tarjadia ruthae* than the fan-shaped
337 neural spines of *Parringtonia gracilis* (although a widening of the neural spine is present in
338 the most posterior preserved dorsal vertebra [D6] of NMS G.1992.37.1). The neural spines
339 are constant in height along the cervical and dorsal series but are more posteriorly displaced
340 in the dorsals. As noted by Benton & Walker (2002), the apices of the neural spines of the
341 cervical vertebrae are transversely expanded to form 'spine tables'; this is also the case for
342 the anterior dorsal vertebrae. The dorsal surfaces of the spine tables are concave with a deep
343 pit in the centre. However, the morphology of the spine table varies across the cervical-dorsal
344 transition. The cervical spine tables are rectangular (transversely wider than anteroposteriorly
345 long) in dorsal view, but more posteriorly the spine tables gradually become trapezoidal (with
346 a wider anterior margin) in D3–D5, before disappearing in D6 (Fig. 4). Similarly, the pits on
347 the dorsal surface of the spine tables become shallower along the dorsal series and no pit is
348 present in D6 (Fig. 4). These features may be significant because the neural spines of the
349 caudal vertebrae of BGS GSM Elgin A lack spine tables or pits, unlike those of other
350 erpetosuchids (e.g. *Parringtonia gracilis* and *Tarjadia ruthae*) that possess both.
351 Unfortunately, the posterior half of the skeleton is missing in all confirmed specimens of
352 *Erpetosuchus granti*, making it impossible to make direct comparisons with BGS GSM Elgin
353 A.

354   Both the cervical and dorsal series of NMS G.1992.37.1 are associated with two rows
355 of parasagittal osteoderms, as in the holotype (NHMUK PV R3139) (Figs 3–4). However,
356 this is the first time that the lateral series of osteoderms in NMS G.1992.37.1 has been
357 revealed: the μCT scans shows that they are still completely embedded in the matrix, and
358 thus they were not visible in the physical moulds of the specimen (Figs 3–4).

359   **2.1.2. Scapula.** The shoulder girdle of *Erpetosuchus granti* is reasonably well
360 preserved in the holotype (NHMUK PV R3139), so little additional information can be added
361 to the description of Benton & Walker (2002). Both scapulae are preserved in life position in
362 NMS G.1992.37.1 and are larger than those of the holotype (37 mm in maximum length in
363 NMS G.1992.37.1 *versus* 33 mm in NHMUK PV R3139), indicating that the NMS individual
364 was marginally larger than the holotype (Fig. 3). The completeness of the scapulae of NMS

365 G.1992.37.1 allows a more precise quantification of the proportions of this element. Uniquely

366 within Erpetosuchidae, the scapula of *Erpetosuchus granti* is extremely elongated with a total

367 length / anteroposterior width >13 (character [Ch.] 387: 1→2). This is greater than in other

368 relatively gracile taxa such as *Parringtonia gracilis*, where the ratio is ~8–11 (Nesbitt &

369 Butler 2013).

370 **2.1.3. Humerus.** Both humeri of NHMUK PV R3139 have incomplete distal ends but

371 were each estimated to be 38 mm long (Benton & Walker 2002). The humeri in NMS

372 G.1992.37.1 are preserved in articulation with the pectoral girdle, and whereas only the

373 mould of the proximal third of the left humerus is preserved in the block, the entire right

374 humerus (46.5 mm in length) is visible in the μCT scans (Figs 3–4). The distal end is narrow

375 transversely, reaching ~20% of the total humeral length. In addition to the description of

376 Benton & Walker (2002), we report that the deltopectoral crest of both specimens is well

377 developed (extends to ~1/3 of the total humeral length). No entepicondylar foramen or

378 supinator process is visible at the distal end of the humerus, but the condyles are separated by

379 a clear trochlear groove. A deeply excavated, long groove is visible on the posterior surface

380 of the distal end and extends for ~1/3 of total humeral length (Fig. 3).

381 **2.1.4. Ulna.** The ulna and radius of the holotype of *Erpetosuchus granti* (NHMUK

382 PV R3139) are missing their proximal ends, whereas they are completely preserved, in life

383 position with the rest of the right forelimb, in NMS G.1992.37.1 (Fig. 3). The ulna of NMS

384 G.1992.37.1 is long and gracile, weakly flattened and only slightly shorter than the humerus

385 (37 mm in length excluding the olecranon process, 40 mm with this process included, against

386 46.5 mm, respectively). The proximal half of the ulna exhibits a weak curvature that gives the

387 bone a sigmoidal outline in anterior and posterior views (Fig. 3D–E) (not straight, *contra*

388 Benton & Walker 2002). Its proximal end bears a prominent olecranon process that is

389 completely fused with the shaft and a weakly developed lateral (radial) tuber (Fig. 3), just

390 above a concave articular surface for the radius.

391 **2.1.5. Radius.** The radius of NMS G.1992.37.1 is also completely preserved, allowing

392 for a more precise assessment of its proportions, and comparison with the humerus and ulna.

393 The radius is subequal in length to the ulna (36.2 mm *versus* 37 mm excluding the olecranon

394 process, 40 mm with this process included). The radius has a narrow shaft and proximal end

395 that is more expanded than the distal one (Fig. 3).

396   **2.1.6. Manus.** The manus of *Erpetosuchus granti* is very well preserved in the

397   holotype and has been described thoroughly (Benton & Walker 2002). To this description we

398   add that the ratio of metacarpal distal width and length is ~0.27 (2.5 mm / 7.35 mm in

399   metacarpal I), and that we could not identify extensor pits on any of the distal ends of the

400   metacarpals. Although the manus of NMS G.1992.37.1 is not as complete as that of NHMUK

401   PV R3139, it is notable because of a rarely-seen pathology (Fig. 3). Specifically, NMS

402   G.1992.37.1 exhibits polydactyly, with a manus possessing six metacarpals where

403   'metacarpal I' is composed of two fused metacarpals. The same pathology seems to also

404   affect the first phalanx (Fig. 3F).

405

406   **2.2. New information on *Erpetosuchus* sp. (AMNH 29300)**

407   AMNH 29300, from the New Haven Formation of Connecticut (Hartford Basin, Newark

408   Supergroup) of the USA, is the only specimen outside the LSF to be referred to

409   *Erpetosuchus*. In general, we agree with the previous descriptions of this material by Olsen *et*

410   *al.* (2001), and we use this section to update the anatomical description of this specimen

411   based on examination of our CT scans, which, for the first time, allowed access to the medial

412   side of the skull (the whole skull is exposed in left lateral view). This exercise allowed us to

413   update scores for 20 new character states for this specimen in our phylogenetic analysis (see

414   Supplementary Information).

415   AMNH 29300 should still be referred to *Erpetosuchus* sp. based on the small size, and

416   the extremely elongated posterior process of the jugal (Fig. 5) (Ch. 100-2) with an

417   anteroposterior length/dorsoventral thickness ratio (measured at the base of the process) >

418   ~4 , which is higher than in all other erpetosuchids (e.g. it scores '1' = 1.57–3.77 in *Tarjadia*

419   *ruthae*: Ezcurra *et al.* 2017). AMNH 29300 may also differ from *Erpetosuchus granti* in

420   having a maxilla that reaches as far as the anterior orbital border (Fig. 5), whereas it reaches

421   between the posterior and anterior orbital border in *Erpetosuchus granti* and all other

422   erpetosuchids. However, this region of the skull is damaged in AMNH 29300, so we were not

423   able to score this character confidently. Because of this difference, and a lack of overlap in

424   other diagnostic features, we cannot refer AMNH 29300 to *Erpetosuchus granti,* but only to

425   *Erpetosuchus* sp.

426   **2.2.1. Maxilla.** The maxilla of AMNH 29300 has been thoroughly described and we

427   can add little detail to the Olsen *et al.* (2001) description. Its medial side is mounted against a

428 support. Unfortunately, the maxilla is incomplete and broken across the medial side of the

429 alveoli. Based on the hidden alveolar margins we can confirm the presence of ~7/8 teeth

430 sitting in sockets and not fused to the maxilla. The antorbital fossa frames the anterior and

431 ventral borders of the antorbital fenestra as it also does in *Erpetosuchus granti* and other

432 erpetosuchids. The ventral margin of the fossa is a sharp ridge/shelf, which is highly

433 vascularised and pierced by several foramina, as also seen in *Tarjadia ruthae* (Ezcurra *et al.*

434 2017) and *Parringtonia gracilisis* (NMT RB28). There is no evidence for a secondary

435 antorbital fenestra (Fig. 5), which is seen in some erythrosuchids (i.e. *Guchengosuchus*

436 *shiguaiensis*, *Shansisuchus shansisuchus* and *Chalishevia cothurnata*; Ezcurra 2016; Butler *et*

437 *al*. 2019a). The contact of the maxilla with the jugal is unclear due to a fracture running

438 across the relevant area.

439   **2.2.2. Jugal.** As observed by Olsen *et al.* (2001), the jugal of AMNH 29300 is almost

440 identical to that of *Erpetosuchus granti*. The posterior process, although broken at its base,

441 has a distinct lateroventral orientation with respect to the anterposterior axis of the skull. This

442 process lies distinctly ventral to the quadratojugal and extends posteriorly to nearly reach the

443 quadrate condyles, as observed in some erpetosuchids and ornithosuchids (e.g. *Erpetosuchus*

444 *granti,* BGS GSM Elgin A; Fig. 5, compare with Fig. 15) (see Von Baczko & Desojo 2016;

445 Ezcurra *et al.* 2017; Lacerda *et al.* 2018). This process extends posteriorly beyond the

446 occipital border of the lower temporal fenestra. The medial side of the jugal shows pneumatic

447 structures, specifically a series of hollow cavities and trabeculae (Fig. 5I–J). The jugal of

448 AMNH 29300 is in close association with a very well preserved ectopterygoid, which

449 articulates along most of the length of the medioventral edge of the orbital margin (Fig. 5).

450   **2.2.3. Ectopterygoid.** The ectopterygoid of AMNH 29300 is completely concealed in

451 the matrix surrounding the specimen. The main body is anterodorsally curved (much more so

452 than in BGS GSM Elgin A) and broken (but closely associated) with a well-developed,

453 trapezoidal posterior expansion that extends posteriorly to the base of the jugal posterior

454 process (Fig. 5). The anterior process is intact and, as in BGS GSM Elgin A, is short and peg-

455 like (Fig. 5E–F, compare with Fig. 9). In AMNH 29300, this process does not reach the

456 maxilla.

