

1 Phylogenetic and Environmental Context of a Tournaisian Tetrapod Fauna

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24

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<sup>1,2</sup> for a hiatus of approximately 25 million years  
45 (Myr)<sup>3</sup> 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<sup>4,5</sup>. By that time, tetrapods were ecologically diverse, and were terrestrially  
49 capable. With five or fewer digits, some had gracile limbs<sup>6,7</sup>, unlike the polydactylous  
50 predominantly aquatic fish-like tetrapods of the Late Devonian<sup>8</sup>. 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 regime<sup>9</sup> or lack of successful collecting  
55 in Tournaisian strata<sup>2</sup>.

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<sup>10,11</sup>, only a small fraction has been fully described<sup>12</sup>. The only other Tournaisian  
59 tetrapod material was the articulated skeleton of *Pederpes finneyae*, from the  
60 Tournaisian Ballagan Formation near Dumbarton, western Scotland<sup>13,14</sup>. More recently,  
61 new taxa from this formation in the Borders Region of Scotland were reported<sup>2</sup>, 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<sup>15,16</sup> (**Supplementary Fig 7**). This varied environment  
74 persisted over the 12 million years of the Tournaisian<sup>3</sup>. 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*<sup>17</sup>. 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*<sup>18</sup>.

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*<sup>19-21</sup>. 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*<sup>19</sup> and *Ichthyostega*<sup>20</sup>. 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*<sup>22</sup>,  
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<sup>e.g.21</sup>, 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 individuals<sup>23</sup>. 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 11095<sup>24</sup>). Its gracile limbs,  
220 metapodial bones and phalanges resemble *Colosteus* rather than *Greererpeton*.  
221 Clavicular ornament is similar to that of other colosteids<sup>25,26</sup>. 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 deleted<sup>27</sup>. 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  $K$ <sup>28</sup> 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 amphibians<sup>29-31</sup>, but see<sup>32,33</sup> 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 studies<sup>29-33</sup>,  
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<sup>2,34</sup>. 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 siltstone<sup>16</sup> 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)<sup>15,16</sup>. 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 architecture<sup>35-37</sup>. 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 hypothesis<sup>9</sup> 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 Scotia<sup>38</sup> as  
296 indicating O<sub>2</sub> 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 O<sub>2</sub>  
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 O<sub>2</sub> was stable across this time interval, directly  
310 refuting hypoxia<sup>9</sup> 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 groups<sup>39</sup>, 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<sup>40,41</sup>.

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 Scotia<sup>12</sup>.

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<sup>42,43</sup> 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 lungfish<sup>40</sup> and chondrichthyans<sup>41</sup> as they adapted to a post-extinction world.

330 The occurrence of probable plesiomorphic members of the Crassigyrinidae<sup>2</sup> and  
331 Colosteidae indicates an inception 20-24 Myr earlier than the Late Mississippian as  
332 previously considered<sup>44</sup>. 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 trackways<sup>38</sup> and challenge suggestions of a prolonged period of reduced body size in  
344 vertebrates following the DC extinction event<sup>45</sup>.

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 conditions<sup>46</sup>. 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  $\mu$ 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  $\mu$ 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<sup>14,29-31,44,47,48</sup>. 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. 1.1<sup>49</sup>.  
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 reweighting<sup>28</sup>, 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<sup>50,51</sup>. Diverse palaeosols<sup>15</sup> 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)<sup>27-31,52</sup>. The  
809 saline-hypersaline lake deposits in the Ballagan Formation have been interpreted to  
810 represent brackish marginal marine or hypersaline<sup>52-56</sup> conditions. Other dolomitic units  
811 from the Mississippian are interpreted as saline coastal marshes<sup>56-61</sup>. Erosive-based,  
812 cross-bedded sandstone units (one to tens of metres thick) with basal conglomerate lags  
813 cut into all other facies<sup>34</sup>. The lags contain disarticulated vertebrate material including  
814 acanthodian, rhizodont and tetrapod bones<sup>16</sup>.

815

#### 816 Charcoal Analysis

817 Dispersed organic matter (DOM) was extracted by standard palynological  
818 demineralisation techniques<sup>62</sup>. 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 Petrology<sup>63</sup>.

