

1 Phylogenetic and Environmental Context of a Tournaisian Tetrapod Fauna

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25 Summary

26 The end-Devonian to mid-Mississippian time interval has long been known for its
27 depauperate palaeontological record, especially for tetrapods. This interval encapsulates
28 the time of increasing terrestriality among tetrapods, but only two Tournaisian localities
29 previously produced tetrapod fossils. Here we describe five new Tournaisian tetrapods
30 (*Perittodus apscanditus*, *Koilops herma*, *Ossirarus kierani*, *Diploradus austiumensis*
31 and *Aytonerpeton microps*) from two localities in their environmental context. A
32 phylogenetic analysis retrieved three taxa as stem tetrapods, interspersed among
33 Devonian and Carboniferous forms, and two as stem amphibians, suggesting a deep split
34 among crown tetrapods. We also illustrate new tetrapod specimens from these and
35 additional localities in the Borders Region of Scotland. The new taxa and specimens
36 suggest that tetrapod diversification was well established by the Tournaisian.
37 Sedimentary evidence indicates that tetrapod fossils are usually associated with sandy
38 siltstones overlying wetland palaeosols. Tetrapods were probably living on vegetated
39 surfaces subsequently flooded. We show that atmospheric oxygen levels were stable
40 across the Devonian/Carboniferous boundary, and did not inhibit the evolution of
41 terrestriality. This wealth of tetrapods from Tournaisian localities highlights the
42 potential for discoveries elsewhere.

43

44 The term “Romer’s Gap” was coined^{1,2} for a hiatus of approximately 25 million years
45 (Myr)³ in the fossil record of tetrapods from the end-Devonian to the Mid-Mississippian
46 (Viséan). Following the end-Devonian, the earliest terrestrial tetrapod fauna was known
47 from the early Brigantian (late Viséan) locality of East Kirkton near Bathgate,

48 Scotland^{4,5}. By that time, tetrapods were ecologically diverse, and were terrestrially
49 capable. With five or fewer digits, some had gracile limbs^{6,7}, unlike the polydactylous
50 predominantly aquatic fish-like tetrapods of the Late Devonian⁸. Fossils representing
51 transitional morphologies between these disparate forms was almost entirely lacking,
52 limiting both understanding of the acquisition of terrestrial characteristics and the
53 relationships between the diverse mid-Carboniferous taxa. Alternative hypotheses to
54 explain the hiatus have included a low oxygen regime⁹ or lack of successful collecting
55 in Tournaisian strata².

56 Although isolated tetrapod limb bones, girdle elements, and trackways are
57 known from the Tournaisian of the Horton Bluff Formation at Blue Beach, Nova
58 Scotia^{10,11}, only a small fraction has been fully described¹². The only other Tournaisian
59 tetrapod material was the articulated skeleton of *Pederpes finneyae*, from the
60 Tournaisian Ballagan Formation near Dumbarton, western Scotland^{13,14}. More recently,
61 new taxa from this formation in the Borders Region of Scotland were reported², but
62 further collecting from five localities (**Supplementary Fig. 1**) has since produced more
63 data about the fauna, its environment, and climatic conditions.

64 Our analysis shows that the Tournaisian included a rich and diverse assemblage
65 of taxa which included close relatives of some Devonian forms on the tetrapod stem, and
66 basal members of the amphibian stem. We diagnose, name and analyse five taxa (Figs 1-
67 5), and summarize at least seven others that are distinct but undiagnosable at present
68 (Fig. 6, **Supplementary Figs 2-6**).

69 Tetrapods occupied a juxtaposed mosaic of microhabitats including ponds,
70 swamps, streams, and floodplains with highly variable salinity and water levels in a

71 sharply contrasting seasonal climate. Their fossils are most closely associated with
72 palaeosols and the overlying sandy siltstones. These indicate exposed and vegetated land
73 surfaces that were then flooded^{15,16} (**Supplementary Fig 7**). This varied environment
74 persisted over the 12 million years of the Tournaisian³. We show that atmospheric
75 oxygen levels were stable across the Devonian/Carboniferous boundary, and did not
76 therefore compromise terrestrial faunal life (contra ref 9).

77 Differential diagnoses below give the characters in which each differs from all
78 other tetrapods in its combination of autapomorphic and derived (relative to Devonian
79 taxa) characters.

80 This published work and the nomenclatural act it contains have been registered in
81 Zoobank: <http://www.zoobank.org/pub:4BFFB544-7B0B-4F2F-80EC-11226C0FDAAB>

82 Tetrapoda Goodrich, 1930 indet.

83 ***Perittodus apscanditus*** gen. et sp. nov. Clack and Smithson T.R. Fig. 1 e-g.

84 Smithson et al., 2012 (fig. 4), new taxon A.

85 *LSID*. urn:lsid:zoobank.org:act 69DB72E5-F9BD-49C6-B471-CD8E03767732

86 **Etymology.** Genus from *perittos* (Greek) ‘odd’ and *odus* (Greek) ‘tooth’ referring to the
87 unusual dentition of the mandible. Species from *apscanditus* (Latin) ‘covert, disguised,
88 hidden, secret or concealed’, referring to the fact that key parts were only discovered by
89 micro-CT scanning.

90 **Holotype.** UMZC 2011.7.2 a and b. Cheek region of skull, lower jaw, and postcranial
91 elements in part and counterpart.

92 **Locality and Horizon.** Willie’s Hole, Whiteadder Water near Chirnside. Ballagan
93 Formation. Early mid Tournaisian.

94 **Diagnosis.** Autapomorphies: unique adsymphysial and coronoid dentition –
95 adsymphysial with two tusks and at least two smaller teeth, anterior coronoid with two

96 or three larger tusks, middle coronoid with two larger and two or three smaller teeth,
97 posterior coronoid row of small teeth; lozenge-shaped dorsal scales bearing concentric
98 ridges centred close to one edge nearer to one end. Derived characters: deeply excavated
99 jugal with narrow suborbital bar; lateral line an open groove on jugal.

100 **Plesiomorphies & characters of uncertain polarity:** No mesial lamina of postspenial
101 (state of angular not known); 35 dentary teeth including spaces; 29 maxillary teeth
102 including spaces; room for possibly 6 teeth on premaxilla; marinal teeth similar in size;
103 short broad phalanges, rounded unguals longer than wide with ventral ridge.

104 **Attributed specimen.** UMZC 2016.1. Isolated dentary and adsymphysial (in micro-CT
105 scan) from Burnmouth Ross end cliffs, 373.95 m above the base of the Ballagan
106 Formation. Mid Tournaisian.

107 **Remarks:** Lower jaw length 68 mm. Maxilla of holotype visible in micro-CT scan.
108 UMZC 2016.1 is almost identical in size and dentition to the holotype. The pattern is
109 most similar to but not identical with, that of the Devonian taxon *Ymeria*¹⁷. A distinct
110 denticulated ridge on the prearticular is set off from the remainder of the bone by a
111 ventral groove. Radius and ulna are of approximately equal length. A partial ischium
112 reveals similarities to that of *Baphetes*¹⁸.