457   **2.2.4. Quadratojugal.** The quadratojugal is very similar in morphology to that of

458 BGS GSM Elgin A, and is still in articulation with the quadrate and closely associated with

459 the posterior process of the jugal. The posteromedial extent of the quadratojugal overlaps the

460 lateral side of the quadrate and does not reach the ventral condyles of the quadrate. The

461 occipital surface of the quadratojugal of AMNH 29300 is not perforated by a foramen, unlike

462 that of BGS GSM Elgin A (Fig. 5G–H, compare with Fig. 8F–K).

463   **2.2.5. Lower jaw.** Only the posterior half of the mandible is preserved in AMNH

464 29300 and most of its dorsal side is hidden by the jugal. However, once the skull and matrix

465 are digitally removed, the details of its dorsal and medial sides become available. As in other

466 erpetosuchids, ornithosuchids and proterochampsids the lower jaw has a strongly developed

467 surangular shelf (Trotteyn *et al.* 2013; Ezcurra 2016; Von Baczko & Ezcurra 2016; Ezcurra *et*

468 *al.* 2017). The mandibular fenestra is not completely preserved but most of its dorsal side is

469 intact and shows it was long compared to the overall lower jaw length. The dorsal margin of

470 the surangular is straight. The angular is widely exposed in lateral view and not fused with

471 the prearticular, which is also separated from the articular. The articular is pierced by a

472 foramen on the medial side and has a medioventrally directed process. The retroarticular

473 process is well developed and extends directly posterior to the glenoid fossa (Fig. 5).

474

475   Archosauria Cope, 1869, *sensu* Gauthier & Padian 1985

476   Pseudosuchia Zittel, 1887–1890, *sensu* Sereno *et al.* 2005

477   Suchia Krebs, 1974, *sensu* Nesbitt 2011

478   Erpetosuchidae Watson, 1917, *sensu* Nesbitt & Butler 2013

479

480   Erpetosuchidae gen. et sp. indet.

481

482   **Referred material.** The disarticulated skeleton of BGS GSM Elgin A is embedded in

483 BGS GSM 91072–81, 91085–6 (Figs 1, 2, 6–14). It consists of: left premaxilla; frontals; left

484 lacrimal; right quadrate; left quadratojugal; right posterior lower jaw (articular, angular,

485 surangular and associated fragments); ectopterygoid; ?pterygoid (two fragments); ?radius;

486 fragments of dorsal vertebrae and associated osteoderm series; incomplete dorsal ribs;

487 articulated series of middle–distal caudal vertebrae with intact osteoderms; parts of both

488 femora (a short fragment of the shaft of the right, and the complete left); left tibia; left fibula;

489   proximal portion of the ?pubis; three left metatarsals (two preserved as moulds). All of these

490   elements are embedded in 10 small blocks of sandstone (Figs 1–2).

491   **Locality and horizon.** BGS GSM 91072–82, 91085–6 was collected at Spynie

492   Quarries (NJ 223657), near to Elgin (Moray, Scotland, United Kingdom). The aeolian

493   sandstones exposed in the quarry belong to the Lossiemouth Sandstone Formation (Upper

494   Triassic: ~upper Carnian/lower Norian; but see Benton & Walker 2011).

495

496   **2.3. Description of BGS GSM Elgin A**

497   **2.3.1. Skull.** Many of the skull bones are largely complete and three-dimensionally

498   preserved. The cranial remains are disarticulated, but closely associated in five blocks (BGS

499   GSM 91074–8) (Figs 1–2, 6–9). The maxilla, nasal, jugal, prefrontal, most of the palate and

500   the braincase are missing.

501   Premaxilla. The left premaxilla is nearly completely preserved within BGS GSM

502   91076 (Fig. 6A–F). It is <10 mm long in lateral view and 5 mm wide in anterior view. In

503   lateral view, the main body of the premaxilla is horizontally oriented (not downturned), has a

504   rectangular shape (proportions: ~1.5 longer anteroposteriorly than deep dorsoventrally) and

505   possesses two thin processes arising from its anterodorsal and posterodorsal margins (Fig.

506   6A).

507   The lateral surface of the main body of the premaxilla is pierced by a comparatively

508   large (relative to the size of the premaxilla) foramen, positioned a short distance above the

509   alveolar margin between the first and second premaxillary alveoli (P1 and P2) (Fig. 6A). This

510   feature is shared with *Parringtonia gracilis* (NMT RB28), and potentially also other

511   erpetosuchids (see Discussion). The μCT scans reveal that this foramen opens into a channel

512   that extends through the premaxilla, trending dorsoventrally and exiting the bone within the

513   external naris, along the posterior side of the base of the anterodorsal process. A

514   proportionately smaller foramen ('anterior premaxillary foramen') can be found in the narial

515   fossae of some early dinosaurs such as *Eoraptor lunensis* (Sereno *et al.* 1993, 2013) and

516   *Buriolestes* (Cabreira *et al.* 2016). An additional opening, that superficially appears to be a

517   large foramen (Fig. 6A: for?), is present on the ventral margin of the external nares, but it

518   likely is an artefact of preservation, unlike the genuine foramen present in the 'rauisuchian'

519   pseudosuchian archosaur *Vivaron haydeni* (Lessner *et al.* 2016).

520   The premaxilla bears four alveoli, but only two erupted teeth are present. These are
521   set in sockets and the bases are not cemented to the alveolar margin (i.e. thecodont
522   implantation: Fig. 6C, F). The four alveoli occupy the entire ventral margin of the premaxilla
523   (Fig. 6F). There is neither an edentulous anterior margin nor a posterior subnarial diastema,
524   which are present in aetosaurs (*Stagonolepis, Neoaetosauroides, Desmatosuchus*) and
525   Ornithosuchidae, respectively (Desojo *et al.* 2013; Von Bazcko & Ezcurra 2013).
526   Unfortunately, due to the small size of the specimen, few details of the dentition are
527   available, but the teeth are weakly compressed mediolaterally, ventrally directed and are
528   weakly recurved towards their apices; it is not clear if they have serrations. The μCT scans
529   show a small replacement tooth medial to P2 (Fig. 6F). A small, dorsoventrally compressed
530   palatal process projects medially and posteriorly, dorsal to alveoli P3–P4. Its posterior border
531   is concave (Fig. 6C, F). It is unclear whether interdental plates were present on the medial
532   side of the premaxilla.

533   The anterior margin of the main body of the premaxilla is sub-vertical in lateral view
534   (Fig. 6A). Above it the thin, elongate anterior process (= nasal process) extends
535   posterodorsally at ~60° to the horizontal in lateral view (Fig. 6A, C). This process (measured
536   from base of external nares to its posterior end) is shorter than the anteroposterior length of
537   the premaxilla and forms the anterior and dorsal margins of the external nares. Its lateral
538   surface bears an unusually long, slot-like articular surface for the nasal (Fig. 6A); the anterior
539   extent of this surface indicates that the nasal would have participated in the anterodorsal
540   margin of the external nares. The shape and orientation of this slot indicates that the nasals
541   were separated from each other anteriorly by thin processes of the premaxillae that met along
542   the midline. Finally, as is common in archosaurs, the relative positions of the nasal
543   articulation and the posterior border of the main body of the premaxilla indicate that the nasal
544   reached further anteriorly than the maxilla in lateral view (Fig. 6A, E).

545   The posterodorsal (= maxillary or subnarial process) process is thinner in lateral and
546   posterior views than the anterior process (Fig. 6A, C). The posterodorsal process initially
547   projects posteriorly at a low angle (~30°) before bending sharply dorsally to become sub-
548   vertical. This morphology is unusual and creates a distinctive 'step-like' contact between the
549   premaxilla and maxilla that is, to our knowledge, unique within Pseudosuchia (Nesbitt 2011;
550   Ezcurra 2016; Roberto-da-Silva *et al.* 2016), and which is similar to the condition in the early
551   dinosaur *Eoraptor lunensis* (see Sereno *et al.* 1993, 2013). However, this part of the
552   posterodorsal process is often broken in many specimens. The posterodorsal process forms

553   the posterior margin of the external naris and excluded the maxilla from participating in the

554   border of this opening (Fig. 6A). The exclusion of the maxilla from the border of the external

555   naris is plesiomorphic in Archosauriformes and the maxilla participates in the border only in

556   a small number of taxa (e.g. all aetosaurs except *Aetosauroides*, *Batrachotomus*

557   *kupferzellensis*, *Effigia, Arizonasaurus*) (Gower 1999; Nesbitt 2011; Desojo *et al.* 2013).

558   The external nares are positioned at the anterior end of the snout, open laterally and

559   are triangular in lateral view (this is a potential autapomorphy of BGS GSM Elgin A within

560   Erpetosuchidae) (Fig. 6A); by contrast, they are normally circular or oval in other archosaurs.

561   The ventral, anterodorsal and posterior margins of the external naris are formed, respectively,

562   by the premaxilla main body, premaxillary anterior process and nasal, and premaxillary

563   posterodorsal process. There is no evidence of either a substantial narial fossa or a subnarial

564   fenestra between the premaxilla and maxilla (Fig. 6A). The subnarial fossa is commonly

565   found in dinosaurs such as *Eoraptor*, *Herrerasaurus,* sauropodomorphs and theropods

566   (Nesbitt 2011), but only rarely in pseudosuchians (e.g. *Batrachotomus kupferzellensis*: Gower

567   1999).

568   Frontal. Both frontals of BGS GSM Elgin A are well preserved and easily identifiable

569   in BGS GSM 91077 (left) and BGS GSM 91075 (right) (Fig. 6G–P). The right frontal (Fig.

570   6G–L) is nearly complete and ~15 mm long anteroposteriorly, whereas the left element is

571   missing its anterior tip (Fig. 6M–P). The frontals are separate (i.e. unfused along the midline)

572   and are longer than wide. Their dorsal surfaces are densely sculptured by a random (non-

573   radial) pattern of ridges and grooves similar to those of early suchians (e.g. *Gracilisuchus* –

574   MCZ 4117; *Parringtonia* – Nesbitt *et al.* 2018), and lack any distinguishable ridge or fossa

575   near the midline (Fig. 6H, N), in contrast to the presence of these features in *Batrachotomus*,

576   *Postosuchus* and some crocodylomorphs (e.g. *Dromicosuchus, Hesperosuchus*,

577   *Sphenosuchus*; Clark *et al.* 2000; Sues *et al.* 2003; Nesbitt 2011), which are characterised by

578   a distinct midline fossa. The orbital margin of the frontal is slightly raised relative to the rest

579   of the dorsal surface. The frontal is as transversely wide along its anterior portion as it is

580   medial to the orbital margin, as in most archosauriforms (e.g., ornithosuchids, phytosaurs,

581   aetosaurs, gracilisuchids: Walker 1964; Nesbitt 2011; Desojo *et al.* 2013; Butler *et al.* 2014;

582   Stocker & Butler 2014). However, the frontal expands laterally posterior to the narrowest

583   interorbital distance, such that the posterior end is nearly twice the width of the anterior end

584   (Fig. 6H, N). This gives the combined frontals a trapezoidal outline in dorsal view (Fig. 6Q–

585   R).

586   The anterior suture with the nasal is such that the frontals would have projected a

587   short distance between the nasals, whereas the posterior margins of both frontals form an

588   interdigitated ('W'-shaped) suture with the parietals (Fig. 6G, M). Along its posteromedial

589   margin there is no evidence that the frontal participated in the supratemporal fenestra.

