Postcranial anatomy and histology of *Seymouria*, and the terrestriality of seymouriamorphs

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Seymouria is the best known of the seymouriamorphs, a group of Permo-Carboniferous reptiliomorphs with both terrestrial and aquatic taxa. The majority of research on *Seymouria* has focused on cranial anatomy, with few detailed descriptions or illustrations of the postcrania. We utilized neutron computed tomography (nCT) and histological sampling to provide updated, detailed illustrations that clarify details of the postcranial anatomy and to assess the development and internal anatomy of *Seymouria* through specimens from the early Permian Richards Spur locality. The histological data indicate rapid metamorphosis, with the youngest specimen being definitively postmetamorphic despite being substantially younger than pre-metamorphic individuals of *Discosauriscus*, the only other seymouriamorph to have been histologically sampled. The data also substantiates the hypothesis that *Seymouria* was terrestrial based on interpretation of external features, although the persistence of a modestly developed medullary spongiosa in comparison to either *Discosauriscus* or to other co-occurring terrestrial tetrapods suggests additional nuances that require further exploration. In the absence of clearly recognizable postmetamorphic stages in several seymouriamorph taxa, it is difficult to determine the evolution trajectory of terrestriality within the clade, but taken together, our analysis provides novel information regarding the life history of *Seymouria* and highlights the need for further study of seymouriamorph ontogeny.

1 **Postcranial anatomy and histology of *Seymouria*, and the terrestriality of seymouriamorphs**

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Abstract

Seymouria is the best known of the seymouriamorphs, a group of Permo-Carboniferous reptiliomorphs with both terrestrial and aquatic taxa. The majority of research on *Seymouria* has focused on cranial anatomy, with few detailed descriptions or illustrations of the postcrania. We utilized neutron computed tomography (nCT) and histological sampling to provide updated, detailed illustrations that clarify details of the postcranial anatomy and to assess the development and internal anatomy of *Seymouria* through specimens from the early Permian Richards Spur locality. The histological data indicate rapid metamorphosis, with the youngest specimen being postmetamorphic despite being distinctly younger than premetamorphic individuals of *Discosauriscus*, the only other seymouriamorph to have been histologically sampled. The data also substantiates the hypothesis that *Seymouria* was terrestrial based on interpretation of external features, although the persistence of a modestly developed medullary spongiosa in comparison to either *Discosauriscus* or to other co-occurring terrestrial tetrapods suggests additional nuances that require further exploration. In the absence of clearly recognizable postmetamorphic stages in several seymouriamorph taxa, it is difficult to determine the evolutionary trajectory of terrestriality within the clade, but taken together, our analysis provides novel information regarding the life history of *Seymouria* and highlights the need for further study of seymouriamorph ontogeny.

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38 **Introduction**

39   Seymouriamorphs are among the best-known stem amniotes and are known primarily

40 from Lower Permian deposits in North America, Europe, and Russia (Broili, 1904; Amalitzky,

41 1921; Vaughn, 1966; Berman, Reisz, & Eberth, 1987; Berman & Martens, 1993; Sullivan &

42 Reisz, 1999; Bulanov, 2014). Within seymouriamorphs, only the monotypic family

43 Seymouriidae is known from both North America and Eurasia (Broili, 1904; Vaughn, 1966;

44 Berman & Martens, 1993). Of the North American localities, the materials of *Seymouria* with the

45 greatest detail of preservation are known from the Dolese Brothers Limestone quarry near

46 Richards Spur, Oklahoma (Sullivan & Reisz, 1999; Bazzana et al., in press). However, the only

47 previously described postcranial material from this locality consists of a few isolated elements

48 (Sullivan & Reisz, 1999). Furthermore, the most detailed description of the postcrania of

49 *Seymouria* from any locality is arguably that completed by White (1939). Subsequent authors

50 have provided focused descriptions of the atlas-axis complex (Berman, Reisz, & Eberth 1987;

51 Sumida, Lombard, & Berman, 1992) and the manus and pes (Berman et al., 2000), but White's

52 (1939) work remains the most thorough description of the postcranial skeleton in its entirety.

53 While the interpretations made by White (1939) have been largely supported by subsequent

54 authors, his illustrations were unlabelled, somewhat stylized, and from slightly angled, non-

55 standard perspectives, which collectively limits their utility. As stem amniotes that are well-

56 documented in the fossil record, seymouriamorphs provide a relatively accessible window

57 through which to examine morphological changes associated with terrestrial lifestyles in

58 Paleozoic tetrapods.

59   Here we describe new postcranial material of *Seymouria* from the early Permian Richards

60 Spur locality, including several articulated vertebrae and a complete humerus, femora, and

61 fibula, and provide updated descriptions, illustrations, and images of the postcrania. Analysis of

62   several limb elements and vertebra using neutron computed tomography (nCT) and histological

63   sampling provides important details regarding the development and internal anatomy of the

64   postcrania of *Seymouria* and contributes to our understanding of the extent to which these stem

65   amniotes were adapted to terrestrial lifestyles.

66   **Materials & Methods**

67   **Neutron tomography.** Neutron tomography measurements were performed at the DINGO

68   thermal-neutron radiography/ tomography/imaging station (Garbe et al., 2015) at the Australian

69   Nuclear Science and Technology Organisation's (ANSTO) 20 MW OPAL nuclear research

70   reactor, Sydney, Australia. The instrument was equipped with an Iris 15TM Large Field of View

71   sCMOS camera (5056 x 2968 pixel, 16-bit) and Zeiss Ikon 100 mm f/2.0 Makro Planar lens.

72   Based on a desired spatial resolution of ~60 μm across the partially-embedded ROMVP 80915

73   and ROMVP 80917, a maximum sample width of 48.5 mm and minimum sample-to-detector

74   distance of 28 mm, the DINGO instrument was configured with a 30 μm thick terbium-doped

75   Gadox scintillator screen (Gd2O2S:Tb, RC Tritec AG) and $25.2 \times 25.2 \times 25.2$ μm voxels for a

76   Field-of-View of 100 x 74.5 mm. For OMNH 79348, the achieved voxel size was 72.0 x 72.0 x

77   72.0 μm. To maximise counting statistics and minimise subsequent noise in the tomographic

78   reconstruction, a collimation ratio (*L/D*) of 500 was used, where *L* is the neutron aperture-to-

79   sample length and *D* is the neutron aperture diameter. This high-flux configuration traditionally

80   illuminates a 200 mm x 200 mm area around the sample area with 4.75×10^7 neutrons cm-2s-1,

81   leading to high background radiation and zingers on the detector. A newly installed slit system

82   was implemented to restrict the neutron-irradiated area about the specimen to achieve optimum

83   scan conditions and a divergence-limited spatial resolution of 56 μm. A total of 900 equally-

84   spaced angle shadow-radiographs were obtained every 0.20° as the sample was rotated 180°

85   about its vertical axis. Both dark (closed shutter) and beam profile (open shutter) images were

86   obtained for calibration before initiating shadow-radiograph acquisition. To reduce anomalous

87   noise, a total of three individual radiographs with an exposure length of 4.0 s were acquired at

88   each angle (Mays, Bevitt, & Stilwell, 2017) for a total scan time of 4.6 h.

89   The individual radiographs were summed in post-acquisition processing using the

90   'Grouped ZProjector' plugin in ImageJ v.1.51h in accordance with our previous measurements;

91   this plugin was developed by Holly (2004). Tomographic reconstruction of the 16-bit raw data

92   was performed using commercially available Octopus Reconstruction v.8.8 software package

93   and the filtered back-projection algorithm to yield virtual slices perpendicular to the rotation

94   axis. When these slices are stacked in a sequence, they form a three-dimensional volume image

95   of the sample. The reconstructed volume data were downsampled by a factor of 2 in ImageJ to

96   reduce computation time, then rendered and segmented with Avizo Lite 9.3.0.