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 figure<sup>64-68</sup>. As an alternative, fossil charcoal (fusinite) is used by several authors as a

826 proxy for atmospheric oxygen<sup>69-72</sup>, as wildfire activity, and hence charcoal production,  
827 is proportional to oxygen supply<sup>73</sup>. Controlled burning experiments<sup>73</sup> have  
828 demonstrated that when O<sub>2</sub> 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% O<sub>2</sub> and switched off completely below 16%, even in  
832 very dry conditions<sup>73</sup>. The most comprehensive attempt thus far to reconstruct  
833 Phanerozoic O<sub>2</sub> in this way<sup>69</sup> indicated 25.6% O<sub>2</sub> 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 light<sup>74</sup>; 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 origin<sup>75</sup>, 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](mailto: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

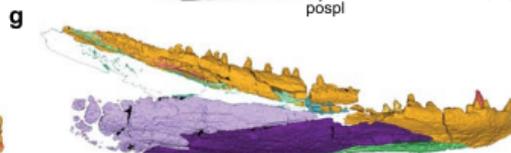
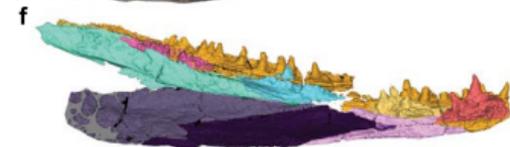
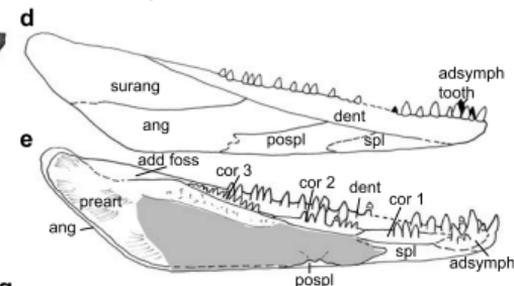
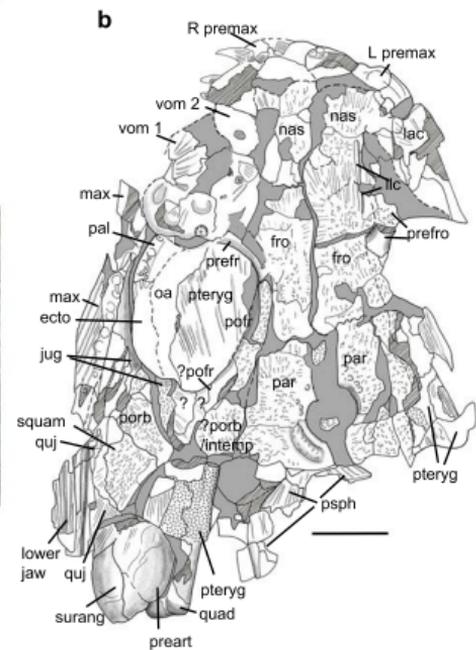
879 JAC is corresponding author and lead PI and with TRS, JAC, BKAO, and KZS  
880 collected, described and analysed the tetrapod specimens. CEB, TIK, SJD and DM  
881 contributed to the stratigraphical, sedimentological and environmental studies. JEAM,  
882 DKC, and EJR contributed to the charcoal, 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.