113

114 ***Koilops herma*** gen. et sp. nov. Clack and Smithson T.R. Fig. 1 a-b.

115 Smithson et al., 2012 (fig. 2C), ‘probable new taxon’.

116 **LSID.** urn:lsid:zoobank.org:act 8C43E66A-3822-49B4-B3B5-E43C79FA9C70

117 **Etymology.** Genus from *koilos* (Greek) ‘hollow or empty’, and *ops* (Greek) ‘face’,
118 referring to the skull mainly preserved as natural mould. Species from *herma* (Greek)
119 ‘boundary marker, cairn, pile of stones’. The specimen, from the Borders Region of
120 Scotland, has transitional morphology between Devonian and Carboniferous tetrapods.

121 **Holotype.** NMS G. 2013.39/14. Isolated skull mainly as a natural mould.

122 **Locality and Horizon.** Willie's Hole, Whiteadder Water near Chirnside. Ballagan
123 Formation. Early mid Tournaisian.

124 **Diagnosis.** Autapomorphies: fine irregular dermal ornament with conspicuous curved
125 ridges around the parietal foramen and larger pustular ornament anterior to parietal
126 foramen. Derived characters: deeply excavated jugal with narrow suborbital bar; large
127 parietal foramen.

128 **Plesiomorphies & characters of uncertain polarity:** Orbit oval with slight anterior
129 embayment; prefrontal-postfrontal contact narrow, anterior to orbit mid-length; about 8
130 premaxillary teeth recurved, sharply pointed, ridged towards base; closed palate,
131 denticulated pterygoid; vomers bearing tusks and smaller teeth, at least four moderately
132 large teeth on palatine; short rounded snout, only slightly longer than maximum orbit
133 length.

134 **Remarks.** Skull length 80 mm. The dermal bones are robust and well integrated so the
135 individual was almost certainly not a juvenile.

136

137 ***Ossirarus kieranii*** gen. et sp. nov. Clack and Smithson T.R. Fig. 2.

138 **LSID.** urn:lsid:zoobank.org:act FC9FAB5C-CC3E-4D0D-B7D7-8030FBAA4F0C

139 **Etymology.** Genus from *ossi* (Latin) 'bones' and *rarus* (Latin) 'scattered or rare.'

140 Specific name to honour Oliver and Betty Kieran, representing the Burnmouth
141 community, who have supported us and encouraged local interest and co-operation.

142 **Holotype.** UMZC 2016.3. A single block containing scattered skull and postcranial
143 remains.

144 **Locality and Horizon.** Burnmouth Ross end cliffs, 340.5 m above the base of the
145 Ballagan Formation. Mid Tournaisian.

146 **Diagnosis.** Autapomorphies: tabular elongate triangle forming a conspicuous tabular
147 horn with a convex lateral margin. Derived character: tabular-parietal contact;
148 exoccipital separate from basioccipital.

149 **Plesiomorphies & characters of uncertain polarity:** Jugal with extensive posterior
150 component, with anteriorly placed shallow contribution to orbit; lozenge-shaped
151 interclavicle; humerus with elongate and oblique pectoralis process comparable with the
152 ventral humeral ridge of elpistostegalians and *Acanthostega*; multipartite vertebrae with
153 diplospondylous widely notochordal centra and neural arches as unfused bilateral
154 halves.

155 **Remarks:** Estimated skull length 50 mm based on comparisons with *Acanthostega*,
156 *Ichthyostega* and *Greererpeton*¹⁹⁻²¹. The primitive jugal morphology, with an elongated
157 postorbital region and an anteriorly placed orbital margin contributing less than 25% of
158 the orbit margin, is similar to that in *Acanthostega*¹⁹ and *Ichthyostega*²⁰. The tabular has
159 an elongated posterior process, but its lateral margin does not show an embayment for a
160 spiracular notch. The bones are robust, with well defined overlap areas for
161 interdigitating sutures. Though disarticulated, these suggest that the individual was not a
162 juvenile. The specimen shows the earliest known occurrence of a separate exoccipital.
163

164 ***Diploradus austiumensis*** gen. et sp. nov. Clack and Smithson T.R. Fig. 3.
165 *LSID.* urn:lsid:zoobank.org:act 268DDD4F-289D-4F83-8172-1A18A1007B7C

166 **Etymology.** Genus from *diplo* (Greek) ‘double’ and *radus* (Greek) ‘row’ referring to the
167 double coronoid tooth row. Species from *austium* (Latin) ‘mouth of a river or stream’
168 referring to Burnmouth.

169 **Holotype.** UMZC 2015.55.4. Small disrupted skull with lower jaw, palate and skull
170 roofing bones.

171 **Locality and Horizon.** Burnmouth Ross end cliffs, 373.95 m above the base of the
172 Ballagan Formation. Mid Tournaisian.

173 **Diagnosis.** Autapomorphies: lower jaw with irregular double row of denticles along the
174 coronoids; around 51 dentary teeth and spaces, with enlarged tusk at position 3 and the
175 largest teeth in positions 8-13; parietals short, pineal foramen anteriorly placed; ?narrow
176 curved pre- and postfrontals. Derived characters: deeply excavated jugal with narrow
177 suborbital bar; parasphenoid with broad, flattened posterior portion with lateral wings,
178 earliest known occurrence of a parasphenoid crossing the ventral cranial fissure,
179 cultriform process flat, narrow.

180 **Attributed specimen.** UMZC 2016.4 a and b. The anterior end of a mandible from 341
181 m above the base of the Ballagan formation at Burnmouth.

182 **Plesiomorphies & characters of uncertain polarity:** Unsutured junction between
183 prearticular and splenial series; adductor fossa dorsally placed; adsymphysial plate
184 possibly lacking dentition; closed, denticulated palate; broad pterygoid, quadrate ramus
185 narrow with vertically orientated medial ascending lamina; ossified hyobranchial
186 elements; maxilla and premaxilla with spaces for 35 and 10-12 teeth respectively;
187 maxilla-premaxilla contact narrow, lacking interdigitations; dermal ornament with low
188 profile, irregular on skull table, ridged on squamosal and quadratojugal.

189 **Remarks.** Lower jaw length 30 mm, superficially resembling that of *Sigournea*²²,
190 although a relationship is not supported by cladistic analysis. The thinness of the bones
191 and their distribution suggest a juvenile.

192

193 *Aytonerpeton microps* gen. et sp. nov. Otoo, Clack and Smithson T.R. Fig. 4.

194 *LSID.* urn:lsid:zoobank.org:act E1E094A8-FAC0-4A2A-A13D-487D7775FB E1

195 **Etymology.** Genus name from Ayton, the parish in the Scottish Borders from which the
196 specimen came, and *erpeton* (Greek) ‘crawler’ or ‘creeping one’. Species name from
197 *micro* (Greek) ‘small’ and *ops* (Greek) ‘face’.