97

98   **Histology.** Histological preparation followed standard procedures (Padian & Lamm, 2013). All

99   specimens were photographed prior to embedding in EP4101UV resin (Eager Polymers), which

100   was allowed to cure for 24 hours. ROMVP 80916 (partial femur), ROMVP 81198 (vertebra), and

101   ROMVP 81199 (vertebra) were prepared at the Royal Ontario Museum (ROMVP), Toronto,

102   Canada. Specimens were cut on the IsoMet 1000 precision saw (Buehler) and mounted to frosted

103   plexiglass slides with cyanoacrylate adhesive. For the femora, the cut was made at the

104   approximate region of the minimum diaphyseal circumference; for the vertebra, the first cut was

105   made sagittally (anteroposteriorly) down the midline, and the second cut was made transversely

106   through one of the two halves of the block. For ROMVP 80916 (larger, partial femur), the

107 section is taken slightly proximal to the inferred minimum circumference due to the incomplete

108 specimen's nature.

109   Mounted blocks were trimmed using the IsoMet and ground on the Hillquist Thin

110 Sectioning Machine lapidary wheel. Manual polishing using 1000-mesh grit on glass plates and a

111 combination of 1-μm and 5-μm grit on polishing cloths was used to remove scratches. ROMVP

112 81200 (partial femur) was prepared in a similar fashion but with a different equipment setup at

113 the University of Toronto Mississauga. Cutting was performed on the Metcut-5 low speed saw

114 (MetLab), initial grinding on the Metcut-10 Geo (MetLab), and manual grinding on a cutlery

115 whetstone block. Imaging was done on a Nikon AZ-100 microscope with a DS-Fi1 camera and

116 NIS Elements-Basic Research software registered to David C. Evans.

117   Preparation of the specimens was performed by Diane Scott and Bryan M. Gee using pin

118 vises and air scribes. Figures were prepared using Adobe Illustrator and Photoshop.

119

120 **Systematic Paleontology**

121 Order Seymouriamorpha Watson, 1917

122 Family Seymouriidae Williston, 1911

123 Genus *Seymouria* Broili, 1904

124

125 **Horizon and locality.** Dolese Brothers Limestone Quarry near Richards Spur, Oklahoma, USA.

126 Early Permian (Artinskian).

127

128 **Referred specimens.** OMNH 74721, right humerus; OMNH 79346, complete vertebra; OMNH

129 79347, string of 11 articulated vertebrae; OMNH 79348, string of three articulated vertebrae;

130   OMNH 79349, complete vertebra; OMNH 79350, partial vertebra; OMNH 79351, complete

131   vertebra; OMNH 79352, partial vertebra; OMNH 79353, partial vertebra; ROMVP 81198,

132   complete vertebra; ROMVP 81199, complete vertebra; ROMVP 80915, left femur; ROMVP

133   80916, proximal left femur; ROMVP 80917, left fibula; ROMVP 81200, distal left femur.

134

Description

136   **Vertebrae.** OMNH 79346, OMNH 79349, OMNH 79350, OMNH 79353, ROMVP 81198, and

137   ROMVP 81199 are isolated presacral vertebrae between the tenth and twenty-second positions

138   (Fig. 1). OMNH 79346 and OMNH 79349 are mostly complete, whereas OMNH 79350 and

139   OMNH 79353 are incomplete. OMNH 79351 and OMNH 79352 are complete vertebrae from

140   the third to ninth vertebral positions (Fig. 2). OMNH 79347 consists of 11 articulated presacral

141   vertebrae, likely between the tenth and twenty-second positions (Fig. 3A). OMNH 79348

142   consists of the last presacral position, the first sacral vertebra, and a possible second sacral

143   vertebra in articulation (Fig. 3B-E).

144   All the vertebrae described here exhibit the swollen pre- and postzygapophyses that are

145   characteristic of *Seymouria* (White, 1939). The first sacral vertebra in OMNH 79348 exhibits the

146   transition from the expanded zygapophyses of the trunk series to the more transversely

147   constricted morphology characteristic of the caudal series (White, 1939), with the

148   prezygapophyses being slightly more than twice the width of the postzygapophyses (Fig. 3B).

149   The neural spine of OMNH 79349 is strongly deflected to the right, as has been noted in other

150   specimens of *Seymouria* (Sullivan & Reisz, 1999). Both OMNH 79351 and 79352 display the

151   broadly expanded diapophyses characteristic of the anteriormost presacral vertebrae in

152   *Seymouria* (Fig. 2). In OMNH 79352, the neural spine is bifurcated; the neural spines of the

153   other specimens are either broken or missing. *Seymouria* has been previously described as

154   having an irregular distribution of bifurcated and single spines along the vertebral column, from

155   the tenth position to the twenty-second position (White, 1939). OMNH 79352 appears to be the

156   first record of bifurcation of the neural spine in a vertebra from the anteriormost trunk. Although

157   the seemingly complete co-ossification of the neural arch and centrum suggests skeletal maturity,

158   the maturity of these vertebrae cannot be more definitively established given the known

159   challenges of applying skeletochronology to vertebral elements (Danto et al., 2016).

160   ROMVP 81198, an isolated presacral neural arch of a small-bodied individual (Fig. 1E),

161   and ROMVP 81199, a presacral neural arch with centrum of a larger individual (Fig. 1F), were

162   histologically sectioned. The transverse profile reveals a similar microanatomy and histology to

163   that of a previously sampled specimen (OMNH 73499) from Richards Spur (Danto et al., 2016).

164   The pleurocentrum of ROMVP 81199 is formed by two domains (Fig. 4), a compact periosteal

165   domain along the ventrolateral margin of the element that is formed by a thin layer of lamellar

166   bone, and a less dense and more disorganized endochondral domain with trabeculae; this is

167   captured in both sagittal and transverse sections. Although the suture between the pleurocentrum

168   and the neural arch is not clearly defined externally, it is very apparent in the transverse section

169   in which the separation was largely cartilaginous at the time of death. Neither the notochordal

170   canal nor the neural canal were captured in the half-transverse section. The neural arches of

171   ROMVP 81198 and 81199 are very similar in transverse section. Each arch is comprised of a

172   spongy bone texture with a hollow interior. In the smaller ROMVP 81198, the ventral portion of

173   the arch is poorly ossified, with a sparse network of trabecula (Fig. 5). The sagittal sections are

174   also generally comparable, but a few differences may be noted. Indentations on the anterior and

175   posterior surfaces representing the vestiges of the supraneural canal are present; these

176 indentations are more prominent in the larger ROMVP 81199, and in each specimen, the anterior

177 indentation is more pronounced. In both specimens, the neural arch is much thicker along the

178 posterodorsal surface behind the neural spine and extending down to the posterior indentation of

179 the supraneural canal when compared to the anterior surface. The thickened region is far more

180 developed in the larger ROMVP 81199. The neural spines are very poorly ossified. The ventral

181 portion of the arch, which roofs the neural canal, is thin in both specimens and with distinct

182 remodelling (Figs. 4B, 5B). Remodelling is otherwise found mostly near the geometric center of

183 the element (Fig. 5B). A pair of closely spaced, distinctive growth lines can be identified in the

184 thickened region of ROMVP 81199 (Fig. 4A).

185   The three articulated vertebrae of OMNH 79348 were digitally sectioned using the

186 neutron tomography data (Fig. 6). Viewed in transverse section, the data reveal pronounced

187 differences in the compactness of the diapophyses; the diapophyses of the first sacral vertebra are

188 not only greatly expanded, as is visible externally, but are also composed of substantially more

189 compact bone than those of either the presacral or the possible second sacral, suggesting that the

190 first sacral undergoes the majority of the stress loading. The identity of the vertebra immediately

191 posterior to the first sacral has been historically debated; White (1939) and Berman et al. (2000)

192 identified the element as a second sacral, while Williston (1911), Watson (1918), and Berman,

193 Reisz, and Eberth (1987) identified it as the first caudal. White's (1939) argument was based on

194 the presence of a rib extending anteriorly from the vertebra in question to contact the rib of the

195 first sacral, stating unequivocally that it must have had a strong cartilaginous connection and was

196 doubtlessly a functional second sacral vertebra (p. 354). In contrast, Berman, Reisz, and Eberth

197 (1987) noted that the rib of the debated element curved posteriorly and thus could not contact the

198 ilium or the rib of the first sacral, negating any possibility of it forming a true second sacral. In

199 the absence of a preserved rib in OMNH 79348, we are unable to comment on whether the

200 vertebra immediately following the first sacral represents a definitive second sacral or the first

201 caudal vertebra.