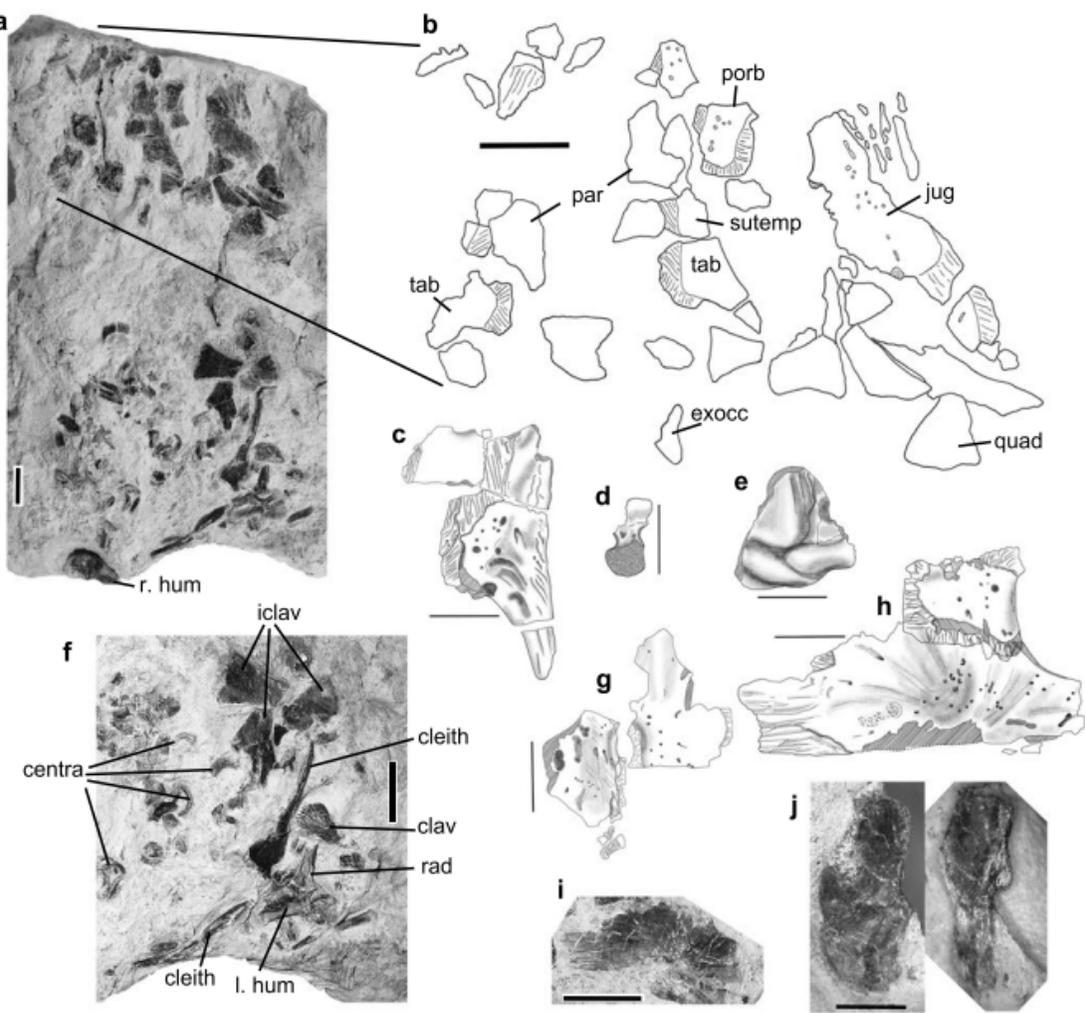
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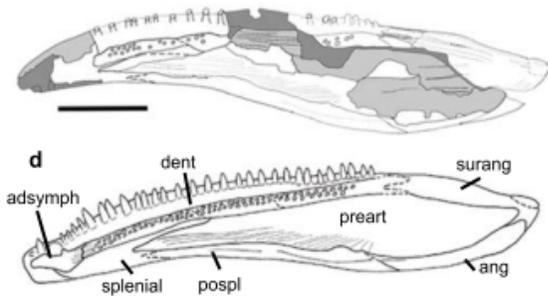
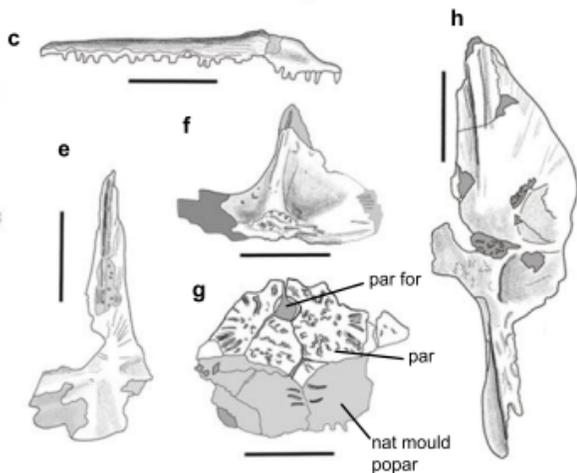
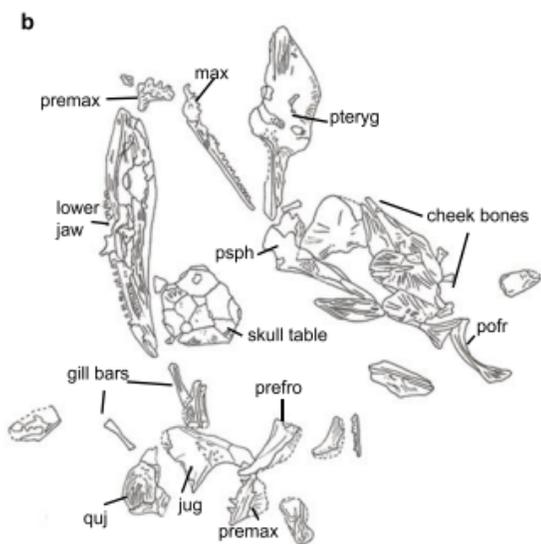
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