198 **Holotype.** UMZC 2015.55.8. Partial skull and scattered postcrania visible only in micro-
199 CT scan (**Supplementary Movie Files**)

200 **Locality and Horizon.** Burnmouth Ross end shore exposure, 340.6 m above the base of
201 the Ballagan Formation. Mid Tournaisian.

202 **Diagnosis.** Autapomorphies: two enlarged premaxillary teeth plus one large tooth space
203 at posterior end of premaxilla; 5 teeth on premaxilla; adsymphysial with a single tooth;
204 coronoids apparently lacking shagreen; L-shaped lacrimal; vomer with at least one tooth,
205 palatine with one large fang but lacking smaller teeth; ectopterygoid with at least two
206 teeth and possible smaller teeth. Derived characters shared with colosteids: course of
207 lateral line on maxilla and nasal; dentary teeth larger and fewer than upper marginal
208 teeth; single large Meckelian fenestra; interpterygoid vacuities longer than wide; single
209 large parasymphysial fang on dentary; ilium with a single strap-shaped iliac process.

210 **Remarks.** Reconstructed skull length about 50 mm. Other distinguishing features: short
211 snout, approximately similar in length to orbit diameter; naris and choana both very
212 large relative to skull size – relatively larger than in *Greererpeton*. The enlarged
213 premaxillary teeth prefigure those of more derived colosteids^{e.g.21}, but the dentary lacks
214 the corresponding reciprocal notch. This appears an early expression of a feature that
215 becomes more elaborate in later taxa. All coronoids bear at least one tooth. Some
216 colosteids lack coronoid teeth, and instead bear shagreen, a variable condition among
217 individuals²³. The small size of the skull but the strong integration of the lower jaw
218 bones suggest a subadult or adult in which case the large orbit is unlikely to be a

219 juvenile feature (c.f. juvenile *Greererpeton* CMNH 11095²⁴). Its gracile limbs,
220 metapodial bones and phalanges resemble *Colosteus* rather than *Greererpeton*.
221 Clavicular ornament is similar to that of other colosteids^{25,26}. The single iliac process is
222 shared with other colosteids and with temnospondyls. The earliest known occurrence of
223 this feature.

224

225 **Results**

226 **Cladistic Analysis**

227 We performed parsimony and Bayesian analyses of a new data matrix (**Supplementary**
228 **Data Character list and Data matrix**) incorporating the new tetrapods. No taxon could
229 be safely deleted²⁷. Parsimony with all characters unordered and equally weighted
230 produced 4718 shortest trees, a poorly resolved strict consensus (Fig. 5, **Supplementary**
231 **Fig. 8**), and moderate branch support.

232 Four parsimony analyses with implied weighting, each using a different value (3,
233 4, 5, 10) of the concavity constant K ²⁸ produced many fewer trees (Fig. 5a, b), with
234 novel topologies and increased stability for most of the new taxa. In these analyses, the
235 relative positions of *Ossirarus*, *Perittodus*, and *Diploradus* remain unaltered (**Methods**
236 **and Supplementary Fig. 8**). Except in the analysis with $K=10$, *Koilops* and
237 *Aytonerpeton* emerge as stem amphibians²⁹⁻³¹, but see^{32,33} with *Aytonerpeton* close to
238 *Tulerpeton*+colosteids. With characters reweighted by their rescaled consistency index,
239 all new taxa emerge as stem tetrapods.

240 We also performed a Bayesian analysis (Fig. 5c). The results were largely similar
241 to the parsimony analysis, except for the position of *Ossirarus*. In the Bayesian analysis,
242 *Ossirarus* appears as a stem amniote, whilst *Perittodus*, *Diploradus*, *Koilops*, and

243 *Aytonerpeton* are stem tetrapods.

244 Despite inconsistencies, these results imply a substantial reshuffling of the
245 branching sequence of Carboniferous stem tetrapods relative to previous studies²⁹⁻³³,
246 with interspersed Carboniferous and Devonian taxa pointing to a more ramified stem of
247 tetrapod diversification. If corroborated by further evidence, a firmer placement of
248 *Aytonerpeton* and *Koilops* within crown tetrapods would suggest a deep split between
249 stem amphibians and stem amniotes within the Tournaisian..

250

251 **Geology and Environment**

252 The Ballagan Formation (Inverclyde Group) underlies much of the Midland Valley of
253 Scotland and the northern margin of the Northumberland Basin. At Burnmouth the
254 vertically dipping strata probably span the entire Tournaisian^{2,34}. Environmental
255 interpretation was based on a 490 m core from a borehole through the formation, a
256 complete logged succession at centimetre scale intervals through 520 m at Burnmouth,
257 and an 8 m section at Willie's Hole (Fig. 6, **Methods and Supplementary Fig. 7**).

258 *Perittodus apscanditus* occurs within a 6 cm thick laminated grey siltstone¹⁶ that
259 contains a network of cracks filled with sandy siltstone identical to that of the overlying
260 bed. Occurring within laminated siltstones, this may record an autochthonous lake
261 dweller. Associated fossils comprise plants, actinopterygians, myriapods and ostracods.
262 *Koilops* occurs within a unit comprising four beds of alternating black and green
263 siltstone in which abundant palaeosol clasts indicate erosion and transport of land-
264 surface sediment during flooding events.

265 *Diploradus* occurs in a 40 cm thick, bedded, black sandy siltstone that lies
266 between pedogenically modified grey siltstones. Associated fossils comprise fish scales,
267 abundant plant fragments, megaspores, and shrimp and scorpion cuticle.

268 *Ossirarus* and *Aytonerpeton* occur within a complex 15 cm thick grey-black
269 sandy siltstone that overlies a gleyed palaeosol and grades upwards into a laminated
270 grey siltstone with brecciation cracks (Fig. 6, **Methods and Supplementary Fig. 7**).
271 *Ossirarus* occurred just above the palaeosol in a light grey clay-rich sandy siltstone,
272 whereas *Aytonerpeton* occurred within an overlying black sandy siltstone with abundant
273 plant material. Associated fauna comprise abundant plants, megaspores, unusually
274 abundant rhizodont bones and scales, actinopterygians, chondrichthyans (*Ageleodus*,
275 *Gyracanthus*), dipnoans, eurypterids and ostracods.

276 An association between wetland palaeosols and tetrapod-bearing facies has
277 emerged from our studies, significant because those horizons indicate a vegetated land
278 surface (Fig. 6)^{15,16}. The flood-plain environments of semi-permanent water bodies,
279 marsh, river banks and areas of dry land with trees were laid down at a time of change in
280 the land plant flora of the Mississippian following the end-Devonian extinctions. The
281 new flora initiated a change in fluvial and floodplain architecture³⁵⁻³⁷. Progymnosperms
282 had been almost eliminated in the extinctions, but thickets and forests were re-
283 established in the early-mid Tournaisian with lycopods as the dominant flora. At
284 Burnmouth many beds with abundant spores of the creeping lycopod *Oxroadia* include
285 tetrapods. Terrestrial ground-dwelling arthropods, such as myriapods and scorpions
286 fossils of which have been found at Burnmouth and at Willie's Hole, formed a possible
287 food supply for tetrapods..