202

203 **Humerus.** OMNH 74721 is a complete right humerus, exhibiting the tetrahedral shape typical of

204 many reptiliomorphs (Fig. 7). The overall morphology matches that described by previous

205 authors (White, 1939; Sullivan & Reisz, 1999) in being short and robust with the deltopectoral

206 crest following an L-shaped path. The proximal and distal ends are broadly expanded and are set

207 at an approximately 45-degree angle to each other with no distinct shaft separating the epiphyses.

208 The supinator process is oval in cross-section and located just distal to the short arm of the

209 deltopectoral crest (Fig. 7C). OMNH 74721 exhibits a keel that extends along the anteroventral

210 surface from the deltopectoral crest to the entepicondylar foramen (Fig. 7D); a similar crest has

211 been described by Sullivan & Reisz (1999) but was not mentioned by White (1939). The

212 entepicondylar ridge runs along the ventral edge and expands proximally to form what may

213 represent the insertion site for the subcoracoscapularis on the posterior surface of the humerus,

214 near the glenoid articulation (Fig. 7B). Dorsal to this expansion is a pronounced tubercle for the

215 insertion of the latissimus dorsi muscle. The absence of an ectepicondylar foramen, the proximal

216 position of the insertions for the subcoracoscapularis and the latissimus dorsi muscles, and the

217 position and shape of the supinator process all correspond exactly to the descriptions of

218 *Seymouria* given by White (1939) and Sullivan and Reisz (1999).

219   Compared to the smaller and presumably more immature humerus (FMNH PR 2054) that

220 was previously described from Richards Spur (Sullivan & Reisz, 1999: fig. 2), many features on

221 OMNH 74721 are more developed. In FMNH PR 2054, the capitellum is indicated only by a

222   slight swelling, whereas in OMNH 74721 it is a distinct hemispherical facet. Mirroring this

223   disparity, the supinator process of FMNH PR 2054 remains connected to the capitellum by a

224   ridge of unfinished bone, whereas the process of OMNH 74721 is clearly delineated from the

225   distal articular surfaces by an emargination of smoothly finished bone.

226

227   **Femur.** ROMVP 80915 is a complete left femur (Fig. 8), the morphology of which corresponds

228   to previous descriptions (White, 1939; Sullivan & Reisz, 1999). The element is short and robust.

229   The insertion for the puboischiofemoralis muscle is visible on the dorsal surface of the head (Fig.

230   8B, D). As is known in *Seymouria* (White, 1939; Sullivan & Reisz, 1999), the adductor crest

231   extends posterolaterally along the ventral surface of the femur from the trochanter to near the

232   tibial condyle (Fig. 8F). The smaller femur that was previously described by Sullivan and Reisz

233   (1999; FMNH PR 2053) was stated to have a prominent trochanter. This appears to remain

234   constant throughout ontogeny, as little difference in the relative size of the trochanter is seen

235   between the smallest (ROMVP 81200) and largest specimens (ROMVP 80915 and 80916). The

236   distal articular surface has been described as following an M-shaped curve (White, 1939), but

237   this may not be entirely accurate. In ROMVP 80915, ROMVP 81200, and a smaller, more

238   immature femur (FMNH PR 2053; Sullivan & Reisz, 1999: fig. 3), the distal surface is V-

239   shaped, with the tip of the anterior arm being bent ventrally (Fig. 8G), as opposed to the

240   illustration given by White (1939: fig. 28) that reconstructs this surface with both ends curving

241   ventrally. However, it is possible that the shape of the distal surface is ontogenetically variable,

242   and disparities in length suggest that the specimen described by White (1939), measuring 6.4 cm

243   in length, may be more mature than ROMVP 80915 (5.5 cm), the largest complete femur from

244   Richards Spur.

245   ROMVP 80916 and ROMVP 81200 are partial left femora (Fig. 9); ROMVP 80916 is

246   equivalent in size to ROMVP 80915 and is broken distal to the trochanter, while ROMVP 81200

247   is substantially smaller and is broken proximal to the trochanter. ROMVP 80916 was

248   histologically sectioned slightly proximal to the minimum diaphyseal circumference (Fig. 10),

249   while ROMVP 81200 was sectioned at this minimum region (Fig. 11). ROMVP 80915 was

250   digitally sectioned at the minimum circumference (Fig. 12). All three femora are relatively

251   similar in their microanatomical and histological features. The cortex is relatively compact,

252   comprised primarily of lamellar bone; the tissue is distinctly less organized in the smaller

253   ROMVP 82100, reflecting its immaturity and presumed faster growth rate. Secondary osteons

254   and vascular canals are present in both specimens (Figs. 10-11); the latter decrease in abundance

255   in the larger ROMVP 80916 (Fig. 11). Remodelling is found at the boundary of the medullary

256   cavity in both specimens (Figs. 10C, 11C), but there is distinctly more parallel-fibered bone

257   along the margin of the cavity in the larger ROMVP 80916 (Figs. 10-11). The medullary cavity

258   is relatively open, although there is a network of trabeculae throughout; secondary remodelling is

259   present within this network, but calcified cartilage is absent. The trabecular network appears to

260   be less dense in the digital section of ROMVP 80915 than in the histological section of ROMVP

261   80916, but this may be a combination of a slightly more proximal plane of section in the latter

262   and limitations on scanning resolution (25.2 μm). Histological features (e.g., lines of arrested

263   growth) are not resolvable in ROMVP 80915. A confident determination of lines of arrested

264   growth (LAGs) is complicated in these specimens; most lines appear not to extend for the full

265   circumference or are disrupted by secondary remodelling. In the smaller ROMVP 81200, at least

266   four lines of arrested growth are identifiable. In the larger ROMVP 80916, at least seven lines

267   are identifiable.

268

269   **Fibula.** ROMVP 80917 is a complete left fibula (Fig. 13). Previous descriptions (White, 1939;

270   Sullivan & Reisz, 1999) have commented only on the general shape of the element, to which

271   ROMVP 80917 corresponds exactly in that the medial surface is deeply concave, the lateral

272   surface is mostly straight with only a slight concavity, and the distal articular surface is more

273   expanded than the proximal surface, which itself is crescentic with its dorsal margin being

274   convex and its ventral margin being concave. Features that have not been described previously in

275   *Seymouria* but that are present in ROMVP 80917 are the pronounced muscle scar along the

276   proximal half of the lateral surface, which may represent the insertion site for the iliofibularis

277   muscle (Fig. 13A-B, D; Romer, 1956), and the twisting of the fibular shaft such that the proximal

278   and distal heads lie in planes that are at an approximately 45-degree angle to each other (Fig.

279   13E-F).

280

281   **Discussion**

282   **Comparative external anatomy.** The vertebrae of *Seymouria* bear a number of marked

283   differences from those of other seymouriamorphs. In *Ariekanerpeton*, the presacral vertebrae

284   differ in the level of ossification of the neural arch, with the arches of the third to fifth vertebrae

285   remaining separate and the sixth to ninth arches being strongly co-ossified (Klembara & Ruta,

286   2005). The neural spines of *Kotlassia* are much higher than in *Seymouria* (Bystrow, 1944),

287   whereas in *Discosauriscus* the spines are short (Klembara & Bartík, 2000), and in

288   *Ariekanerpeton* the spines are either low or unossified altogether (Laurin 1996b). The vertebrae

289   of *Utegenia* have been described as indistinguishable from those of *Discosauriscus* (Klembara &

290   Ruta, 2004). The oval cross-section of the diapophyses is shared between *Seymouria* (White,

291   1939) and *Kotlassia* (Bystrow, 1944). However, in *Seymouria* the diapophyses remain the same

292   size but transition in orientation from vertical to horizontal along the vertebral column (White,

293   1939), whereas the diapophyses of *Kotlassia* maintain the same orientation but decrease in size

294   along the column (Bystrow, 1944). Unlike *Seymouria* in which the articular surfaces of the

295   prezygapophyses and the postzygapophyses face directly dorsally and ventrally, respectively

296   (White, 1939), the surfaces of *Discosauriscus* and *Ariekanerpeton* face dorsomedially and

297   ventrolaterally (Klembara & Bartík, 2000; Klembara & Ruta, 2005). *Seymouria*, *Kotlassia*, and

298   *Discosauriscus* retain an open notochordal canal in adulthood (White, 1939; Bystrow, 1944;

299   Klembara & Bartík, 2000). It is unknown whether the notochordal canals were retained in the

300   other seymouriamorphs (Klembara & Ruta, 2004; 2005; Klembara, 2005; 2009; Bulanov, 2014).