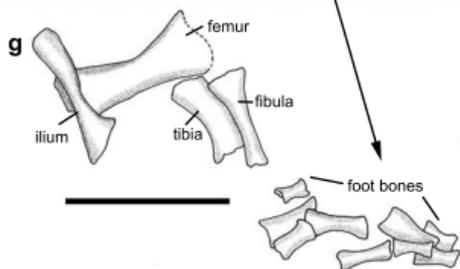
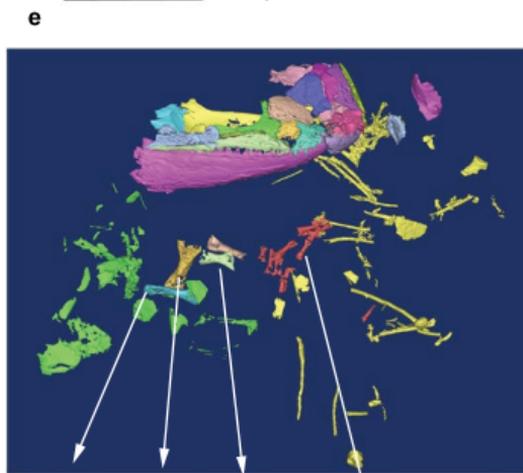
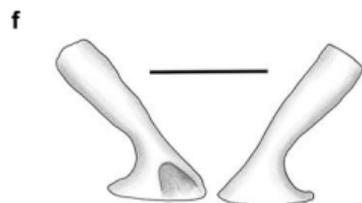
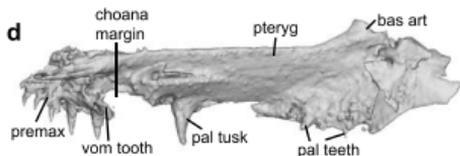
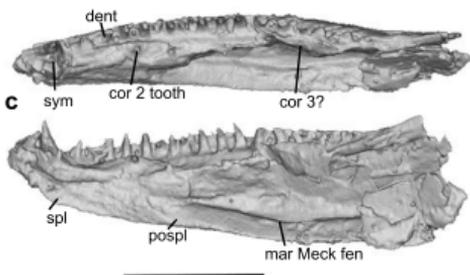
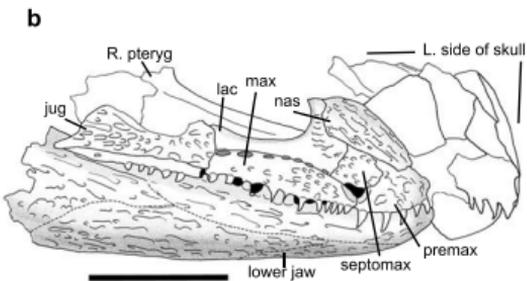