288

289 **Atmospheric oxygen levels in the Tournaisian**

290 To address the low oxygen hypothesis⁹ we examined fossil charcoal (fusinite) in the
291 Ballagan Formation to compare atmospheric oxygen levels in the Tournaisian with the
292 Late Devonian and later Mississippian.

293 Charcoal, either as microscopic dispersed organic matter (DOM) or visible in
294 hand specimens is relatively common at Burnmouth and Willie's Hole. Although
295 charcoal is reported from the Tournaisian Horton Bluff Formation, Nova Scotia³⁸ as
296 indicating O₂ concentrations above 16%, no quantitative study to validate this result has
297 been undertaken.

298 We analysed DOM from 73 rock samples from Burnmouth shore and Willie's
299 Hole. For comparison with wildfire activity before and after Romer's Gap, we also
300 analysed 42 samples from the Viséan of East Fife, Scotland (Strathclyde Group) and 9
301 samples from the Famennian of Greenland (Stensiö Bjerg Formation) (**Supplementary**
302 **Fig. 9 and Supplementary Table 1**). All were found to contain fusinite, with a mean
303 abundance relative to total phytoclasts of 2.2%, 2.3% and 2.6% for the Famennian,
304 Tournaisian and Viséan, respectively. We also analysed 12 samples from Willie's Hole
305 which had a mean value of 2.0% (**Supplementary Table 1**). Not only do these results
306 mean that fire activity persisted through Romer's Gap and indicate that atmospheric O₂
307 did not fall below 16%, but also that there was no significant change in charcoal
308 production compared with the Famennian and Viséan (**Supplementary Fig. 9**). This
309 strongly suggests that atmospheric O₂ was stable across this time interval, directly
310 refuting hypoxia⁹ as an explanation for Romer's Gap.

311

312 **Discussion**

313 Although an extinction event at the end of the Devonian saw the demise of many archaic
314 fish groups³⁹, our studies provide new perspectives on the recovery and diversification
315 of surviving groups, which went on to found the basis of modern vertebrate
316 diversity^{40,41}.

317 The new tetrapods show no close relationship to each other, exhibiting different
318 combinations of plesiomorphic and derived characters. Some taxa cluster with Devonian
319 forms, suggesting a possible relict fauna, whereas others appear more crownward, even
320 clustering near the base of the crown group. They imply an early radiation of tetrapods
321 during the Tournaisian, and at the same time, suggest a blurring of the Devonian-
322 Carboniferous (D-C) boundary in respect of tetrapod evolution, a feature also noted in
323 tetrapod remains from Nova Scotia¹².

324 If confirmed, our results imply a deep split between stem amphibians and stem
325 amniotes in the earliest Carboniferous. This accords with most molecular dates for the
326 split that place it at an average of 355 Ma^{42,43} a date only 4 Ma after the end-Devonian.
327 It suggests that the origin of the tetrapod crown group occurred soon after the extinction
328 event as tetrapods began to recover. Their radiation into a range of new taxa parallels
329 that of lungfish⁴⁰ and chondrichthyans⁴¹ as they adapted to a post-extinction world.

330 The occurrence of probable plesiomorphic members of the Crassigyrinidae² and
331 Colosteidae indicates an inception 20-24 Myr earlier than the Late Mississippian as
332 previously considered⁴⁴. Other tetrapod material of uncertain attribution are distinct and
333 increase known tetrapod diversity in the Tournaisian (Fig. 6 and **Supplementary Figs 2-**
334 **6**).

335 The preponderance of small animals throughout the sequence is unusual, notably
336 a very small tetrapod in a horizon 33 m above the D-C boundary, around 1 Myr after the
337 extinction event (Fig. 6). None of the five taxa described above has a skull length of
338 more than 80 mm. This could indicate preservational or collector bias, but they occur
339 throughout different lithologies, horizons and localities (Fig. 6 and **Supplementary Figs**
340 **2-6**). Larger tetrapod taxa are found at Willie's Hole, about one quarter of the way up
341 the sequence, probably representing about 3 or 4 Myr above the D-C boundary. Larger
342 sizes seem to have appeared relatively rapidly in the Tournaisian, as also documented by
343 trackways³⁸ and challenge suggestions of a prolonged period of reduced body size in
344 vertebrates following the DC extinction event⁴⁵.

345 The tetrapods of the Ballagan Formation lived in a mosaic of floodplain
346 environments. Some were under water for long periods, others alternated between land
347 surface and standing water. A recent study of the development of *Polypterus* shows how
348 early in life, their skeletons can be differentially modified in response to exposure to
349 water-based or land-based conditions⁴⁶. Such skeletal flexibility might have contributed
350 to the origin of tetrapod terrestrial morphology in the varied environments of the
351 Ballagan Formation.

352 The wealth and diversity of tetrapod taxa from the Tournaisian refutes the
353 proposal of depauperate Tournaisian stage, and our charcoal studies show that
354 atmospheric oxygen levels, stable from the Famennian to the Viséan, were not a causal
355 factor for the apparent gap. We emphasise the importance of exploring or re-exploring
356 non-marine Tournaisian sites elsewhere in the world, and examining previously
357 overlooked lithologies.

358

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585

586

587 Figure legends

588 **Figure 1. a-b** *Koilops herma* gen. et sp. nov. (National Museum of Scotland NMS G.

589 2013.39/14). **a**, Photograph of specimen, mainly preserved as natural mould. **b**,

590 Interpretive drawing of specimen. **c-g**, *Perritodus apscanditus* gen. et sp. nov.

591 (University Museum of Zoology, Cambridge UMZC 2011.7.2a). **c**, Photograph of main

592 specimen block. **d**, Reconstruction of lower jaw in external view, from scan data and

593 part and counterpart specimens. **e**, Reconstruction of lower jaw in internal view made

594 from scan data and part and counterpart specimens. **f**, Segmented model from scans of

595 lower jaw in internal view. **g**, segmented model from scans of lower jaw in internal

596 view. Colour code in **f**: orange, dentary; red, adsymphyial plate; turquoise, part of

597 prearticular; yellow, first coronoid; blue, second coronoid; cerise, third coronoid; pink,

598 splenial; violet, angular; purple, prearticular; green, splenial; external bones greyed out.

599 In **g**, green, splenial. Scale bar in **a**, **b**, and **c**, 10 mm. Abbreviations: add foss, adductor

600 fossa; adsymph, adsymphyial; ang, angular; cor, coronoid; dent, dentary; ecto,

601 ectopterygoid; fro, frontal; intemp, intertemporal; jug, jugal; l, left; lac, lacrimal; llc,

602 lateral line canal; max, maxilla; oa, overlap area for pterygoid; pal, palatine; par,

603 parietal; pofr, postfrontal; porb, postorbital; pospl, postsplenial; preart, prearticular;

604 prefro, prefrontal; premax, premaxilla; psph, parasphenoid; pteryg, pterygoid; quad,
605 quadrate; quj, quadratojugal; surang, surangular; vom, vomer.