590   Absence of frontal participation in the supratemporal fenestra is the condition in most

591   Triassic archosaurs (Ezcurra 2016). In lateral view, the frontal forms the entire dorsal margin

592   of the orbit (Fig. 6G–P). The posterolateral corner of each frontal has a depression that likely

593   represents the articulation surface for either the postfrontal or postorbital (if the postfrontal

594   was absent) (Fig. 6G–H, L). The ventral surfaces of the frontals have distinct fossae that

595   represent the impressions of the olfactory bulbs (Fig. 6I, O). These are linked to fossae that

596   represent the impressions of the rest of the cerebrum by the hourglass-shaped impressions of

597   the olfactory tracts. The crista cranii that separate the orbits from these endocranial structures

598   are well-developed tall ridges.

599   Lacrimal. The right lacrimal is completely embedded within BGS GSM 91078 (Fig.

600   7), has a triangular outline in lateral view, and is flat and slightly concave medially. One of

601   the extremities, here interpreted as the ventral process, is tubular in cross-section with a low

602   crest extending along the lateral surface and would presumably have articulated with the

603   anterodorsal process of the jugal. This process terminates ventrally in a large foramen that is

604   similar to, but more ventrally placed than, that reported on the lacrimal of the pseudosuchian

605   *Prestosuchus chiniquensis* (Mastrantonio *et al.* 2019). This foramen opens into a canal that

606   extends through the bone and that emerges medially at the dorsal end of the ventral process

607   (Fig. 7B, D, F). The shape of the lacrimal of BGS GSM Elgin A is unusual, in that the

608   posterior prefrontal process is more prominent than in most known archosaurs BGS GSM

609   Elgin A. A shallow fossa is present on the anterior process that is interpreted as part of the

610   antorbital fossa. The gently curved posterior margin forms the anterior edge of the orbit. Sulci

611   and flat articular surfaces, probably for the nasal and prefrontal, are visible on the anterior

612   and posterior processes in lateral and dorsal views (Fig. 7B: a.na, a.prf?).

613   Quadrate. The right quadrate is nearly completely preserved, although its main body

614   (in BGS GSM 91076) has been separated from the medial pterygoid process (in BGS GSM

615   91079) (Fig. 8A–E). The articular condyles and the anterior extremity of the pterygoid

616   process are not as well preserved, although it is unclear whether this is due to poor

617   ossification, diagenetic damage, or both. A large foramen, interpreted as the quadrate

618   foramen (Fig. 8A–C: qf), is visible on the lateral surface near the quadrate-quadratojugal

619 articulation – this feature is present in all non-archosaurian archosauromorphs, and many

620 crown archosaurs, but absent in crocodylomorphs (Nesbitt 2011). Neither the anterior nor

621 posterior surfaces of the quadrate bear significant grooves or crests. The dorsal portion of the

622 quadrate is triangular in dorsal view, with a prominent dorsal and posteriorly directed

623 process.

624 Quadratojugal. The right quadratojugal of BGS GSM Elgin A is preserved in BGS

625 GSM 91077 in close association with a fragment of the lower jaw (Fig. 8F–K). In lateral

626 view, this bone has a characteristic 'L'-shaped outline (Fig. 8G). The angle between the

627 anterior and dorsal processes is acute (~40°), a feature shared by Ornithosuchidae and

628 Erpetosuchidae within Pseudosuchia (Von Baczko & Desojo 2016; Ezcurra *et al.* 2017;

629 Lacerda *et al.* 2018; but see Discussion). The main body of the quadratojugal is an arched

630 thin sheet that in life wrapped around the lateral surface of the quadrate and contacted the

631 posterior process of the jugal ventrally. The anterior surface of the quadratojugal is concave

632 and formed the posterior and ventral walls of the lower temporal fenestra. The posterior

633 surface is also smooth and concave, and pierced by a foramen, which is not seen in other

634 archosaurs (Fig. 8G, J: for?; see Discussion).

635 The articular surfaces for the posterior process of the jugal and the quadrate are both

636 visible (Fig. 8G–K: a.q, a.j). The first is positioned on the ventral surface of the bone,

637 indicating that in life the jugal would articulate on the ventral surface of the anterior process

638 of the quadratojugal, and that the jugal posterior process extended far posteriorly, reaching

639 close to the quadrate condyles. The first character state is shared with crocodylomorphs (e.g.

640 *Dromicosuchus*), *Postosuchus kirkpatricki*, *Polonosuchus* and *Gracilisuchus* (Chatterjee

641 1985; Sues *et al.* 2003; Nesbitt 2011; Weinbaum 2011) among pseudosuchians. The latter

642 character state (i.e. the jugal posterior process extending as far as the quadrate condyles) is

643 shared with erpetosuchids, most phytosaurs, crocodylomorphs (Benton & Walker 2002;

644 Nesbitt 2011; Ezcurra *et al.* 2017; Stocker *et al.* 2017) and some rauisuchians (Gower 1999;

645 Nesbitt *et al.* 2013; but see Discussion). The articular surfaces for the quadrate on the ventral

646 and dorsal parts of the medial surface of the quadratojugal are both well preserved (Fig. 8G,

647 I–K).

648 Ectopterygoid. The right ectopterygoid is preserved in BGS GSM 91079 and is a

649 long, weakly curved, comma-shaped element (Fig. 9A–F). The main body is elongated and

650 bears traces of the articulation with the pterygoid on the posteromedial surface (Fig. 9A–C:

651 a.pt). The lateral process is lost and on the other side, a straight, rod-like process is visible

652 (Fig. 9B–E: a.j). However, based on the preserved element, it is not possible to determine

653 whether the ectopterygoid articulated with the maxilla, nor the extent of its lateral contact

654 with the jugal (the ectopterygoid has an expanded contact with the jugal in *Erpetosuchus*

655 *granti* and *E.* sp. [AMNH 29300]) (Fig. 5) (Olsen *et al.* 2001; Benton & Walker 2002).

656   The ectopterygoid has a single head, as opposed to the 'rauisuchians' *Postosuchus*,

657 *Polonosuchus* and *Batrachotomus*, in which a double head is present (Chatterjee 1985;

658 Gower 1999; Nesbitt 2011; Weinbaum 2011; Nesbitt *et al.* 2013). The ectopterygoid arches

659 anteriorly in dorsal view and maintains a sub-circular to sub-triangular cross-section along

660 most of its length before it tapers and flares laterally at its distal end. In contrast to most

661 archosaurs, the main body of the ectopterygoid is not significantly arched anteriorly or

662 anterodorsally but is mostly straight as in *Revueltosaurus* (Parker *et al.* 2005). The

663 posteromedial surface of the bone shows an articular surface for the lateral and ventral parts

664 of the pterygoid.

665   Pterygoid. Two fragments preserved in BGS GSM 91076 are here interpreted as parts

666 of the pterygoids (Fig. 9G–N). We interpret the first as the lateral part of the right pterygoid

667 (preserving an articular facet for the ectopterygoid) (Fig. 9G–J). The second fragment (Fig.

668 9K–N) is identified as the posterior portion of the left pterygoid, preserving the medial

669 margin of the subtemporal fenestra, part of the basipterygoid articulation, and the damaged

670 base of the quadrate ramus (Fig. 9K: q r.). A complex system of thin crests is visible on one

671 side of the bone. There is no evidence of teeth on either of the preserved pterygoid fragments.

672   **2.3.2. Lower jaw.** The posterior part of the right lower jaw is preserved in BGS GSM

673 91076 and includes parts of the posterior portion of the angular and parts of the surangular

674 (Fig. 10). There is evidence that an external mandibular fenestra was present, but no other

675 internal mandibular cavity could be identified due to the poor preservation. Posterior to this

676 the angular is widely exposed on the lateral surface of the mandibular ramus. Additional

677 useful diagnostic features cannot be assessed due to the poor preservation of the fragments.

678   We identified one of the associated lower jaw fragments as the anterior part of a

679 mediolaterally broad surangular shelf. A similar wide shelf is present in *Parringtonia* (NMT

680 RB 426), *Erpetosuchus* sp. (AMNH 29300, Fig. 5) and some other archosauriforms (see

681 Discussion). Additional bone shards, presumably belonging to the splenial, angular and

682 surangular, are preserved in BGS GSM 91076 and 91079 close to the other mandibular

683 fragments (Fig. 10B, D–E, G). There is no evidence of a surangular foramen in any of these
684 fragments.

685

686 **2.3.3. Vertebral column and osteoderms.** Incomplete fragments of vertebrae and
687 associated osteoderms belonging to BGS GSM Elgin A are found in several blocks (Figs 2,
688 11). A long, fragmented series of osteoderms and broken ribs can be traced along the surface
689 of BGS GSM 91076 and continues on BGS GSM 91073–5 and GSM 91086 (Figs 1–2).
690 Based on their close proximity with the skull fragments, and the orientation of the rest of the
691 skeleton, these are likely associated with the pre-caudal part of the vertebral series.
692 Associated with these are a putative radius/ulna and a possible pubis fragment (Figs 1, 12).

693 Twelve pairs of articulated osteoderms and moulds or fragments of partial vertebrae
694 are present in BGS GSM 91081 and 91085 (Fig. 2). This series presumably represents the
695 posterior dorsal, sacral and anterior caudal vertebrae. Finally, an articulated series of nine
696 distal caudal vertebrae and associated osteoderms are split between BGS GSM 91074 and
697 91072 (Figs 2, 11). This segment is almost certainly the continuation of the previous series,
698 although, as previously mentioned, an unambiguous connection between the blocks BGS
699 GSM 91072/91074 and 91085/91081 has not been recognised (see Introduction).
700 Unfortunately, little information can be gleaned from the presacral series, but the caudal
701 sequence is well preserved and only slightly distorted (Figs 2, 11). These middle–posterior
702 caudals are the only vertebrae that warrant full description (Fig. 11A–K).