301   *Discosauriscus* has only one sacral vertebra (Klembara & Bartík, 2000), as in OMNH 79348. It

302   is unclear whether *Seymouria baylorensis* and *Seymouria sanjuanensis* differ in the number of

303   sacral vertebrae (White, 1939; Berman, Reisz, & Eberth, 1987, 2000), so this character cannot be

304   used to clarify the specific designation of this material.

305   The humerus of *Seymouria* is more extensively ossified than those of *Utegenia* or

306   *Ariekanerpeton* (Laurin, 1996a, 1996b; Klembara & Ruta, 2005), in which the capitellum,

307   trochlea, the supinator process, and the deltopectoral crest are indistinct in even the largest

308   individuals. In particular, the humerus of *Utegenia* has been described as "little more than a

309   stout, subcylindrical lump of bone" (Klembara & Ruta, 2004: 77). It has been noted, however,

310   that the lack of ossification in *Utegenia* may represent ontogenetic immaturity (Klembara &

311   Ruta, 2004). The humerus of *Kotlassia* is the slenderest of the seymouriamorphs and lacks an

312   entepicondylar foramen (Bystrow, 1944). *Makowskia*, *Spinarerpeton*, and *Discosauriscus* exhibit

313   the same massive, L-shaped deltopectoral crest extending from the proximal articular surface as

314   that seen in *Seymouria* (Klembara, 2005, 2009; Klembara & Bartík, 2000). The humeri of

315   *Makowskia* and *Spinarerpeton* are described as having a broad shaft, a proximodistally short

316   entepicondyle, and an entepicondylar foramen that is open distally (Klembara, 2005, 2009); the

317   last feature has been recognized as being likely ontogenetic. *Makowskia*, *Spinarerpeton*, and

318   *Discosauriscus* differ substantially from *Seymouria* in having a well-developed insertion site for

319   the subcoracoscapularis muscle and in lacking a supinator process (Klembara & Bartík, 2000;

320   Klembara, 2005, 2009); in *Seymouria*, the former is represented by only a slight rugosity while

321   the latter is quite pronounced (White, 1939). The humeri of *Discosauriscus* and *Ariekanerpeton*

322   have been reported with a lesser degree of twisting, with the planes of the proximal and distal

323   ends being at an approximately 38-degree angle (Klembara & Bartík, 2000; Klembara & Ruta,

324   2005). The positioning and degree of development of the insertions for the subcoracoscapularis

325   and latissimus dorsi muscles are roughly equivalent in *Discosauriscus* as in *Seymouria*

326   (Klembara & Bartík, 2000).

327   As with the humerus, the femur of *Seymouria* is more ossified than in *Utegenia* or

328   *Ariekanerpeton* (Laurin 1996a, 1996b); the femur of *Utegenia* has been described as featureless

329   (Klembara & Ruta, 2004). The femur of *Makowskia* is known but has only been described as

330   having a crescentic proximal articular surface with a deep intertrochanteric fossa as in *Seymouria*

331   (Klembara, 2005), and the only corresponding figure is a simplified line drawing. The femur of

332   *Spinarerpeton* has been similarly described and figured in limited detail (Klembara, 2009). The

333   femur of *Microphon* is much more gracile than in *Seymouria* with less pronounced expansion of

334   the epiphyses and a proportionally longer, narrower shaft (Bulanov, 2014). *Microphon* also

335   differs from *Seymouria* in that the adductor crest extends towards the fibular condyle (Bulanov,

336   2014), as opposed to the tibial condyle as in *Seymouria* and *Discosauriscus* (Klembara & Bartík,

337   2000). In addition, the intertrochanteric fossa of *Microphon* is approximately one-third the length

338   of the femur (Bulanov, 2014), whereas in *Seymouria* it extends approximately halfway along the

339   element. *Kotlassia* appears to be intermediate between these two conditions and exhibits a

340   starker contrast between the slender shaft and the broadly expanded epiphyses (Bystrow, 1944:

341   fig. 9). A feature found in the femora of *Microphon* and *Kotlassia* and in ROMVP 80915, though

342   perhaps not all specimens of *Seymouria*, is the lesser development of the trochanter (Bystrow,

343   1944); in *Microphon*, the trochanter seems to not be developed at all (Bulanov, 2014). The femur

344   of *Discosauriscus* is similar to that of *Seymouria* in overall morphology but is more gracile

345   (Klembara & Bartík, 2000:fig. 25).

346   The fibulae of *Kotlassia* and *Utegenia* have not been illustrated or described in sufficient

347   detail to allow for accurate comparison with *Seymouria*. The fibula of *Ariekanerpeton* has only

348   been described as being poorly preserved with unfinished epiphyses (Klembara & Ruta, 2005).

349   In *Makowskia* and *Discosauriscus*, the fibula is similar to *Seymouria* in being deeply concave

350   medially with only a slight concavity on the lateral surface (Klembara & Bartík, 2000; Klembara,

351   2005). The fibula of *Spinarerpeton* is unknown (Klembara, 2009).

352

353   **Histological interpretations and comparisons.** In early tetrapods, interpretations of ecology

354   (e.g., aquatic vs. terrestrial) are often based on the presence or absence of features such as lateral

355   line grooves and the degree of development of external features of the limbs (Moodie, 1908).

356   Histology has more recently been utilized as a means to further test these hypotheses by means

357   of comparisons with extant taxa in which ecologies can be definitively observed and with the

358   classically utilized external anatomical features (Germain & Laurin, 2005; Kriloff et al., 2008;

359   Sanchez et al., 2010; Quemeneur, de Buffrénil & Laurin, 2013; Konietzko-Meier, Shelton, &

360   Sander, 2016). *Seymouria* is widely accepted to lack lateral line grooves, although they have

361   been suggested by some to have been present in juveniles (Berman & Martens, 1993, but see

362   Klembara et al., 2006), indicating a transition in ecology throughout ontogeny. Additionally, the

363   limbs are well-developed, with prominent attachment sites for musculature and distinct processes

364   (Figs. 7-8), and the neural arches are greatly expanded compared to other Paleozoic tetrapods

365   and with prominent zygapophyses inferred to have supported the axial column. These features

366   have been used to infer a terrestrial lifestyle (Sullivan & Reisz, 1999). This is further supported

367   by the specific context of the Richards Spur locality, which is dominated by terrestrial fauna

368   (MacDougall et al., 2017).

369   Contextualizing the histological data of the specimens of *Seymouria* is complicated by

370   the paucity of work on other stem amniotes, let alone seymouriamorphs specifically. Limb

371   elements of *Seymouria* have never been histologically analyzed. The only other seymouriamorph

372   femur to be histologically sampled is that of the European *Discosauriscus* (Sanchez et al., 2008).

373   Most individuals of *Discosauriscus* retain lateral line canals, but this may reflect a biased relative

374   abundance of premetamorphic individuals in the fossil record (e.g., Klembara et al., 2006).

375   Previous authors have inferred that *Discosauriscus* underwent metamorphosis (Klembara, 1995)

376   but definitive adults, terrestrial or otherwise, are unknown (Klembara, 2001). Sanchez et al.