606

607 **Figure 2.** *Ossirarus kierani* gen. et sp. nov. (UMZC 2016.3) **a**, Photograph of complete
608 specimen. Leaders point to **b**, Map of skull bones. **c**, Drawing of right tabular,
609 supratemporal and a partial unidentified bone. **d**, Drawing of exoccipital. **e**, Drawing of
610 quadrate. **f**, Photograph enlargement of part of postcranial portion of specimen, **g**,
611 Drawings of left and right parietal bones placed in articulation, **h**, Drawing of jugal and
612 postorbital placed in articulation, **i**, Photograph of jugal. **j**, Photograph enlargement of
613 right humerus. Scale bar in **b** 10 mm, scale bars in **c-j** 5 mm. Abbreviations: clav,
614 clavicle; cleith, cleithrum; exocc, exoccipital; iclav, interclavicle; jug, jugal; par,
615 parietal; porb, postorbital; quad, quadrate; r, right; rad, radius; sutemp, supratemporal;
616 tab, tabular.

617

618 **Figure 3.** *Diploradus austiumensis* gen. et sp. nov. (UMZC 2015.55.4). **a**, Photograph of
619 complete specimen. Scale bar 10 mm, **b**, Map of specimen showing distribution of
620 elements, **c**, Drawing of right maxilla, **d**, Upper, interpretive drawing of specimen;
621 lower, reconstruction of jaw in internal view. **e**, Drawing of parasphenoid. **f**, Drawing of
622 right jugal in internal view. **g**, Drawing of skull table. **h**, Drawing of pterygoid in dorsal
623 view. Scale bars in **b-h**, 5 mm. Abbreviations as for Figures 1 and 2 except for: nat
624 mould popar, natural mould of postparietal.

625

626 **Figure 4.** *Aytonerpeton microps* gen. et sp. nov. (UMZC 2015.55.8). **a**, Still from micro-
627 CT scan of block containing most of the specimen. **b**, Interpretive drawing of right side
628 of skull and palate. **c**, Stills from micro-CT scan of right lower jaw in (upper image)

629 dorsal view and (lower image) mesial view. **d**, Still from micro-CT scan of right palate
630 in approximately ventral view. **e**, Still from micro-CT scan of entire specimen in the
631 main block. Arrows point to elements in **g**. **f**, Enlargement of ilium in lateral (left image)
632 and medial (right image) views. **g**, Elements of hind limb. In **c**, and **d**, note the sutures
633 between pterygoid and marginal palatal bones, and the lower jaw bones, are tightly
634 sutured and difficult to see in the scan. Abbreviations as for Figures 1 and 2, except for:
635 mar Meck fen, margin of Meckelian fenestra; sym, symphysis; septomax, septomaxilla.
636 Scale bars for all except **f** are 10 mm. Scale bar for **f** is 5 mm.

637

638 **Figure 5.** Three cladograms: two from TNT analysis and one from Bayesian analysis. **a**,
639 Single most parsimonious tree obtained from implied weights search with $k=3$ (see text
640 and Supplementary Data for details). **b**, strict consensus of four equally parsimonious
641 trees obtained from implied weights search with $k=4$. **c**, Bayesian analysis tree. See main
642 text, methods, and Supplementary Data for details.

643

644 **Figure 6.** Burmmouth sedimentary log showing palaeosol and tetrapod fossil
645 distribution. Left hand column shows the sedimentary log for Burnmouth with the
646 tetrapod horizons indicated. Right hand column shows the distribution of palaeosols and
647 their thicknesses. Photographs a-g show some of the tetrapod specimens found in
648 addition to those in Figs 1-4.

649 Specimen **a**, an isolated jugal (UMZC 2016.13) from the same bed that yielded the
650 partial *Crassigyrinus*-like jaw in ref 2, horizon approximately 383 m above the base of
651 the Ballagan Formation. This is a thick localized conglomerate lag containing many
652 isolated vertebrate bones, plant remains and charcoal. The shape of the jugal is unique
653 among the tetrapods so far collected from the Ballagan, in its relative contribution to the

654 orbit margin. Probable new taxon 1. Specimens **b-f**, tetrapod specimens from a closely
655 juxtaposed set of horizons beyond the resolution of the log to differentiate, between 340-
656 341m above the base of the Ballagan: **b**, an isolated tetrapod maxilla (UMZC 2016.9); **c**,
657 tetrapod belly scales (UMZC 2016.12) and metapodials/phalanges (UMZC 2016.10, 11);
658 **d**, skull bones and belly scales (UMZC 2016.8); **e**, Micro-CT scan of the two
659 overlapping bones in **d**. They are probable frontal bones of a *Pederpes*-like tetrapod; **f**,
660 partial skull table and postorbitals from slightly above the Burnmouth horizon yielding
661 *Aytonerpeton microps* (UMZC 2016.7). Probable new taxon 2? May be associated with
662 those in **Supplementary Fig. 2**, but not with *Aytonerpeton*. Scale bar 10 mm. (Micro-
663 CT by K. Z. Smithson); **g**, phalanges or metapodials and skull elements of a small
664 tetrapod from Burnmouth (UMZC 2016.5 a, b). Probable new taxon 3. Left hand image,
665 largest elements circled. Right hand image, dentigerous bone near top left corner. Other
666 elements include a probable jugal and rib fragments (not figured). These remains are the
667 earliest post-Devonian tetrapod specimens found in the UK. They come from a horizon
668 approximately 33m above the base of the Ballagan Formation that was probably
669 deposited about 1 Myr after the start of the Carboniferous. Scale bars for all except g are
670 10 mm. Scale for for g is 5 mm. (Photographs by J. A. Clack)

671

672 METHODS

673 Micro-CT data

674 Specimen UMZC 2016.3 *Ossirarus* and NMS G. 2013.39/14 *Koilops* and UMZC
675 2011.7.2a *Perittodus* were prepared mechanically with mounted needle, some matrix
676 was removed from *Ossirarus* with a brush and water, consolidated where necessary with
677 Paraloid B72. Specimens UMZC 2011.7.2a *Perittodus* and UMZC 2015.55.8
678 *Aytonerpeton* were scanned at the Cambridge Tomography Centre with a Nikon

679 XTH225 ST scanner. Scan data:- *Perittodus*: Isotropic voxel size, 0.0444mm.
680 Projections:1080, Filter: 0.25mm Cu, Xray kV:160, Xray μ A: 70, Slices:1647.
681 Exposure: 1000, Gain: 24 dB. UMZC 2015.55.8 *Aytonerpeton*: Isotropic voxel size:
682 0.0609mm. Projections: 1080, Filter: None, Xray kV: 120, Xray μ A: 125, Slices: 1789,
683 Exposure: 1000, Gain: 24 dB. .