703 Vertebrae. The middle and distal caudal vertebrae are intact and only slightly
704 distorted. This caudal series has some peculiar characteristics (Fig. 11A–K). The centra are
705 strongly reduced in size relative to the neural arches with the neurocentral canal being wider
706 and taller than the centra in cross section (Fig. 11F–K). The neural spines are rectangular and
707 low in lateral view and lack any transverse expansion at their dorsal ends (i.e. spine tables are
708 absent). Expansions of the apices of the neural spines are present in many pseudosuchian
709 archosaur lineages (including Rauisuchidae, Phytosauria, Ornithosuchidae, Aetosauria and
710 Erpetosuchidae; but see Discussion). It is noteworthy, however, that complete caudal series
711 are rarely preserved and the spine table character has been assessed primarily on
712 cervical/dorsal and anterior caudal vertebrae. Spine tables are present on some caudals of
713 *Parringtonia gracilis* (see Discussion). No accessory neural spine, haemal arch or lateral

714 processes (caudal ribs) are present on any of these associated vertebrae, indicating that they
715 possibly represent a segment of the middle to distal tail.

716 Osteoderms. Osteoderms are preserved in articulated parasagittally-arranged rows
717 within multiple blocks (BGS GSM 91081, 91085–6, 91072–4, 91077: Figs 2, 11). Each
718 vertebra of the caudal series is associated with two rows of thin osteoderms per side (a
719 paramedian and lateral row per side: Fig. 11E, L–O). The dorsal surface of each osteoderm is
720 conspicuously ornamented with pits and grooves, but the ventral surface is smooth. The
721 paramedian osteoderms are approximately square in shape (only slightly longer than wide),
722 with a visible keel along the midline that is also the hinge of a weak mediolateral curvature
723 (Fig. 11N–O: see Discussion). The lateral osteoderms are narrower, rectangular and their
724 lateral edge is irregular; they are also smaller and, in contrast to the paramedian osteoderms,
725 they are flat and lack a clear longitudinal keel (Fig. 11L–M). Successive rows of paramedian
726 osteoderms are imbricated, with the anterior margin of each osteoderm being minimally
727 covered by the posterior margin of the previous one. Based on the combined number of
728 osteoderm rows and the one-to-one association with vertebrae of the caudal region, the tail
729 would comprise at least 20 vertebrae. There is no indication of appendicular osteoderms,
730 although if present they might be too small to be detected in the μCT scans.

731

732 **2.3.4. Forelimb**. The only trace of a possible humerus, as noted by Walker (1964), is
733 preserved on the surface of BGS GSM 91081 and 91085 but is not clearly visible in the μCT
734 datasets. Considering its poor state of preservation, it is not possible to comment further on
735 its morphology.

736 A long and thin element, presumably the radius or ulna, is present in BGS GSM
737 91074 and 91077, lateral to the ribs and osteoderms. No further anatomical details are
738 available (Fig. 2).

739

740 **2.3.5. Pelvic girdle and hind limb.** A putative pelvic girdle element is present at the
741 end of the partial vertebral column segment in BGS GSM 91073–5 and 91086. Parts of both
742 hind limbs are partially exposed in association, with a series of dorsal/caudal osteoderms, and
743 the moulds of the centra of a few vertebrae in BGS GSM 91081. The pelvic girdle elements
744 are so fragmentary that it is impossible to comment further on their morphology.

745   Pelvic girdle. A fragment of what could be the proximal end of the pubis with an
746 obturator foramen is present in BGS GSM 91072 (Fig. 12).

747   Femur. Two femoral fragments are partially exposed on the surface of BGS GSM
748 91081 (Figs 1–2, 13). Neither is complete and both are missing the epiphyses and parts of
749 their shafts. They are both partially exposed in lateral view. The following description is
750 based on the right femur, which is missing only the femoral head and distal condyles (Fig.
751 13A–H). The femur has a weakly sigmoidal outline (Fig. 13B, D). The lateral surface of the
752 shaft is smooth. The femur bears no trace of a trochanteric shelf (possible attachment for the
753 M. iliofemoralis in *Erythrosuchus africanus* and in *Mandasuchus tanyauchen* amongst
754 pseudosuchian archosaurs and dinosauriforms; Gower 2003; Nesbitt 2011; Butler *et al.*
755 2018). Conversely, the attachment for the M. caudofemoralis group (= fourth trochanter) is
756 clearly exposed on the medial (ventral) side of the femur (Fig. 13D: 4t) and trends parallel to
757 the long axis of the bone. This crest is low, distinctly separated from the proximal head and is
758 not associated with an intertrochanteric fossa. These latter features are similar to
759 pseudosuchian archosaurs, which also have a mound-like and symmetrical trochanter (as also
760 in non-archosaurian archosauriforms), as opposed to the morphologies (trochanter is absent
761 or present as a sharp flange) present in avemetatarsalian archosaurs (Langer & Benton 2006;
762 Nesbitt 2011; Ezcurra 2016). The femur of BGS GSM Elgin A is unusually thin-walled, with
763 a thickness/diameter ratio of ~0.225 (Ch. 508–1), which is rare, but not unique amongst
764 pseudosuchian archosaurs (e.g. *Effigia, Arizonasaurus, Poposaurus* and *Terrestrisuchus*: see
765 Nesbitt *et al.* 2007; Nesbitt 2011; Schachner *et al.* 2011) (see Discussion). Although
766 incomplete, the preserved distal end hints that the fibular condyle had a rounded cross-section
767 and was distinctly larger than the tibial condyle, as in most archosauriforms (Fig. 13H). A
768 small groove, here identified as the anterior extensor groove, is present as a small concavity
769 limited to the most distal part of the anterior surface of the bone (Fig. 13B, G).

770   Tibia. The tibia is closely associated with the left femur, fibula and the moulds of
771 three metatarsals. Of the two bones associated with the femur, we identify the larger one as
772 the tibia (Figs 2, 13I–L). The left tibia is a slender bone missing the distal and proximal ends
773 (Fig. 14A–D). It is completely embedded in BGS GSM 91081 so that it is only revealed by
774 μCT scans (Figs 1–2, 13I–L). Its total preserved length (28.3 mm) makes it shorter than the
775 preserved length of the right femur (33.6 mm), even accounting for the missing ends. The
776 estimated length is difficult to assess but the life position of the bones in the matrix hint that
777 the complete femur would be longer than the complete tibia. The femur is longer than the

778 tibia (or fibula) in non-archosaurian archosauriforms, pseudosuchian archosaurs,

779 herrerasaurids and post-Carnian sauropodomorphs (Müller *et al.* 2018). The lateral surface of

780 the bone is smooth and lacks a clearly defined fibular crest. The shaft is subcircular in cross-

781 section.

782   Fibula. The left fibula is associated with the other bones of the left hind limb in

783 approximate life position. It is missing the distal and proximal ends (Fig. 13M–R) but appears

784 to have been transversely compressed. Its width at mid-length is distinctively less than that of

785 the tibia, as in most archosauromorphs except *Tanystropheus longobardicus* (Ezcurra 2016).

786 The attachment of the M. iliofibularis is located on the proximal third of the bone and is

787 visible as a small flattened surface (Fig. 13O: M. i). This condition contrasts with the well-

788 developed tubercle positioned approximately at the midshaft that is present in phytosaurs,

789 ornithosuchids and aetosaurs (Sereno 1991; Parrish 1993; Nesbitt 2011).

790   Foot. The moulds of three undetermined metatarsals are preserved between BGS

791 GSM 91081 and BGS GSM 91080, close to the distal end of tibia and fibula (Figs 2, 14K).

792 Little can be said about them other than they are unfused, considerably shorter than both the

793 tibia and fibula (approximate maximum length of the longest element is ~14.5 mm), and thus

794 are not as elongated as those of most avemetatarsalian archosaurs (Sereno 1991; Nesbitt

795 2011).

796

797 **2.4. BGS GSM Elgin P and indeterminate bones in BGS GSM 91072–82, 91085–6**

798 Within the blocks of BGS GSM 91072–82, 91085–6 there are several bones that cannot be

799 assigned to the unnamed pseudosuchian (BGS GSM Elgin A). We refrain from referring

800 these bones to BGS GSM Elgin A due to differences in anatomical features, size, textures,

801 and location (they are scattered away from the main cluster of that skeleton). Furthermore,

802 these bones are in some cases easily identifiable as representing another taxon.

803   BGS GSM 91072–81, 91085–6 contains a previously unknown specimen of the

804 procolophonid *Leptopleuron lacertinum*. A handful of bones embedded in BGS GSM 91074–

805 78 are identified as damaged cranial elements (dentary, partial anterior snout with teeth and a

806 skull roof: Fig. 14A–C), ribs and other unidentifiable fragments, all belonging to the same

807 individual (BGS GSM Elgin P). The dentary and maxilla show features diagnostic of

808 Procolophonidae, and specifically *Leptopleuron lacertinum*, which is known from the same

809 age and locations (Säilä 2010). These features include: frontal narrow between the

810 orbitotemporal openings; bicusped, labiolingually wide maxillary teeth (with the two cusps

811 linked by a sharp ridge); maxillary tooth (M2) larger than maxillary tooth 1 (M1) (Säilä 2010;

812 Zaher *et al.* 2019) (Fig. 14).

813   Potentially belonging to this specimen (BGS GSM Elgin P) are two closely associated

814 long bones (radius and ulna) in BGS GSM 91077, 91074. Unfortunately, and similar to most

815 of the other long bones in BGS GSM 91072–81, 91085–6, the epiphyses are poorly

816 preserved, so only limited information is available (Fig. 14D–E).

817   Finally, two additional bones, not belonging to either BGS GSM Elgin A or L, are

818 here tentatively identified as humeri. The first lies within in BGS GSM 91076+78, but is

819 separate from the BGS GSM Elgin A bone cluster. Whereas this humerus is missing its distal

820 end, its proximal end is intact, with a visible rounded head (Fig. 14E). The second putative

821 humerus is considerably smaller, with a well-developed deltopectoral crest (Fig. 14F). These

822 apparently underwhelming bones are not clearly referable to any of the known Elgin reptiles.

823 This suggests that they may belong to previously unrecognized taxa in the assemblage,

824 hinting at an underappreciated diversity in the LSF late deposits.