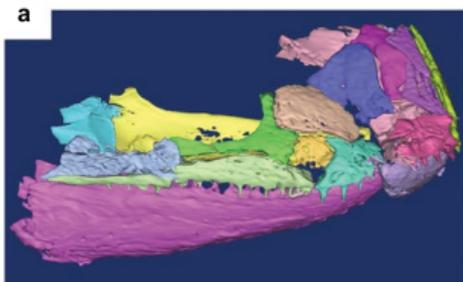
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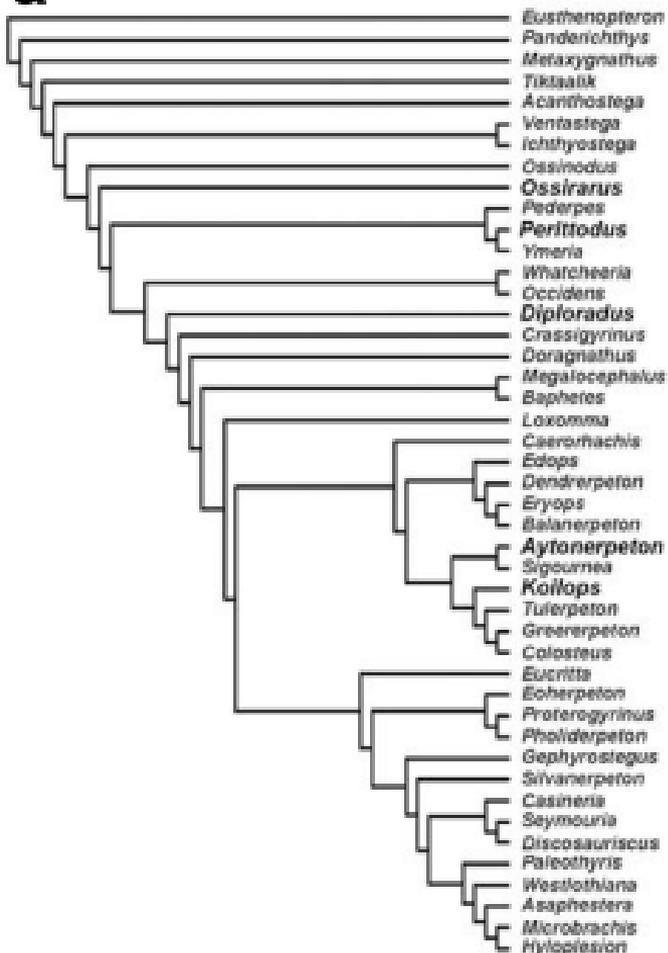
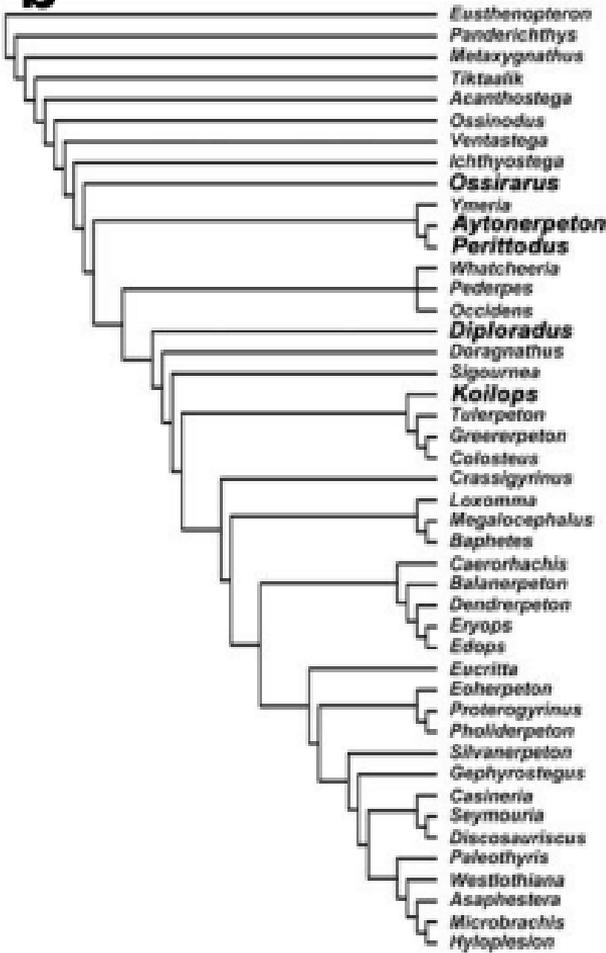
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905









**a****b****c**