684

685 Cladistic analysis

686 A new database of 46 taxa coded for 214 osteological characters (170 cranial, 43
687 postcranial), and was subjected to maximum parsimony analyses. It was designed to
688 include representative early tetrapods. Characters were drawn up to capture the features
689 of the new taxa as far as possible in the context of the range of early tetrapods available
690 for comparison. Most were drawn from recent analyses^{14,29-31,44,47,48}. Some
691 characters were reworded or reformulated and all were independently scored by JAC
692 from personal observation or from the literature. These were checked for accuracy by
693 MR. Characters are arranged in alphabetical order grouped into regions of the anatomy
694 (**Supplementary Data Character list and Data Matrix**).

695 The data matrix was subjected to maximum parsimony analyses in TNT v. 1.1⁴⁹.
696 Several experiments of taxon and character manipulation were carried out, as detailed
697 below, with identical search protocols throughout. Given the size of the matrix, tree
698 searches relied on heuristic algorithms, following a simple series of steps under the
699 ‘Traditional search’ option in the ‘Analyze’ menu in TNT. Before each search, we
700 modified memory requirements under the ‘Memory’ option in the ‘Settings’ menu. One
701 hundred Mbytes of general RAM were allocated, and a total of 50,000 trees were
702 selected as the maximum size of tree space for the exploration of alternative tree
703 topologies. In the initial part of the ‘Traditional search’ (‘Wagner trees’ box ticked), we

704 chose 10,000 replicates (random stepwise addition sequences of taxa), keeping a
705 maximum of five trees at the end of each replicate, using the bisection-reconnection
706 algorithm for tree branch swapping, and retaining all trees found at the end of all
707 replicates. A new round of branch swapping was then applied to all trees retained from
708 the initial search ('trees from RAM' box ticked). For each set of experiments, where
709 applicable, we summarized the results in the form of a strict consensus, a 50% majority-
710 rule consensus.

711 Using the search settings expounded above, we carried out three types of
712 parsimony analysis. The first parsimony analysis, employing all taxa and characters
713 from the original matrix, treated all characters as having equal unit weight (default TNT
714 option). The second analysis, again using all taxa and characters, was based on implied
715 character reweighting²⁸, briefly described as follows. Given a character, its implied
716 weight (W) is given by $K / (K + M - O)$, where M and O represent, respectively, the
717 greatest number of character-state changes and the observed number of character-state
718 changes for that character. The constant of concavity (K) is an integer, the value of
719 which determines the most parsimonious trees as those trees for which W is maximized
720 across all characters. As the selection of K is arbitrary, we experimented with increasing
721 values (K = 3, 4, 5 and 10) (Fig 5, **Supplementary Fig. 8**). We did not report details of
722 searches with other K values, as our goal was to establish whether the Tournaisian taxa
723 showed stable positions within a minimal range of implied weighting increments.
724 However, we ran analyses with values varying between 6 and 10, with mixed outcomes.
725 In some cases, the Tournaisian taxa are heavily reshuffled, in others the branching
726 sequence of other groups revealed implausible arrangements that, we feel, were dictated
727 by varying amounts of homoplasy in the data, although a proper characterization of this
728 phenomenon requires further testing. Topologies with K=10 are reported as an example.

729 In the third analysis, characters were reweighted by the maximum value (best fit)
730 of their rescaled consistency indexes, such as were obtained from the first analysis.

731 Statistical branch support was evaluated through character resampling via
732 bootstrap (resampling with replacement; ref.) and jackknife (resampling without
733 replacement, with 33% of characters removed; ref.), using 1000 replicates in each case
734 and collapsing nodes with less than 50% support.

735 Of all the new Tournaisian taxa, only *Diploradus* appears in a maximum
736 agreement subtree (a taxonomically pruned tree showing only taxa for which all most
737 parsimonious trees agree upon relationships).

738 As for the implied weighting analysis, we found stable mutual arrangements for
739 most Tournaisian taxa with $K = 3, 4$ and 5 . With $K = 10$, the branching sequence of
740 Tournaisian taxa differed from those found with smaller values. In addition, slightly
741 different branching patterns emerge for various early tetrapod taxa/groups following
742 different implied weighting searches. Below, we highlight key differences among
743 various tree topologies.

744 In trees generated with $K = 3, 4$ and 5 , *Ossirarus*, *Perittodus* and *Diploradus*
745 emerge as increasingly crownward taxa, in that sequence, along the tetrapod stem group,
746 whilst *Aytonerpeton* and *Koilops* are placed among stem amphibians and are thus part of
747 the tetrapod crown group. *Ossirarus* is crownward of a (*Ventastega* + *Ichthyostega*)
748 clade, with *Ossinodus* placed either immediately anti-crownward of ($K = 3$), in a
749 polytomy with ($K = 4$), or immediately crownward of *Ossirarus* ($K = 5$). *Perittodus* is
750 the sister taxon to the Devonian *Ichthyostega*-like taxon *Ymeria*, and the (*Perittodus* +
751 *Ymeria*) clade forms the sister group to *Pederpes*. *Diploradus* is immediately crownward
752 of a (*Whatcheeria* + *Occidens*) clade, which in turn occurs crownward of (*Pederpes* +
753 (*Perittodus* + *Ymeria*)). However, the branching sequence of Carboniferous stem

754 tetrapods more crownward than *Diploradus* varies. Thus, in trees with $K = 3$, the
755 branching sequence includes *Crassigyrinus*, *Doragnathus*, (*Megalocephalus* +
756 *Baphetes*) and *Loxomma*. In trees with $K = 4$, the sequence includes only *Crassigyrinus*
757 and *Doragnathus*, whereas all baphetids form a clade on the amphibian stem
758 (*Megalocephalus* + (*Loxomma* + *Baphetes*)). In trees with $K = 5$, the baphetid clade is,
759 once again, on the amphibian stem, but the sequence of stem tetrapods crownward of
760 *Diploradus* differs substantially, and includes (*Eucritta* + *Doragnathus*), *Sigournea* and
761 *Crassigyrinus*. In trees from $K = 3$ and 4, the (*Aytonerpeton* + *Sigournea*) clade forms
762 the sister group to a (*Koilops* + (*Tulerpeton* + (*Greererpeton* + *Colosteus*))) clade. In
763 turn, this wider group joins temnospondyls on the amphibian stem, with *Caerorhachis* as
764 a more immediate sister taxon. In trees from $K = 5$, *Aytonerpeton* is collapsed in a
765 trichotomy with temnospondyls and the (*Koilops* + (*Tulerpeton* + (*Greererpeton* +
766 *Colosteus*))) clade. With $K = 10$, the results match those from the second set of
767 parsimony analyses (reweighting).

768 As for other tetrapod groups, the amniote stem undergoes little reshuffling in
769 trees derived from different K values. The most noticeable difference among such trees
770 is the placement of *Silvanerpeton* and *Gephyrostegus*, both of which are immediately
771 crownward of the ‘anthracosauroids’ (*Eoherpeton* + (*Pholiderpeton* + *Proterogyrinus*))
772 but swap their positions as the first and second most crownward plesion after
773 anthracosauroids.