825

826 3. Discussion

827 3.1. Comparisons of BGS GSM Elgin A with other archosaurs

828 The µCT scans reveal a combination of features (e.g. osteoderms, femur/tibia proportions,

829 presence of a low fourth trochanter) that indicate that BGS GSM Elgin A is a pseudosuchian

830 archosaur (Nesbitt 2011). However, this new information falsifies the original proposal that

831 the specimen is referable to *Ornithosuchus woodwardi* (Walker 1964). Below we discuss

832 how the BGS GSM Elgin A skeleton differs from *Ornithosuchus* and other known

833 ornithosuchids, and discuss the phylogenetic distribution of key characteristics (from our

834 phylogenetic dataset) of BGS GSM Elgin A within Archosauriformes, with a particular

835 emphasis on those widespread in Archosauria and Pseudosuchia:

836 • Horizontally oriented premaxilla (Ch. 29-0) bearing four premaxillary teeth (Ch. 42-2)

837   that occupy the entire length of the premaxilla (Ch. 26-0) (Fig. 15C–E). This condition

838   differs from *Ornithosuchus woodwardi* and other ornithosuchids, which have a

839   downturned premaxilla with three teeth that are separated from the maxilla by a large

840   subnarial gap and a diastema equal to two tooth positions in length (Ch. 13-1 in Nesbitt

841   2011) (Fig. 15A). This combination of character states also allows us to distinguish BGS

842   GSM Elgin A from the following clades: (a) Phytosauria, which have a higher tooth

843   count, extremely elongated premaxillary body, and external nares that are oriented

844   dorsally and retracted along the snout (Stocker & Butler 2013; Stocker *et al.* 2017; Jones

845   & Butler 2018); (b) Aetosauria, which have an edentulous anterior premaxilla, long

846   premaxillary body (Fig. 15B), and higher tooth count (except perhaps for *Stagonolepis*

847   and *Aetosaurus ferratus*) (Desojo *et al.* 2013; Parker 2018); (c) Crocodylomorpha, which

848   have a subnarial gap to receive an enlarged dentary tooth (Nesbitt 2011); and (d)

849   Gracilisuchidae (Butler *et al.* 2014) which have three premaxillary teeth (e.g.

850   *Gracilisucus* – MCZ 4117). However, the combination of premaxillary features seen in

851   BGS GSM Elgin A is not unique among pseudosuchians and can be also found in

852   erpetosuchids (Fig. 16C–E) and some 'rauisuchians' (e.g. *Postosuchus kirkpatricki*;

853   *Batrachotomus kupferzellensis* – SMNS 80260: Nesbitt 2011; Weinbaum 2011; Nesbitt *et*

854   *al.* 2013; Tolchard *et al.* 2019).

855   • The jugal posterior process lies ventral to the quadratojugal (Ch. 105-1) and reaches past

856   the posterior end of the infratemporal fenestra (Ch. 106-1) (Fig. 15C–E). In the

857   ornithosuchids *Ornithosuchus* and *Riojasuchus* the jugal posterior process lies dorsal to

858   the quadratojugal and does not reach the posterior margin of the infratemporal fenestra

859   (Fig. 15A). Within Archosauriformes, the character states present in BGS GSM Elgin A

860   are shared with Erpetosuchidae (Figs 5, 15C–E), Crocodylomorpha, Phytosauria (except

861   *Diandongosuchus fuyuanensis*) (Nesbitt 2011; Stocker *et al.* 2017) and, among

862   'rauisuchians', with *Batrachotomus kupferzellensis* (SMNS 80260) and *Postosuchus*

863   *kirkpatricki* (TTU-P 9000) (Gower 1999; Nesbitt 2011; Weinbaum 2011; Nesbitt *et al.*

864   2013).

865   • The dorsal process (= ascending process) of the quadratojugal is strongly anteriorly

866   inclined at an acute angle (equal to or less than ~40–45°) from the horizontal plane (Ch.

867   636-1) (Fig. 15). BGS GSM Elgin A shares this character state with some members of

868   Ornithosuchidae (e.g. *Ornithosuchus woodwardi* and *Riojasuchus tenuisceps*, but not

869   *Venaticosuchus rusconi*: Walker 1964; Von Baczko & Ezcurra 2013, 2016; Von Bazcko

870   *et al.* 2014, 2018). However, it is worth noting that this feature is a putative

871   synapomorphy shared between Ornithosuchidae and Erpetosuchidae, and is one of the

872   character states that has united these lineages into a clade in recent analyses (see Von

873 Baczko & Desojo 2016; Ezcurra *et al.* 2017; Lacerda *et al.* 2018) (Fig. 15A, C–E). The

874 majority of other archosauriform groups (including 'rauisuchians' and Crocodylomorpha)

875 either have a vertical or only marginally anteriorly inclined process, except aetosaurs (e.g.

876 *Stagonolepis robertsoni*), in which the anterior process of the quadratojugal is posteriorly

877 inclined (Desojo *et al.* 2013) (Fig. 15B).

878 • Extended surangular shelf (Ch. 286-3). Although small, the only surangular fragment

879 found in BGS GSM Elgin A demonstrates that it had a strongly laterally extended

880 surangular shelf (Fig. 9). This character state is present in both Ornithosuchidae and

881 Erpetosuchidae (Von Baczko & Ezcurra 2016; Ezcurra 2016; Ezcurra *et al.* 2017), but

882 also Erythrosuchidae (Butler *et al.* 2019b) and Proterochampsidae (Dilkes & Arcucci

883 2012).

884 • Osteoderms are densely ornamented (Ch. 589-1), have a longitudinal keel (on paramedian

885 osteoderms, Ch. 591-1) and are longitudinally curved (Ch. 598-1) (Fig. 11E, L–O). The

886 osteoderms of BGS GSM Elgin A share these features with other erpetosuchids (Benton

887 & Walker 2002; Nesbitt & Butler 2013; Ezcurra *et al.* 2017). By contrast the osteoderms

888 of *Ornithosuchus woodwardi* have a longitudinal keel, are weakly sculptured and flat

889 (Walker 1964; Von Baczko & Ezcurra 2016).

890 • Fibula: position of the attachment of the M. iliofibularis (Ch. 530-0) (Fig. 13O). The low

891 platform for the attachment of the M. iliofibularis is located near the proximal end of the

892 fibula in BGS GSM Elgin A, the erpetosuchid *Parringtonia gracilis* (NMT RB28),

893 *Gracilisuchus* and *Mandasuchus*, whereas it is located at midshaft or closer to midshaft in

894 phytosaurs, ornithosuchids and most 'rauisuchians' (Nesbitt 2011; Butler *et al.* 2018).

895 The combination of features present in BGS GSM Elgin A, is inconsistent with its original

896 identification as *Ornithosuchus* (Walker 1964), but also unambiguously distinguish it from

897 other ornithosuchids, phytosaurs, aetosaurs 'rauisuchians' and crocodylomorphs. However,

898 even though BGS GSM Elgin A is missing some of the bones that possess the most typical

899 synapomorphies of Erpetosuchidae (e.g. maxilla: alveolar margin of the maxilla restricted to

900 the anterior half of the bone), it possesses a combination of features in the cranial

901 (premaxilla, frontal, quadrate/quadratojugal) and postcranial skeleton (hind limbs and

902 osteoderms) that are unique to Erpetosuchidae. These are: four premaxillary teeth, evenly

903 distributed along the alveolar margin (absence of subnarial gap); strongly ornamented frontal;

904 posterior process of the jugal that reaches close to the quadrate condyles (posterior to the

905 lower temporal fenestra caudal margin), and articulates ventral to the quadratojugal anterior

906 process; strongly anteriorly inclined quadrate axis/quadratojugal anterior process (< 45°); and

907 four rows of strongly ornamented osteoderms per vertebral segment (two per side).

908 There are however also significant differences between BGS GSM Elgin A and other

909 known erpetosuchids, including the sympatric *Erpetosuchus granti*. These include:

910 • The presence of a foramen on the lateral surface of the premaxilla between P1 and P2, the

911 markedly triangular external nares and the 'step-shaped' posterodorsal process of the

912 premaxilla) (all represent potential autapomorphies within Erpetosuchidae) (Fig. 6).

913 These features of BGS GSM Elgin A are previously unreported in *Erpetosuchus granti*

914 (although this may be also due to the lack of details in the holotype moulds) or any other

915 erpetosuchid (Fig. 15D). However, a foramen above P1/P2 is present in specimens of

916 *Parringtonia* and it is unclear whether *Tarjadia* also has one. Additionally, in BGS GSM

917 Elgin A the palatal process of the premaxilla is concave posteriorly (Fig. 6F), as opposed

918 to straight in *Erpetosuchus granti* (NHMUK PV R3139: Benton & Walker 2002).

919 • Unfused frontals and contact with the parietal (Ch.112-0 and Ch.116-2) (Fig. 6H–S).

920 Similar to *Tarjadia ruthae* and *Parringtonia gracilis*, the frontals of BGS GSM Elgin A

921 are unfused along the midline (see Ezcurra *et al.* 2017). Benton & Walker (2002) reported

922 that the frontals are fused in *Erpetosuchus granti*, but we could not confidently confirm

923 this in our examination of the specimen. The frontals also have a complex interdigitating

924 contact with the parietal (rather than the simple or weakly concave contact seen in all

925 other erpetosuchids) (Benton & Walker 2002; Ezcurra *et al.* 2017; Nesbitt *et al.* 2018).

926 Furthermore, their shape differs from *Erpetosuchus granti* in that they are relatively short

927 and have a simple anterior contact with the nasal. Finally, the posterolateral corner of the

928 frontal in BGS GSM Elgin A has an articular surface for the postfrontal (or postorbital)

929 (Fig. 6H–J). This condition is seen in all erpetosuchids, except *Erpetosuchus granti*

930 (NHMUK PV R3139) in which the postfrontal is considered to be absent (fused with the

931 frontal: Benton & Walker 2002). However, it is noteworthy that fine details as the sutures

932 are hard to see in any of the moulds of any Elgin specimen.

933 • Frontals in ventral view (Ch. 121-1) (Fig. 6L, Q). The crista cranii that separate the orbits

934 from the olfactory bulbs and cerebrum structures are well-developed and tall ridges

935 delimit the constricted the olfactory tract canal. This feature differs from the low crests

936 seen in *Parringtonia gracilis* (Nesbitt *et al.* 2018). However, these are the only two

937 erpetosuchids where this condition can be assessed confidently.

938 • Foramen on the posterior surface of the quadratojugal (potential autapomorphy) (Fig. 8).
939 BGS GSM Elgin A has a foramen on the posterior body of the quadratojugal, which is not
940 present in any other erpetosuchid with a preserved quadratojugal (see *Erpetosuchus* sp. in
941 Fig. 5). This feature is, to our knowledge, unreported in any other pseudosuchian.