377   (2008) defined the age bracket at which they believed metamorphosis to a terrestrial adult to

378   have occurred. The general histology and microanatomy of *Discosauriscus* is similar to that of

379   *Seymouria*, but the cortex of the former is more compact and with more organized lamellar bone,

380   indicating a slower growth and a protracted aquatic larval stage in this taxon (Sanchez et al.,

381   2008). In contrast, the individuals of *Seymouria* that were analyzed here are regarded as being

382   definitively postmetamorphic in spite of at least one (ROMVP 81200) being distinctly younger

383 than the onset of metamorphosis in *Discosauriscus* (Sanchez et al., 2008). This disparity may

384 reflect the different environments in which these taxa are found, as *Seymouria* is primarily found

385 in fluvial environments of North America that probably experienced marked seasonality, and

386 *Discosauriscus* is primarily found in lacustrine settings in Europe that may have been more

387 environmentally stable. Histological sections also indicate a less developed trabecular network in

388 the medullary cavity of *Discosauriscus* (Sanchez et al., 2008:fig. 2); the significance of this is

389 unclear in the absence of additional data.

390   Comparisons with other Paleozoic tetrapods are also limited by a paucity of comparative

391 work. Of the major Paleozoic clades (e.g., pelycosaurian synapsids, 'lepospondyls'),

392 temnospondyls are the best-sampled (Sanchez et al., 2010a; Sanchez et al., 2010b; McHugh,

393 2014; Konietzko-Meier, Shelton & Sander, 2016). The relative thickness of the cortex and the

394 development of the medullary spongiosa are most comparable to that of the co-occurring

395 trematopid *Acheloma dunni*, a terrestrial taxon (Sanchez et al., 2010b; Quemeneur, de Buffrénil

396 & Laurin, 2013). The spongiosa is less developed than in either definitively aquatic taxa such as

397 the late Permian rhinesuchid *Rhinesuchus* (McHugh, 2014) or in controversially aquatic taxa

398 such as the early Permian eryopid *Eryops* (Sanchez et al., 2010b; Quemeneur, de Buffrénil &

399 Laurin, 2013; Konietzko-Meier, Shelton & Sander, 2016), and the cortex is not extensively

400 thickened as in the definitively aquatic dvinosaur *Trimerorhachis* (Sanchez et al., 2010b;

401 Quemeneuer et al., 2013). A large number of Mesozoic temnospondyls, which are predominantly

402 aquatic, have also been sampled (Steyer et al., 2004; Konietzko-Meier & Sander, 2012; Sanchez

403 & Schoch, 2013). Many of these taxa exhibit similar structure to that of *Trimerorhachis*, often

404 with a high degree of pachyostotic development and with greatly reduced or nearly absent

405 medullary cavities. The small-bodied Early Triassic lydekkerinid *Lydekkerina* and the

406   amphibamiform *Micropholis*, both widely regarded as being terrestrial, were sampled by

407   McHugh (2015) and exhibit a similar histological and microanatomical organization to that of

408   terrestrial Paleozoic temnospondyls and to that of *Seymouria*. Collectively, the temnospondyl

409   comparisons support an inferred terrestrial lifestyle of *Seymouria*. However, it is important to

410   note that the spongiosa of *Seymouria* is more developed than in any of the co-occurring

411   terrestrial temnospondyls at Richards Spur (Castanet et al., 2003; Quemeneur, de Buffrénil &

412   Laurin, 2013; Richards, 2016) in which the spongiosa is either weakly developed (Trematopidae)

413   or virtually non-existent (Dissorophidae, Amphibamiformes). The significance of this is

414   uncertain at present and warrants further work to compare co-occurring taxa.

415   The vertebral histology is also difficult to compare with closely related taxa. For one,

416   vertebrae are uncommon in histological studies compared to limb elements, and most studies that

417   that have examined the vertebrae of Paleozoic tetrapods have focused on the inter- and

418   pleurocentra (Konietzko-Meier, Danto & Gadek, 2014; Danto et al., 2017, 2019). However, both

419   the centra and the neural arches contribute valuable information regarding the ecology of

420   *Seymouria*. Previous workers have often suggested that the neural arch would have been subject

421   to greater, more direct biomechanical constraints during locomotion in early tetrapods

422   (Rockwell, Evans & Pheasant, 1938; Olson, 1976; Holmes, 1989). The prominent expansion of

423   the neural arch and the development of the zygapophyses in *Seymouria* lends support to this

424   hypothesis. *Discosauriscus* is the only other seymouriamorph to have its internal vertebral

425   anatomy examined (Danto et al., 2016). The main difference is in the construction of the neural

426   arch, which is comprised of thick, compact lamellar bone in *Discosauriscus*; in contrast, the

427   neural arch of *Seymouria* is largely hollow. Based on the size of the sampled *Discosauriscus*

428   material, the individual was likely premetamorphic and still aquatic, which would explain the

429   higher degree of ossification. Whether this might have changed in later stages of ontogeny when

430   individuals metamorphosed into a presumably terrestrial adult form remains unknown. Beyond

431   seymouriamorphs, neural arches have not been sampled in many clades, which may be because

432   most Paleozoic tetrapod clades have multipartite vertebrae in which the arch readily detaches

433   from the centra during preservation. Furthermore, isolated neural arches have not traditionally

434   been utilized as an ideal case study for exploring histological questions compared to either the

435   centra or to other postcranial elements. Danto et al. (2016) sampled a number of Paleozoic

436   lepospondyl taxa in which neural arches were preserved. Some of the aquatic taxa (e.g., an

437   indeterminate nectridean) exhibit a similar spongy bone composition of the arch, but the interior

438   of the arch is relatively well-ossified with little empty space.

439   The centra also contribute information through inferences on the skeletal mass of the

440   element(s). The two traditionally utilized criteria are the thickness of the periosteal domain and

441   the presence or absence of calcified cartilage. Greatly thickened domains (pachyostosis) and

442   retention of calcified cartilage throughout ontogeny are frequently seen in large-bodied aquatic

443   temnospondyls and probably served to increase the skeletal mass for buoyancy control (Danto et

444   al., 2016). In both *Discosauriscus* and *Seymouria*, the periosteal domain is relatively thin, and

445   calcified cartilage is primarily found around the notochordal canal (Danto et al., 2016). In

446   *Seymouria*, this is the only location of this tissue, whereas calcified cartilage occurs sporadically

447   in the endochondral domain of at least immature individuals of *Discosauriscus*.

448   What then can be concluded regarding the histological data from *Seymouria* postcrania

449   and the ecology of the taxon? The femoral microanatomy, specifically the relatively thin cortex

450   and the modest development of the medullary spongiosa, is more compatible with that of a

451   terrestrial animal by comparison with other Paleozoic tetrapods (primarily temnospondyls) that

452   have been inferred to be terrestrial. Based on studies of femoral and tibial microanatomy in

453   extant tetrapods (Kriloff et al., 2008; Quemeneur, de Buffrénil & Laurin, 2013), these features

454   also support a primarily terrestrial lifestyle. Collectively, this corroborates the conclusions of

455   previous authors that *Seymouria* was most likely a terrestrial animal (White, 1939; Berman &

456   Martens, 1993; Sullivan & Reisz, 1999; Marchetti, Mujal & Bernardi, 2017). The vertebral

457   histology also confers support for a terrestrial lifestyle. The periosteal domain is thin, calcified

458   cartilage is sparse and confined to the margin of the notochordal canal, and the neural arch is

459   largely hollow. These data correspond favorably with the broad expansion of the arch and the

460   zygapophyses, which Sullivan & Reisz (1999) interpreted to be for the stiffening of the axial

461   column following White (1939).

462

463   **Terrestriality in seymouriamorphs.** Assessing the range of ecologies among seymouriamorphs

464   from a macroevolutionary standpoint is important because the group has historically been

465   regarded as being well-situated for understanding the associated skeletal modifications

466   associated with terrestriality. *Seymouria* is one of the best seymouriamorphs for examining such

467   modifications because complete, articulated skeletons are known (e.g., Berman, Reisz, & Eberth,

468   1987), but it then becomes important to assess whether a terrestrial or aquatic lifestyle is the

469   plesiomorphic state among seymouriamorphs. Given that seymouriamorphs, and reptiliomorphs

470   more broadly, are frequently used as exemplars for the skeletal changes associated with

471   terrestrial adaptation, clarifying the primitive condition of this group is critical for informing

472   accurate comparisons. A conceptual phylogeny is presented in Figure 14 which illustrates the

473   distribution of terrestriality among seymouriamorphs.