774 With characters reweighted by the maximum value of the rescaled consistency
775 index, we found three trees differing only in the relative positions of *Whatcheeria*,
776 *Pederpes* and *Occidens*, all of which form a clade. In those trees, all new Tournaisian
777 taxa appear on the tetrapod stem. In particular, *Aytonerpeton* and *Perittodus* are sister
778 taxa, and together they join *Ymeria*. In crownward order, the sequence of stem tetrapods

779 includes: *Acanthostega*, *Ossinodus*, *Ventastega*, *Ichthyostega*, *Ossirarus*, the (*Ymeria*
780 (*Aytonerpeton* + *Perittodus*)) clade, the (*Whatcheeria*, *Pederpes*, *Occidens*) clade,
781 *Diploradus*, *Doragnathus*, *Sigournea*, a (*Koilops* + (*Tulerpeton* + (*Greererpeton* +
782 *Colosteus*))) clade, *Crassigyrinus*, and a baphetid clade. *Caerorhachis* and *Eucritta*
783 appear as the earliest diverging plesions on the amphibian and amniote stem groups,
784 respectively.

785

786 Sedimentological and Environmental Interpretation

787 The borehole was located at Norham near Berwick-Upon-Tweed (British National Grid
788 Reference [BNGR] 391589, 648135), and the Burnmouth section is at BNGR 396000-
789 661000.

790 The stratigraphical position of the succession at Willie's Hole is inferred from a
791 nearby borehole (Hutton Hall Barns, BGS Registered number NT85SE1. The exact
792 stratigraphical position of the Willie's Hole (WH) section is uncertain within the overall
793 succession. No direct correlation with the succession recorded in the Hutton Hall Barns
794 borehole is possible because the borehole is an old one and the level of detail
795 insufficient, plus the fact that distinctive markers are not present in the Ballagan
796 Formation. However, that borehole proved 142.5m of Ballagan Formation strata - the log
797 is good enough to define precisely where the base is, resting on Kinnesswood Formation.
798 The proximity of WH to the borehole allows us to infer that the WH section lies
799 approximately 150m above the base of the Ballagan Formation. The palynological
800 samples from WH contained *Umbonatisporites distinctus*, a spore that is only found in
801 the lower part of our borehole core. We argue that therefore the WH section belongs to
802 the lower part of the Ballagan Formation. We indicated some uncertainty in the figure
803 and gave an approximate range.

804 The dominance of actinopterygians and rhizodonts within these lakes indicates
805 brackish-freshwater salinity levels^{50,51}. Diverse palaeosols¹⁵ and palynology suggest
806 habitats including forest, low-growing and creeping flora, wetland and desiccating pools
807 traversed by rivers (predominantly meandering channels) and saline-hypersaline lakes
808 depositing cementstones and evaporites (Fig. 6 and Supplementary Fig. 7)^{27-31,52}. The
809 saline-hypersaline lake deposits in the Ballagan Formation have been interpreted to
810 represent brackish marginal marine or hypersaline⁵²⁻⁵⁶ conditions. Other dolomitic units
811 from the Mississippian are interpreted as saline coastal marshes⁵⁶⁻⁶¹. Erosive-based,
812 cross-bedded sandstone units (one to tens of metres thick) with basal conglomerate lags
813 cut into all other facies³⁴. The lags contain disarticulated vertebrate material including
814 acanthodian, rhizodont and tetrapod bones¹⁶.

815

816 Charcoal Analysis

817 Dispersed organic matter (DOM) was extracted by standard palynological
818 demineralisation techniques⁶². Measurement of maceral reflectance in oil was by means
819 of a Zeiss UMSP 50 Microspectrophotometer, housed in the School of Ocean and Earth
820 Science, National Oceanography Centre Southampton, University of Southampton
821 Waterfront Campus. Measurements were made under standard conditions as defined by
822 the International Committee for Coal Petrology⁶³.

823 Model-based estimates of atmospheric oxygen concentration during the early
824 Tournaisian vary from 10 – 20%, with more recent models favouring the higher
825 figure⁶⁴⁻⁶⁸. As an alternative, fossil charcoal (fusinite) is used by several authors as a

826 proxy for atmospheric oxygen⁶⁹⁻⁷², as wildfire activity, and hence charcoal production,
827 is proportional to oxygen supply⁷³. Controlled burning experiments⁷³ have
828 demonstrated that when O₂ exceeds the present atmospheric level (PAL) of 20.9%, fire
829 activity rapidly increases and reaches a plateau at around 24%; therefore, we infer that
830 fusinite abundance is likely insensitive to any further increase. Conversely, fire activity
831 is strongly suppressed below 20% O₂ and switched off completely below 16%, even in
832 very dry conditions⁷³. The most comprehensive attempt thus far to reconstruct
833 Phanerozoic O₂ in this way⁶⁹ indicated 25.6% O₂ during Romer's Gap – substantially
834 higher than PAL and exceeding the presumed upper limit of fusinite sensitivity (24%).
835 However, this study was based on the inertinite (= microscopic fusinite) content of
836 coals, which are infrequent during the Tournaisian, so sampling density was relatively
837 low. Furthermore, we assume that large-scale forest fires will have a far greater
838 influence on coal deposits, formed in situ in forest mires, than on the more distal
839 deposits of the kind examined here.

840 By focusing on DOM extracted from sedimentary rocks other than coal, fusinite
841 content can be measured through stratigraphic successions in which coals are rare or
842 absent. The values reported here represent the proportion of fusinite within the organic
843 matter isolated from each 5g shale sample, based on examination of 500 organic (i.e.
844 plant derived) macerals. This indicates the proportion of plant-derived material in the
845 sample which has been burned at high temperatures, and is therefore independent of
846 sediment supply.

847 The specific Famennian and Viséan sampling localities chosen were selected because, as
848 well as being of the required age:

- 849 • The stratigraphic context of the sampled formations is well understood, with

850 well-established biozonation (**Supplementary Table 1**).

- 851 • Thermal maturity in these successions is low. This is essential, because with
852 increasing thermal maturity the reflectance of non-pyrolitic macerals (most
853 notably vitrinite) increases, eventually rendering them indistinguishable from
854 fusinite.
- 855 • Both localities represent largely terrestrial environments, containing a succession
856 of fluviodeltaic, lacustrine or nearshore marine deposits (**Supplementary Table**
857 **1**). Sediments deposited in such environments represent an accumulation point
858 for river-transported organic material derived from the wider region; this
859 mitigates the distorting effect of local fire activity,

860 The organic maceral fusinite is considered synonymous with charcoal and can be
861 distinguished from other maceral types by its reflectance under incident light⁷⁴; we have
862 focused solely on fusinite for this study because, although most other members (semi-
863 fusinite) of the inertinite group are also accepted as pyrolitic in origin⁷⁵, their
864 reflectance forms a continuum between that of vitrinite and fusinite and forms the bulk
865 of the organic matter. This makes the % sum of semi-fusinite and fusinite very large
866 (>90%) and less reliable.