942 • Ectopterygoid (Figs 5E–F, 9A–F). The ectopterygoid of BGS GSM Elgin A is unlike
943 those of most archosauriforms in lacking a strong curvature. Within erpetosuchids the
944 ectopterygoid is well preserved and strongly curved in *Erpetosuchus* sp. (AMNH 29300)
945 (Fig. 5).

946 • Lack of spine table (potential autapomorphy within Erpetosuchidae) (Fig. 11). All of the
947 available vertebrae of BGS GSM Elgin A (middle and distal caudals) lack the
948 characteristic concave spine tables that are present in other erpetosuchids (e.g.
949 *Erpetosuchus granti*, *Parringtonia gracilis*, *Tarjadia ruthae*) (Figs 2–3) (see Benton &
950 Walker 2002; Nesbitt & Butler 2013; Ezcurra *et al.* 2017). Note that this character is
951 normally assessed on the cervical and dorsal vertebrae, whereas the only available
952 vertebrae in BGS GSM Elgin A are caudals. Furthermore, caution is warranted because
953 NMS G.1992.37.1 shows that *Erpetosuchus granti* has spine tables only on the cervical
954 and anterior dorsal series (Figs 2–3). This contrasts with *Parringtonia gracilis* and
955 *Tarjadia ruthae*, which have a well-developed spine table on the available anterior caudal
956 vertebrae (see Nesbitt & Butler 2013; Ezcurra *et al.* 2017), suggesting that this feature
957 extends posterior to the dorsal vertebrae. Thus, it is possible that the lack of spine tables
958 in dorsal (middle and posterior) and caudal vertebrae characterises BGS GSM Elgin A
959 and *Erpetosuchus granti*, although this needs to be confirmed in more complete
960 specimens.

961 • Shape and thickness of the osteoderms (Ch. 595-1 and Ch. 592-1) (potential
962 autapomorphy within Erpetosuchidae) (Fig. 11L–O). The paramedian osteoderms of BGS
963 GSM Elgin A are slightly longer than wide, as in *Parringtonia gracilis* (NHMUK PV
964 R8646) and *Erpetosuchus granti* (NHMUK PV R3139), unlike the condition in *Tarjadia*
965 *ruthae*, *Archeopelta arborensis*, *Pagosvenator candelariensis* and other specimens
966 referred to *Parringtonia gracilis* (NMT RB426; NMT RB28), which either have square or
967 wider-than-long osteoderms (Benton & Walker 2002; Nesbitt & Butler 2013; Ezcurra *et*
968 *al.* 2017; Lacerda *et al.* 2018). The osteoderms of BGS GSM Elgin A are notably thin
969 (Fig. 11N–O), contrasting with the thicker osteoderms of other erpetosuchids (although
970 this may be due to the smaller body size of BGS GSM Elgin A compared to most other

971 erpetosuchids except *Erpetosuchus* and *Dyoplax arenaceous*) (Lucas *et al.* 1998; Benton

972 & Walker 2002; Maisch *et al.* 2013). Their positions (e.g. alignment relative to the

973 vertebral column, imbrication), and ornamentation are similar to those of other

974 erpetosuchids.

975 • Thin walled-femur (Ch. 508-1) (potential autapomorphy within Erpetosuchidae). Perhaps

976 linked with its gracile morphology (shared with *Erpetosuchus granti* and likely

977 *Parringtonia gracilis,* but not *Tarjadia ruthae*), the femora of BGS GSM Elgin A is

978 uniquely thin walled (thickness/diameter ratio <0.3 at the midshaft). This is thinner than

979 in the femora of *Parringtonia gracilis* (NMT RB28, NMT RB426) and *Tarjadia ruthae*.

980

981 **3.2. Results of the phylogenetic analyses**

982 Our phylogenetic analysis found 110 MPTs with lengths of 3410 steps, consistency index

983 (CI) = 0.256 and retention index (RI) = 0.636. BGS GSM Elgin A is recovered within

984 Erpetosuchidae, closely related to *Erpetosuchus* and *Parringtonia* (Fig. 16, Supplementary

985 Information, Fig. S2). Overall, Erpetosuchidae is supported by one unambiguous (present in

986 all MPTs) and 22 ambiguous (not shared in all MPTs) synapomorphies, five of which can be

987 scored in BGS GSM Elgin A: 1) prominent ornamentation of the dorsal surface of the skull

988 (frontal) (Ch. 5: 1→2); 2) orbital margin of the frontal is slightly raised above the skull table

989 (Ch. 7: 0→1); 3) multiple rows of dorsal osteoderms (Ch. 588: 2→3) – reversed to state 2 in

990 BGS GSM Elgin A; 4) strongly ornamented osteoderms (Ch. 589: 0 →1); 5) thick

991 paramedian osteoderms (Ch. 592: 0→1) –reversed to state 0 in *Parringtonia*, *Erpetosuchus*

992 and BGS GSM Elgin A. The relationships within Erpetosuchidae are largely consistent,

993 although weaker (see Bremer values in Fig. 16 and Supplementary Information, Fig. S2) with

994 those recovered in previous iterations of the phylogenetic dataset: erpetosuchids are divided

995 into two clades (*Pagosvenator candelariensis* (*Tarjadia ruthae* + *Archeopelta arborensis*)

996 and (*Erpetosuchus* + *Parringtonia*) (Müller *et al.* 2020). However, these groups are in a

997 polytomy with *Dyoplax arenaceous*, differing from the results of Ezcurra *et al.* (2017) and

998 Müller *et al.* (2020), both of which found *Dyoplax arenaceous* to be the earliest diverging

999 erpetosuchid. BGS GSM Elgin A is in a polytomy with specimens of *Erpetosuchus* spp. and

1000 *Parringtonia gracilis* (holotype: NHMUK PV R8646; NMT RB28; NMT RB426) (Fig. 16)

1001 (Fig. 16, Supplementary Information, Fig. S2).

As in other recent studies, Erpetosuchidae is recovered as the sister taxon to Ornithosuchidae (Von Baczko & Desojo 2016; Ezcurra *et al.* 2017; Lacerda *et al.* 2018; Müller *et al.* 2020) in a clade supported by six unambiguous and nine ambiguous synapomorphies. However, unlike these other studies, the relationships of this clade with others in Pseudosuchia are unclear. Specifically, whereas we recovered other historically well-established clades such as Phytosauria, Aetosauria, Gracilisuchidae, Poposauroidea and Rauisuchidae (the latter in a poorly defined suchian clade with paracrocodylomorphs), all of these these clades are all found in an unresolved polytomy with *Nundasuchus songeaensis* and (Ornithosuchidae + Erpetosuchidae). Note that the support for these clades remains moderate to high (Bremer support ranging from 2–5) when they are considered individually (Supplementary Information, Fig. S2), meaning that the changes in our datasets affected only their relative positions within Pseudosuchia. The monophyly of Pseudosuchia is supported by six unambiguous and 14 ambiguous synapomorphies (see Supplementary Information) and the clade has a Bremer support of 2.

The poor resolution in this area of the tree is not entirely surprising given the historical low support for relationships at the base of Pseudosuchia (Fig. 16, Supplementary Information, Fig. S2) (Nesbitt 2011; Irmis *et al.* 2013; Ezcurra 2016; Ezcurra *et al.* 2017; Müller *et al.* 2020). The addition of the new terminal taxa may have weakened support by introducing a series of issues into the analyses including: polarity, which is aggravated by the limited taxonomic sampling of some lineages (e.g. Suchia, Paracrocodylomorpha, Crocodylomorpha); character conflicts introduced with the updated scores of old and new operational taxonomic units (particularly in postcranial characters); and high homoplasy amongst pseudosuchian lineages. We suggest that the inclusion of more complete paracrocodylomorph and crocodylomorph terminal taxa and the addition of novel characters – as outlined for Crocodylomorpha by Irmis *et al.* (2013) – would help to resolve the relationships of well-established groups within Pseudosuchia.

3.3. Erpetosuchidae indet., *Erpetosuchus granti* or a new species?

As shown above, BGS GSM Elgin A shares synapomorphies with Erpetosuchidae and *Erpetosuchus granti,* but also differs from other erpetosuchids and therefore could potentially represent a new species. Specifically, BGS GSM Elgin A differs from other erpetosuchids in having: a large foramen on the lateral side of the premaxilla between P1/P2 (also present in

1034 *Parringtonia gracilis* and potentially in *Tarjadia ruthae*; other erpetosuchids are too poorly

1035 preserved to verify this character); a 'step-shaped' posterior edge of the premaxilla in lateral

1036 view, with the posterior margin of the premaxilla anterior to the posteroventral corner of the

1037 external nares; external nares that are triangular in shape; a straight body of the

1038 ectopterygoid; a foramen on the occipital surface of the quadratojugal; an unusually thin

1039 femoral wall (transverse thickness of bone wall/femoral diameter <0.3); thin osteoderms

1040 (shared with *Erpetosuchus granti* and *Parringtonia gracilis*); and neural spines of the caudal

1041 vertebrae that lack spine tables (potentially shared with *Erpetosuchus granti*). BGS GSM

1042 Elgin A, is considerably smaller than *Tarjadia*, *Parringtonia* and *Pagosvenator*, and is

1043 comparable in size only with *Dyoplax* and other *Erpetosuchus* specimens (Fig. 17).

1044 Nevertheless, we refrain from assigning BGS GSM Elgin A to *Erpetosuchus granti* or

1045 erecting a new taxon because the limited overlap between BGS GSM Elgin A and the

1046 specimens referred to *Erpetosuchus* prevents us from fully comparing these specimens.

1047 Unfortunately, most of putative autapomorphies of BGS GSM Elgin A are lost or

1048 impossible to assess in coeval specimens of *Erpetosuchus granti* (Fig. 17A–D). Indeed, BGS

1049 GSM Elgin A and all known specimens of *Erpetosuchus granti* have very few elements in

1050 common (predominantly cranial), and even these are difficult to compare due to differential

1051 preservation. Whereas BGS GSM Elgin A comprises disarticulated cranial bones, a posterior

1052 vertebral column and hind limb material, only portions of the anterior skeletons of

1053 *Erpetosuchus granti* (NHMUK PV R3139 and NMS G.1992.37.1) are known (e.g. complete

1054 articulated skull, forelimbs, cervical and anterior-to-middle dorsal vertebrae, and associated

1055 osteoderms) – note also that the dorsal vertebrae of NMS G.1966.43.4 are damaged so that

1056 their neural spines are not preserved. To complicate the matter, the only known cranial

1057 material of *Erpetosuchus granti* is preserved in the type specimen (NHMUK PV R3139), as

1058 the mould of an articulated skull, along with the cervical series, pectoral girdle and

1059 hindlimbs. Thus, the only way to study this specimen is through casts (see Benton & Walker

1060 2002), in which the surface details (including sutures and ornamentation) are often lost or

1061 difficult to interpret (even in first-generation casts).