474   Our data provide strong evidence at the histological and the microanatomical scales to

475   support the longstanding hypothesis of terrestriality in *Seymouria*. This is not a particularly

476   controversial idea; numerous aspects of the external morphology, such as the well-ossified limbs

477   and the massively expanded vertebrae have long been cited as evidence for this ecology (Romer,

478   1956). Although Berman and Martens (1993) described a possible indication of a lateral line

479   system in juvenile specimens of *S. sanjuanensis* from Germany, subsequent work (Klembara et

480   al. 2006) on an early juvenile did not find any evidence for a lateral line system in other *S.*

481   *sanjuanensis* from the same locality. As such, while it is often inferred that *Seymouria* underwent

482   metamorphosis as with other seymouriamorphs and a number of other terrestrial tetrapods (e.g.,

483   some temnospondyls), definitive aquatic larval forms and morphological transitions associated

484   with the presumed metamorphosis are unknown.

485   At least one other seymouriamorph, *Karpinskiosaurus*, is also represented only by

486   specimens that lack lateral line grooves (Klembara, 2011). *Kotlassia* has also been historically

487   regarded as lacking lateral line grooves (e.g., Bystrow, 1944), but the *Kotlassia* of most previous

488   authors is actually a combination of material referable to the type species, *Kotlassia prima*, and

489   material properly referable to *Karpinskiosaurus* (see Bulanov, 2002 and Klembara, 2011, for

490   discussion). Whether these grooves are definitively absent in the holotype of *Ko. prima* is not

491   apparent from previous works that accounted for this historical discrepancy. For

492   *Karpinskiosaurus* and *Seymouria*, it has been proposed that these taxa underwent metamorphosis

493   relatively early in their development and lived on land for the majority of their lives (Klembara,

494   2011).

495   In contrast, most other seymouriamorphs are known from individuals with lateral line

496   grooves, including *Ariekanerpeton* (Klembara & Ruta, 2005), *Discosauriscus* (Klembara, 1996),

497   *Spinarerpeton* (Klembara, 2009), and *Utegenia* (Malakhov, 2000). The most recent phylogenetic

498   analysis that focused on seymouriamorph phylogeny is that of Klembara (2011), which followed

499   a series of anatomical work that re-described virtually all known seymouriamorphs. Mapping the

500   distribution of ecologies onto this topology suggests that seymouriamorphs are primitively

501   aquatic (*Utegenia* being the earliest diverging taxon) and with two separate shifts to terrestriality,

502   one in *Karpinskiosaurus* and one in *Seymouria* (Fig. 14). However, caution must be exercised in

503   inferring the phylogeny of a clade in which metamorphosis is known to occur because biases in

504   the record of premetamorphic larval forms versus that of postmetamorphic terrestrial adults can

505   produce misleading data. As with *Seymouria* (Berman et al., 2000), it has been proposed that

506   *Discosauriscus* transitioned from an aquatic to terrestrial lifestyle throughout its ontogeny, but

507   even the largest known specimens of *Discosauriscus* are believed to be juveniles, and none have

508   been recovered from the terrestrial environments that the adult individuals may have inhabited

509   (Klembara, Martens & Bartik, 2001). This may relate to a relatively protracted larval stage

510   recovered by the histological work of Sanchez et al. (2008) in which metamorphosis may not

511   have begun until year six of an individual's life. The latest phylogenetic analyses (Klembara,

512   2011) do not bear out the slippage that is predicted when coding taxa based on immature

513   specimens (i.e. *Discosauriscus* is a highly nested seymouriamorph), but this does not negate the

514   potential for this disparity to affect the phylogeny. *Ariekanerpeton*, *Spinarerpeton*, and *Utegenia*

515   are also likely represented only by juveniles (Klembara & Ruta, 2003, 2005; Klembara, 2009),

516   which warrants consideration.

517   Histology offers one avenue for exploring the diversity of life histories within a clade

518   through well-documented taxa (e.g., *Discosauriscus, Seymouria*) and for improving hypotheses

519   and predictions regarding those of more poorly represented taxa with limited ontogenetic data.

520   Our histological data substantiate the hypothesis that *Seymouria* was a rapidly metamorphosing

521   taxon that spent most of its life on land (Klembara, 2011), which may explain why it is

522   predominantly found in fluvial deposits of south-southwestern North America and the upland

523   Bromacker locality along with other highly terrestrial tetrapods whereas the slower growing

524   *Discosauriscus* is restricted to lacustrine environments of Europe. Additionally, the Richards

525   Spur locality preserves almost exclusively terrestrial taxa (MacDougall et al., 2017), and thus it

526   is reasonable to infer that all known *Seymouria* material belonged to postmetamorphic

527   individuals. The absence of larval forms of *Seymouria* may be explained by a short larval stage

528   and the probable spatial separation of larvae from the fluvial environments that preserved the

529   adults (niche partitioning between life stages).

530   In the sense that terrestriality in adults of *Seymouria* has not been widely questioned, our

531   most novel data, the histological data, are not necessarily surprising. However, this should not

532   diminish the value of these data; testing hypotheses using multiple approaches is important for

533   assessing the rigor of such hypotheses. The existing histological framework and understanding of

534   seymouriamorph development remains largely confined in traditional interpretations of relative

535   maturity based on external features and their development, and there is an extensive precedent

536   for the utility of histology (among other more recently accessible methods) to further explore

537   paleobiological attributes of extinct taxa. Our interpretations of the data are somewhat limited, in

538   part by sample size, but also in part by the absence of a substantive body of comparative data. It

539   is unclear, for example, what to make of the persistence of a modestly developed medullary

540   spongiosa in the femur of *Seymouria*, either compared to *Discosauriscus* or to other more

541   distantly related terrestrial tetrapods. Our ontogenetic trends are more accurately stated as two

542 partial points within the developmental trajectory, and the opportunity remains to explore

543 ontogeny further within *Seymouria* across all regions of the skeleton.

544

Institutional Abbreviations

546 **OMNH**   Sam Noble Oklahoma Museum of Natural History, Norman, OK, USA

547 **ROMVP**   Royal Ontario Museum, Toronto, ON, Canada

548

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553

554 *Note to reviewers/editor: embargoed data during review can be viewed on MorphoBank using a*

555 *special log-in: username "3549" and password "ROMVP80915".*

556

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Figure 1

Posterior presacral vertebrae of *Seymouria*.