867 Supplementary Data Table 1b gives the samples taken from Famennian sites,
868 Burnmouth, Willie's Hole and Visean sites. These were analysed for charcoal content.
869 Mean abundance was 2.0%, which is within error of data obtained from Burnmouth
870 Shore, suggesting that the contribution from local fire activity (if any) was similar at
871 both sites (**Supplementary Table 1 and Supplementary Fig. 9**).

872

873 Data availability statement. Correspondence and requests for materials should be
874 addressed to Jennifer A. Clack j.a.clack@zoo.cam.ac.uk. Specimen information is

875 available from the respective housing institutions. Micro-CT scan data to be placed in
876 the NERC National Geoscience Data Centre.

877

878 Author contributions

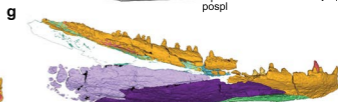
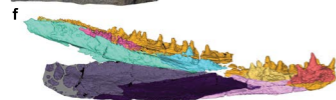
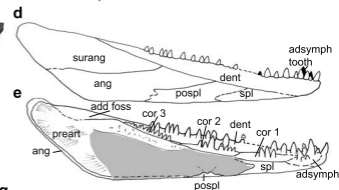
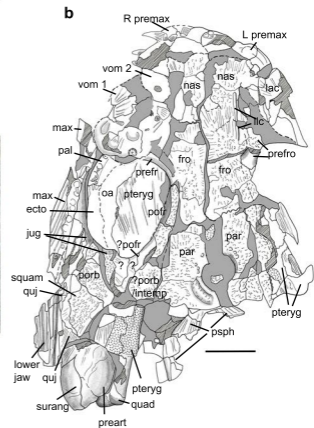
879 JAC is corresponding author and lead PI and with TRS, JAC, BKAO, and KZS
880 collected, described and analysed the tetrapod specimens. CEB, TIK, SJD and DM
881 contributed to the stratigraphical, sedimentological and environmental studies. JEAM,
882 DKC, and EJR contributed to the charcoal, palynological and stratigraphical studies. MR
883 and JAC contributed to the phylogenetic analysis. AJR contributed information on the
884 arthropods, SAW provided additional work on micro-CT scan data. AJR, SAW and
885 NCF organised the Willie's Hole excavation that provided sedimentological
886 information. All authors contributed to discussion, preparation and writing the paper.

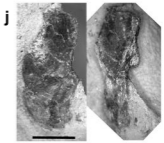
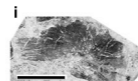
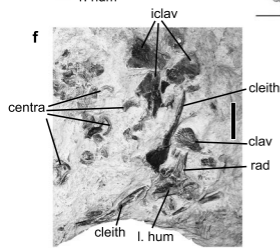
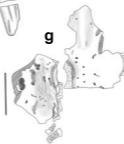
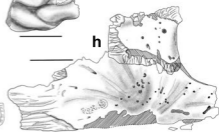
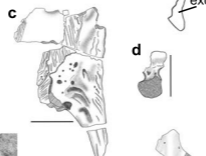
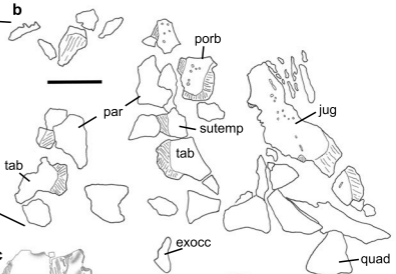
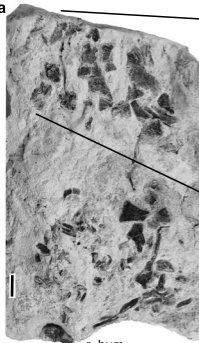
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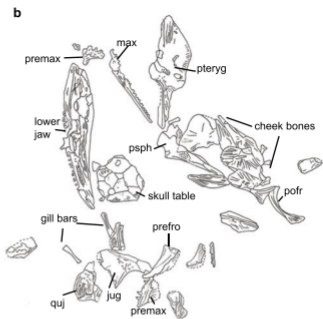
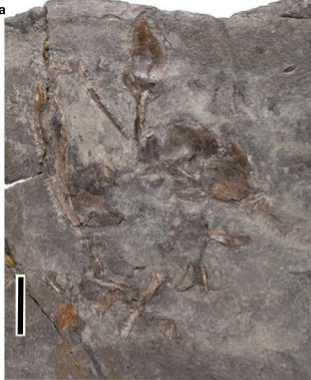
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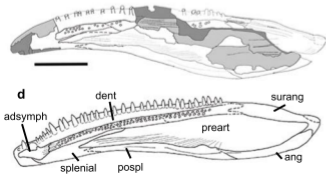
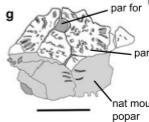
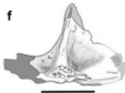
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905

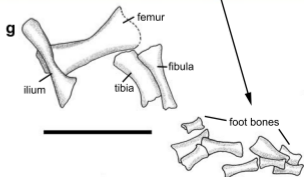
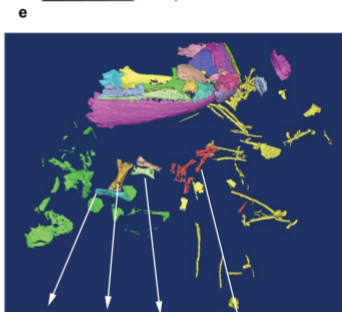
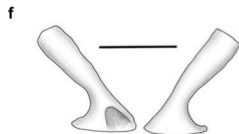
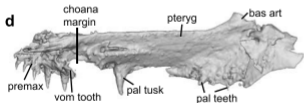
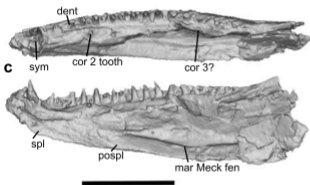
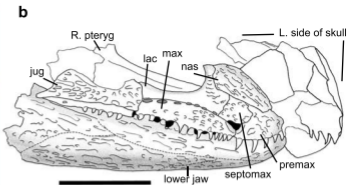
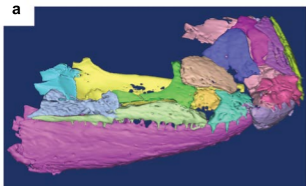


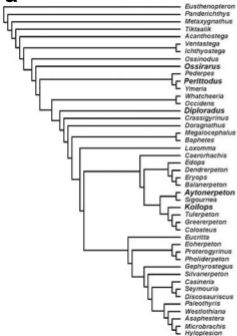
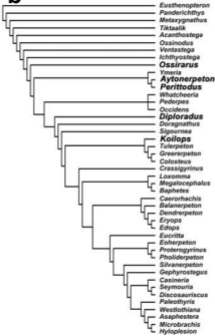




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