1062 On the basis of our proposed diagnosis of *Erpetosuchus granti*, BGS GSM Elgin A

1063 differs from *E. granti* in both of the character states for which the specimens can be assessed.

1064 Specifically: (1) the angle between the alveolar margin and the anterior margin of the

1065 premaxilla in lateral view is acute in BGS GSM Elgin A and obtuse in *Erpetosuchus granti*;

1066 and (2) the paramedian osteoderms of *Erpetosuchus granti* have an unornamented anterior

1067 lamina that is absent in the osteoderms of BGS GSM Elgin A. However, as previously

1068 reported, the neural arches of the caudal vertebrae of BGS GSM Elgin A lack spine tables, a

1069 feature that might unite it with *Erpetosuchus granti* – but that cannot be confirmed in the

1070 absence of more complete specimens.

1071   The CT scans of *Erpetosuchus* sp. (AMNH 29300) are also of limited use. The

1072 elements common to both BGS GSM Elgin A and AMNH 29300 (quadratojugal,

1073 ectopterygoid, surangular shelf) are very similar and, if informative, they not diagnostic

1074 below the family level (Figs 5, 8, 10–11, 15). The only differences we notice are that the

1075 curvature of the ectopterygoid in BGS GSM Elgin A is less pronounced than that of AMNH

1076 29300, and the foramen on the quadratojugal of BGS GSM Elgin A is absent in AMNH

1077 29300 (compare Fig. 5G–H, 8).

1078   Overall, the series of features that distinguish BGS GSM Elgin A from other taxa (eg.

1079 P1/P2 foramen; the shape of the posterodorsal process of the premaxilla; the shape of the

1080 external nares; unfused frontals; suture and ornamentation of the frontal; the curvature of the

1081 ectopterygoid) are unfortunately missing or inaccessible in other specimens referred to

1082 *Erpetosuchus*. Thus, we find the previously discussed verifiable differences and similarities

1083 insufficient to conclusively prove that BGS GSM Elgin A distinct from *Erpetosuchus granti*.

1084 Nevertheless, it is useful to summarise the two possible options:

1085   (a) BGS GSM Elgin A is a new species. In this case, the differences noted between BGS

1086   GSM Elgin A and *Erpetosuchus* specimens are not simply expressions of intraspecific

1087   variation. This might hint at a higher diversity for the Lossiemouth Sandstone reptile

1088   assemblage than previously realised. Moreover, it would represent the first example

1089   of two sympatric erpetosuchids, perhaps indicating niche partitioning (see below).

1090   (b) Alternatively, BGS GSM Elgin A is referable to *Erpetosuchus granti*. In this case the

1091   unique features of BGS GSM Elgin A would represent individual variation within

1092   *Erpetosuchus granti* or perhaps the expression of an earlier ontogenetic stage or

1093   features of the taxon that are not visible in other specimens lacking these elements.

1094   One line of evidence that points towards BGS GSM Elgin A being sub-adult comes

1095   from the impressions left by the brain on the frontal (Fig. 6I). In living crocodylian

1096   species there is a close relationship between the brain and skull roof in early

1097   ontogeny, with lengthening and separation of the olfactory lobes from the rest of the

1098   cerebrum during early adulthood (Jirak & Janacek 2017). Adult crocodylian brain

cavity endocasts largely represent the dural cavity (Witmer *et al.* 2008), and lack the impression of the bony ridge that records the position of the interhemispheric fissure. Since BGS GSM Elgin A exhibits clear separation of the telencephalic fossa and an elongate olfactory tract, it seems likely that the individual was neither a young juvenile nor fully adult. However, since adult retention of a paedomorphic condition is also possible, this evidence remains inconclusive. If this were confirmed by any further discoveries in the future, the putative autapomorphies of BGS GSM Elgin A could help to refine the diagnosis of *Erpetosuchus*.

These questions only can be answered with the discovery of better-preserved specimens with elements shared in common with the currently known specimens of *Erpetosuchus* and BGS GSM Elgin A.

4. Conclusions

We present a revision of some of the erpetosuchid material from the LSF using µCT scans. This work includes the first description of the fossil content of BGS GSM 91072–81, 91085–6. We show that numerous bones belonging to at least two different species are hidden therein. The original identification of one of these skeletons (BGS GSM Elgin A) as *Ornithosuchus* is rejected, and we show instead that it is a gracile, small-bodied (perhaps juvenile) erpetosuchid. Detailed osteological comparisons between BGS GSM Elgin A and the coeval *Erpetosuchus granti* reveal strong similarities, but also some crucial differences. In addition, we provide new descriptive information for *Erpetosuchus granti* based on new µCT scans of a referred specimen. This work revealed previously unknown characteristics of the forelimb and allowed us to propose an updated diagnosis for *Erpetosuchus granti*. Our phylogenetic analysis suggests that BGS GSM Elgin A is closely related to *Erpetosuchus* but does not clarify whether or not it represents a new taxon, an issue exacerbated by the lack of anatomical overlap between key specimens. Under these circumstances the evidence is insufficient to choose between the competing hypotheses that BGS GSM Elgin A is either a small or juvenile *Erpetosuchus granti,* or a new taxon. Nevertheless, we identified a number of potentially diagnostic features for BGS GSM Elgin A in the hope that they could be used as a guide to clarify the relationships of BGS GSM Elgin A and *Erpetosuchus* in the light of future discoveries.

The second specimen (BGS GSM Elgin P) included in these blocks is a new specimen of the procolophonid parareptile *Leptopleuron lacertinum*. The significance of the fossil content of the BGS GSM 91072–81, 91085–6 therefore goes beyond their taxonomic and systematic importance. By identifying these 'new' specimens in historical material, our study suggests that the richness of the 'Elgin reptile fauna' might have been seriously underestimated. It is possible that – concealed within collections and the few active exposures – similar remains are more common than previously thought.

Finally, our study demonstrates that μCT scanning techniques are an invaluable tool for extracting new and heretofore inaccessible data from small-to-medium-sized Elgin specimens regardless of their preservation and preparation history.

5. Data availability

All 3D models and μCT datasets used in this studied were uploaded to Morphosource (https://www.morphosource.org/) and can be freely accessed at [MORPHOSOURCE link to be added here upon acceptance] (Davis *et al*. 2017).

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Figure captions

Figure 1. (A) Map of Great Britain showing the position of the 'Elgin' quarries, with a

geological map of the Elgin area (Moray, Scotland, UK). (B–C) Field photographs of the

Spynie quarries, with white arrows and dashed line indicating the fossiliferous layer

identified on one of the active faces of the quarry; (D) photographs of the articulated blocks

comprising BGS GSM 91072-81, 91085-6; (E) schematic representations of the distribution

of the fossil content (each colour corresponds to a different individual) in the sandstone

blocks. The geological map was redrawn from Benton & Walker (1985). Silhouettes from

www.phylopic.org. Scale bars in (B–C) = 5 cm.

Figure 2. Detailed fossil content of BGS GSM 91072-81, 91085-6 based on the digital

reconstruction following the μCT scanning and segmentation. Abbreviations: an, angular; ar,

articular; d, dentary; fr, frontal; ept, ectopterygoid; f, femur; fi, fibula; fr, frontal; h, humerus;

la, lacrimal; lj, lower jaw; mt, metatarsal; mx, maxilla; na, nasal; os, osteoderm; pmx,

premaxilla; pt, pterygoid; q, quadrate; ra, radius; r, rib; san, surangular; vert, vertebra; pp sq,

paroccipital process of the squamosal; pu, pubis; ul, ulna; ti, tibia. In the inset figure bones

are colour-coded to show their distributions within the original composite block: black for

BGS GSM Elgin A; red for BGS GSM Elgin P; blue for indeterminate. Scale bars = 5 cm.

Figure 3. *Erpetosuchus granti,* NMS G.1992.37.1 (referred specimen). (A) cervical

vertebrae, right pectoral girdle and articulated forearm in right lateral view; (B–F) details of

humerus, radius, ulna and manus; (B–C) humerus digital model and line drawing in anterior

(middle row), proximal (top), distal (bottom), and posterior views; (D–E) radius and ulna

digital model and line drawings; (D) anterior (middle row); (E) proximal (top); and distal

(bottom) views. (F) forearm digital model, line drawing and detail showing the cross section

of pathologic metacarpal I. The red arrows indicate the pathology on metacarpal I.

Abbreviations: dpc, deltopectoral crest; g, groove; h, humerus; hh, humeral head; l. os, lateral

osteoderms; ma, manus; mc I-V, metacarpal I to V; pm. os, paramedian osteoderm oc,

olecranon process; ra, radius; rc, radial condyle; rt, radial tuberosity; sc, scapula; uc, ulnar

condyle; ul, ulna; vert, vertebra. Scale bars = 10 mm.

Figure 4. *Erpetosuchus granti,* NMS G.1992.37.1 (referred pecimen). (A) cervical-dorsal

vertebrae, left pectoral girdle and articulated forearm in oblique dorsolateral view; (B) close-

up of the interclavicle; (C) close-up of the ventral osteoderm row; (D–E) schematic

reconstruction of the posterior cervical and anterior dorsal vertebral series in dorsal (top) and

1430 lateral (bottom) views. Abbreviations: co, coracoid; D1–6, first to sixth dorsal vertebra; dp,

1431 diapophysis; hu, humerus; hyp, hypapophysis; icl, interclavicle; l. os, lateral osteoderm; pm.

1432 os, paramedian osteoderm pa, parapophysis; poz, postzygapophysis; prz, prezygapophysis; r,

1433 rib; sc, scapula; st, spine table; v. os, ventral osteoderm. Scale bar = 10 mm.

1434 **Figure 5.** *Erpetosuchus* sp. AMNH 29300. (A) lateral; (B) medial views; (C–D) close-up of

1435 the skull in lateral and medial views; (E–F) ectopterygoid in medial and lateral views; (G–H)

1436 quadrate and quadratojugal in lateral and posterior views; (I–J) jugal in medial view and

1437 coronal section as seen in the µCT scans. The red arrows indicate pneumatic structures

1438 (cavities and trabeculae) of the jugal. Abbreviations: an, angular; aof, antorbital fenestra; a.j,

1439 articulation for the jugal; a.pt, articulation for the pterygoid; den, dentary; emf, external

1440 mandibular fenestra; ept, ectopterygoid; la, lacrimal; ltf, lower temporal fenestra; mx,

1441 maxilla; mx s., maxillary shelf; or, orbit; po, postorbital; pra, prearticular; pt, pterygoid; sq,

1442 squamosal; q, quadrate; qj, quadratojugal; rap, retroarticular process; san, surangular; sas,

1443 surangular shelf. Scale bar in (C–D) equals 10 mm.