A, OMNH 79346; **B,** OMNH 79349; **C,** OMNH 79350; **D,** OMNH 79353; **E,** ROMVP 81198; and **F,** ROMVP 81199 in anterior, posterior, dorsal, ventral, and left lateral views. Scale bar equals 1 cm.
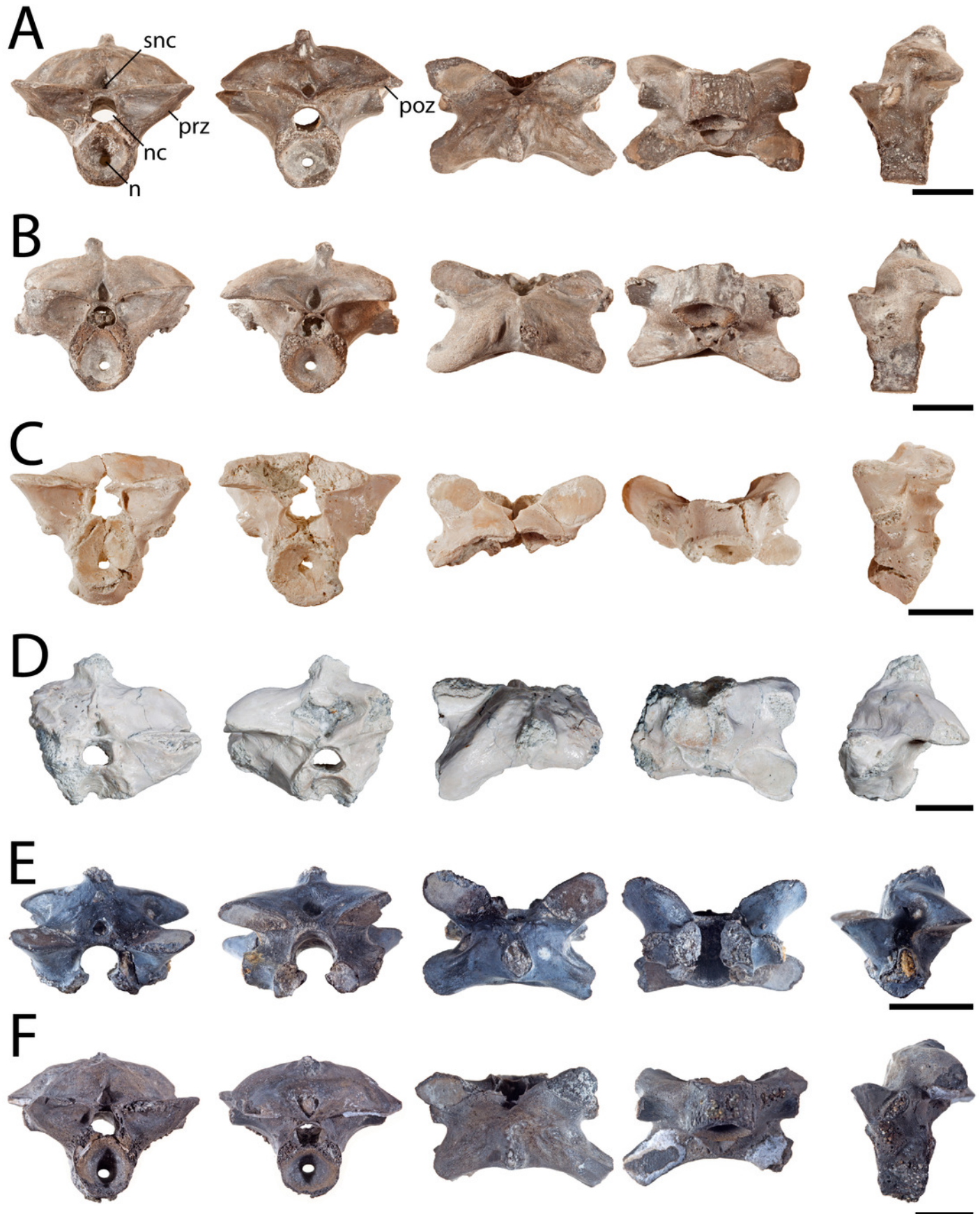
Figure 2

Anterior presacral vertebrae of *Seymouria*.

A, OMNH 79351 and **B,** OMNH 79352 in anterior, posterior, dorsal, ventral, and left lateral views. Scale bar equals 1 cm.
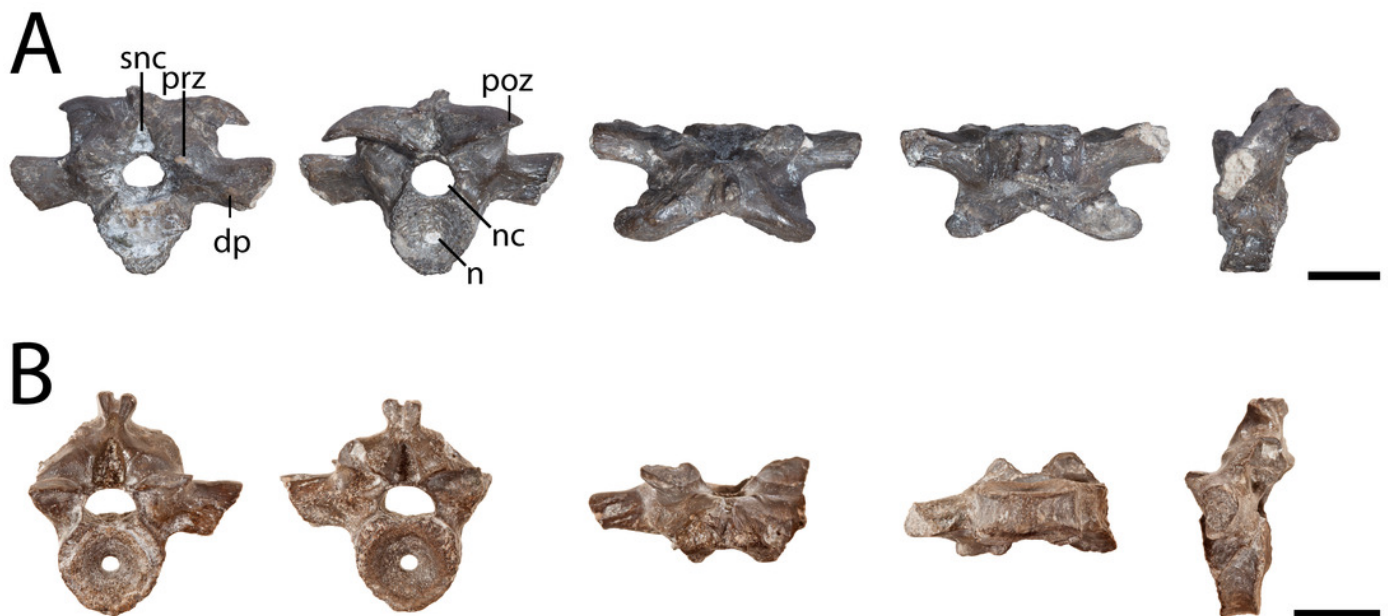
Figure 3

Articulated vertebrae of *Seymouria*.

A, OMNH 79347 in dorsal view; **B,** OMNH 79348 in dorsal view; **C,** the same in ventral view;

D, the same in left lateral view; **E,** the same in right lateral view. Scale bar equals 1 cm.
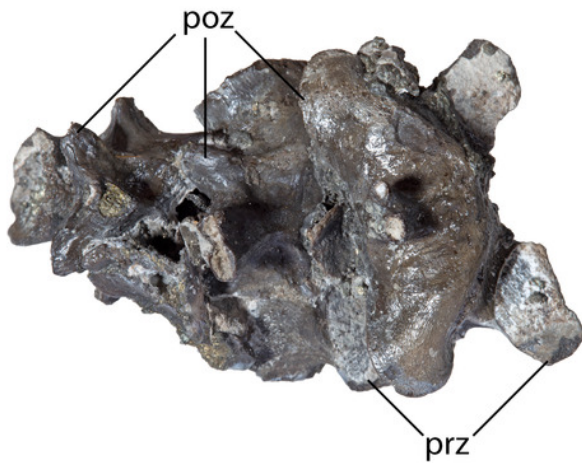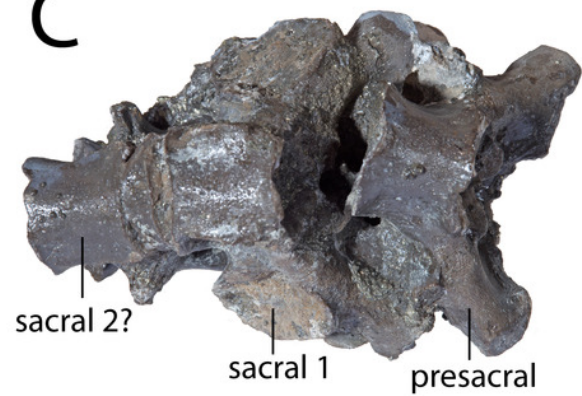
Figure 4