1444 **Figure 6.** Erpetosuchidae indet., BGS GSM Elgin A, premaxilla and frontals. (A–F) Left

1445 premaxilla in (A) anterior, (C) medial, (D) posterior, (E) dorsal, and (F) ventral views; (G–L)

1446 left frontal in (G) dorsal, (H) lateral, (I) ventral, (J) medial, (K) anterior, and (L) posterior

1447 views; (M–P) right frontal in (M) dorsal, (N) lateral, (O) ventral, and (P) medial views; (Q–

1448 R) articulated frontal in (Q) dorsal, and (R) ventral views. Abbreviations: a.na, articulation

1449 for the nasal; a.pf, articulation for the postfrontal; cer, cerebrum; en, external nares; for,

1450 foramen; ob, olfactory bulb; or, orbit; P1-4, premaxillary tooth 1-4; pap, palatal process; pnp,

1451 postnasal process; prp, prenasal process; rt, replacement tooth. Scale bars = 10 mm.

1452 **Figure 7.** Erpetosuchidae indet., BGS GSM Elgin A, right lacrimal. (A–F) lacrimal in (A)

1453 dorsal, (B,) lateral, (C) anterior, (D) medial, (E) posterior, and (F) ventral views.

1454 Abbreviations: a. prf, articulation for the prefrontal; a. mx, articulation for the maxilla; a.na,

1455 articulation for the nasal; l.for, lacrimal foramen; or, orbit; aof, antorbital fenestra. Scale bars

1456 = 10 mm.

1457 **Figure 8.** Erpetosuchidae indet., BGS GSM Elgin A, quadrate and quadratojugal. (A–E)

1458 quadrate in (A) posterodorsal, (B) lateral, (C) anteroventral, (D) medial, and (E) ventral

1459 views; (F-K) quadratojugal in (F) anterior, (G) lateral, (H) posterior, (I) medial, (J) dorsal,

1460 and (K) ventral views. Abbreviations: a.co, articular condyles; a.j, articulation for the jugal;

1461 a.pt, articulation for the pterygoid; a.q, articulation for the quadrate; a.qj, articulation for the

1462 quadratojugal; a.sq, articulation for the squamosal; for, foramen; ltf, lower temporal fenestra

1463 qf, quadrate foramen. Scale bars = 10 mm.

1464 **Figure 9.** Erpetosuchidae indet., BGS GSM Elgin A, left ectopterygoid and two pterygoid

1465 fragments. (A–F) Ectopterygoid in (A) anterior, (B) lateral, (C) posterior, (D) medial, (E)

1466 dorsal, and (F) ventral views; (G-J) middle-left section of the pterygoid; (K–N) posterior

1467 portion of the left pterygoid. Abbreviations: a.bpt, articulation for the basipterygoid; a.ept,

1468 articulation for the ectopterygoid; a.pt, articulation for the pterygoid; a.qj, articulation for the

1469 quadratojugal; q r., quadrate ramus of the pterygoid; sofe, suborbital fenestra; stf,

1470 subtemporal fenestra. Scale bar = 10 mm.

1471 **Figure 10.** Erpetosuchidae indet., BGS GSM Elgin A, posterior right lower jaw fragments in

1472 (A–B) lateral, (C–D) dorsal, (E–F) medial and (G–H) ventral views. Abbreviations: an,

1473 angular; a.cor, articulation for the coronoid; emf, external mandibular fenestra; san,

1474 surangular; sas, surangular shelf; rap, retroarticular process. Scale bars = 10 mm.

1475 **Figure 11.** Erpetosuchidae indet., BGS GSM Elgin A, articulated middle–posterior series of

1476 caudal vertebrae, caudal vertebra and osteoderms. (A–E) series of middle-posterior caudal

1477 vertebrae in (A) dorsal, (B) left lateral, (C) ventral, and (D–E) and right lateral views (E with

1478 associated osteoderms); (F–K) caudal vertebra in (F) dorsal, (G) anterior, (H) left lateral, (I)

1479 posterior (J), right lateral, and (K) ventral views; (L–M) paramedian row of caudal

1480 osteoderms in (L) dorsal and (M) ventral views; N–O close-up of caudal paramedian

1481 osteoderm in (N) anterior and (O) dorsal views. Abbreviation: k, keel. Scale bars = 10 mm,

1482 scale bar in (N–O) = 5 mm.

1483 **Figure 12.** Erpetosuchidae indet., BGS GSM Elgin A, pubis? in (A) dorsal, (B) posterior, (C)

1484 lateral (D) anterior, (E) medial, and (F) ventral views. Abbreviation: of, obturator foramen.

1485 Scale bar = 10 mm.

1486 **Figure 13.** Erpetosuchidae indet., BGS GSM Elgin A, right femur, left tibia, left fibula and

1487 articulated partial left leg. (A, E) right femur in proximal, (B) lateral, (C) posterior (D)

1488 medial, (F) anterior, and (G, H) distal views; (I–L) left tibia in (I) medial, (J) anterior, (K)

1489 lateral, and (L) posterior views; (M–R) left fibula in (M) lateral, (N) anterior, (O) medial, (P)

1490 proximal, (Q) posterior, and (R) distal views; (S) left leg in lateral view. Abbreviations: aeg,

1491 anterior extensor groove; fc, fibular condyle; 4t, fourth trochanter; M. i, attachment for the M.

1492 iliofibularis; pfos, popliteal fossa?; tc, tibial condyle, vl, ventrolateral edge. Scale bar = 10

1493 mm.

Figure 14. *Leptopleuron lacertinum* bones and indeterminate elements in BGS GSM 91072-82, 91085-6 blocks. (A) *Leptopleuron lacertinum*, BGS GSM Elgin P, right dentary and maxilla and bicuspid teeth in lateral view; (B–C) skull roof of *Leptopleuron lacertinum*, BGS GSM Elgin P in (B) dorsal and (C) lateral view; (D–E) radius and ulna of indeterminate taxon in BGS GSM 91074+ 91077; (E) humerus of indeterminate taxon in BGS GSM 91078; (F) humerus of indeterminate taxon in BGS GSM 91074+ 91077. Abbreviations: den, dentary; dpc, deltopectoral crest mx, maxilla; Mn, n^{th} maxillary tooth; Dn, n^{th} dentary tooth; hh, humeral head; ot, orbito-temporal fossa; ra, radius; ul, ulna. Scale bar = 10 mm.

Figure 15. Comparisons of the anterior snout (top row) and jugal-quadratojugal of selected pseudosuchians. (A) *Ornithosuchus woodwardi* (modified from Walker 1964); (B) *Stagonolepis robertsoni* (redrawn and modified from Desojo *et al.* 2013); (C) *Tarjadia ruthae* (redrawn and modified from Ezcurra *et al.* 2017); (D) *Erpetosuchus granti* (redrawn and modified from Benton & Walker 2002); (E) Erpetosuchidae indet., BGS GSM Elgin A. Note the small size of the premaxilla relative to the quadrate in the depicted erpetosuchids. Abbreviations: en, external naris; j, jugal; ltf, lower temporal fenestra; mx, maxilla; na, nasal; or, orbit; pmx, premaxilla; qj, quadratojugal; stf, supratemporal fenestra. Scale bars = 10 mm.

Figure 16. Phylogenetic tree of Pseudosuchia. Comparisons of the strict consensus obtained in this study (left) and Müller *et al.* (2020). Note the change of the position of Phytosauria and *Nundasuchus songaensis* and the loss of definition at the base of Pseudosuchia in this study. Numbers indicate Bremer support values above one.

Figure 17. Skeletal reconstructions showing preserved bones in BGS GSM Elgin A, and specimens referred to *Erpetosuchus*, and size comparisons with other erpetosuchids. (A) *Erpetosuchus granti*, NHMUK PV R3139; (B) *E. granti*, NMS G.1992.37.1; (C) *Erpetosuchus* sp. AMNH 29300; (D) Erpetosuchidae indet, BGS GSM Elgin A; (E) *Tarjadia ruthae*; (F) *Pagosvenator candelariensis*; (G) *Parringtonia gracilis*; (H) *Dyoplax arenaceous*. Silhouettes in (E–G), modified from Ezcurra *et al.* (2017). Scale bar = 5 cm.

1520 **Table 1.** µCT specifications and fossil content of each BGS GSM 91072-82, 91085-6 blocks;
1521 *Erpetosuchus granti* (NMS G.1992.37.1A-B), and *Erpetosuchus* sp. (AMNH 29300). For
1522 further µCT see Table S1 in the Supplementary Information and at [MORPHOSOURCE link
1523 to be added here upon acceptance].

Specimen number	Voxel size [mm]	Fossil content
BGS GSM 91081, 91085	0.0836	BGS GSM Elgin A: femora, tibia, fibula, metatarsals, sacral and caudal vertebrae and associated series of osteoderms
BGS GSM 91086, 91073	0.0234	BGS GSM Elgin A: middle-posterior caudal series and associated rows of osteoderms
BGS GSM 91072	0.0390	BGS GSM Elgin A: posterior dorsal osteoderms, ?pubis and associated vertebral fragments
BGS GSM 91075	0.0489 and 0.0248 (close-up)	BGS GSM Elgin A: frontal (l) BGS GSM Elgin P: anterior snout (dentary, maxilla, premaxilla, teeth), associated skull and vertebral fragments, ribs
BGS GSM 91077,91074	0.0618	BGS GSM Elgin A: frontal (r), quadratojugal, surangular, ribs, dorsal vertebral fragments and associated osteoderms, ?radius INDET: humerus, radius, ulna, ?lacrimal
BGS GSM 91076, 91078	0.0733 and 0.0369 (close-up)	BGS GSM Elgin A: ?nasal/maxilla, lower jaw fragments, quadrate, ?squamosal, lacrimal, pterygoid, ectopterygoid BGS GSM Elgin P: skull roof INDET: humerus
BGS GSM 91080-2, 91085	N/A	N/A
NMS G.1992.37.1A-B	0.0624 (A) and 0.0678 (B)	*Erpetosuchus granti*: (A) right side of cervical-(anterior) dorsal vertebrae with associated ribs and series of paramedian and lateral osteoderms, pectoral girdle, complete right forelimb (missing phalanges); (B) left side of and the same, but with only a partial left humerus.
AMNH 29300	0.0678	*Erpetosuchus* sp.: right articulated side of a partial skull, and posterior right ramus of lower jaw (see Olsen *et al.* 2001)

1524