Histological sections of a presacral vertebra (ROMVP 81199) of *Seymouria.*

A, Full sagittal section; **B,** close-up under cross-polarized light of the ventral border of the neural arch showing remodelling; **C,** close-up under cross-polarized light of the thickened posterior surface; **D,** half transverse section; **E,** close-up under cross-polarized light of the dorsal surface; **F,** close-up under cross-polarized light of the cartilaginous separation between the neural arch and the centrum. Scale bars equal to 1 mm (A, D); 250 µm (B-C, E-F).
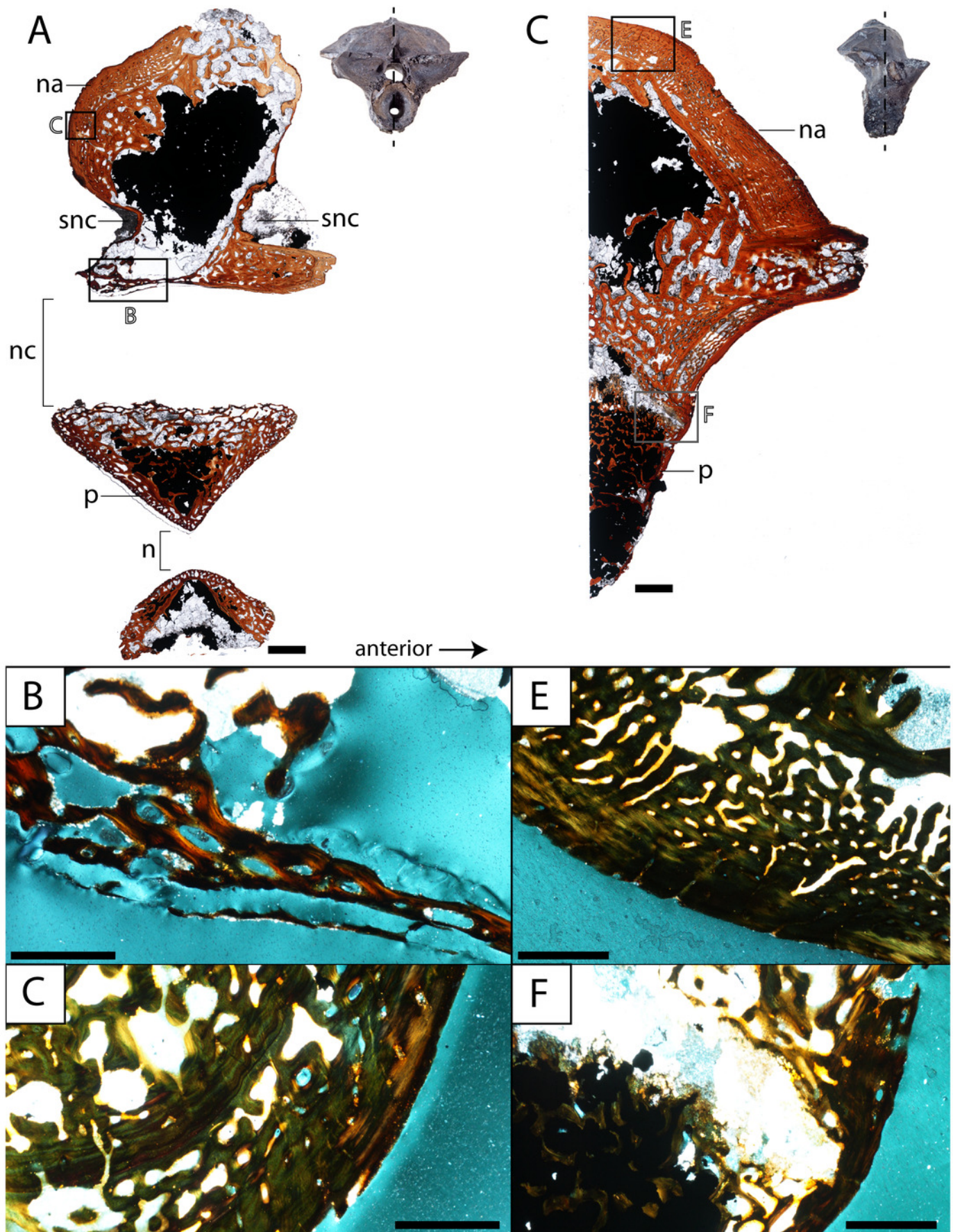
Figure 5

Histological sections of a presacral vertebra (ROMVP 81198) of *Seymouria*.

A, Full sagittal section; **B,** close-up under cross-polarized light of the ventral border of the neural arch showing remodelling; **C,** close-up under cross-polarized light of the thickened posterior surface; **D,** half transverse section; **E,** close-up under cross-polarized light of the dorsal surface; **F,** close-up under cross-polarized light of the geometric center of the neural arch. Scale bars equal to 1 mm (A, D); 250 µm (B-C, E-F).
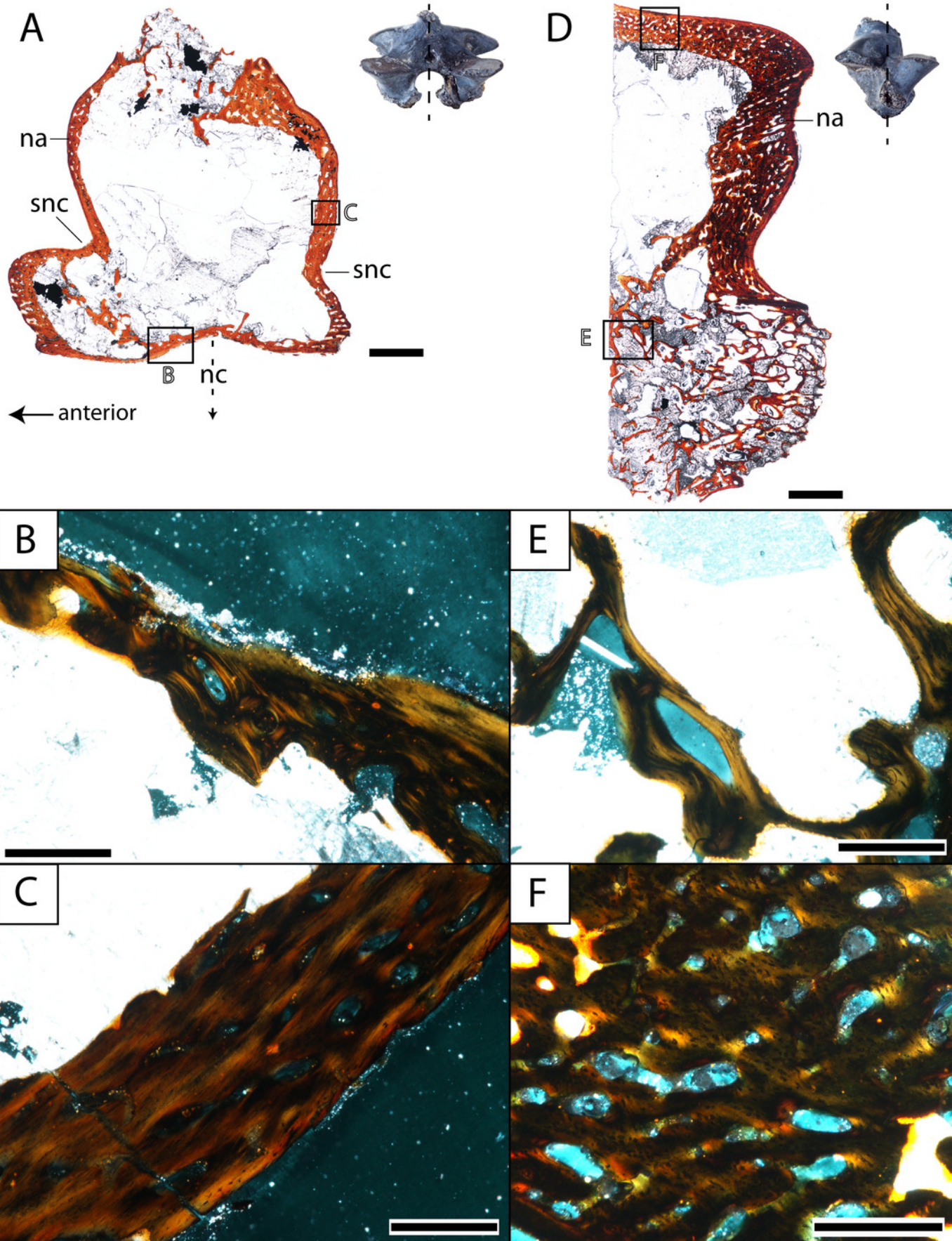
Figure 6

Isolated profiles of OMNH 79348.

A, D, G, digital renderings indicating location of digital sections; **B-C,** sagittal sections of presacral vertebra at mid-centrum (B) and mid-diapophysis (C); **E-F,** sagittal sections of sacral vertebra at mid-centrum (E) and mid-diapophysis (F); **H-G,** sagittal sections of caudal vertebra at mid-centrum (H) and mid-diapophysis (I). Scale bar equals 1 cm.
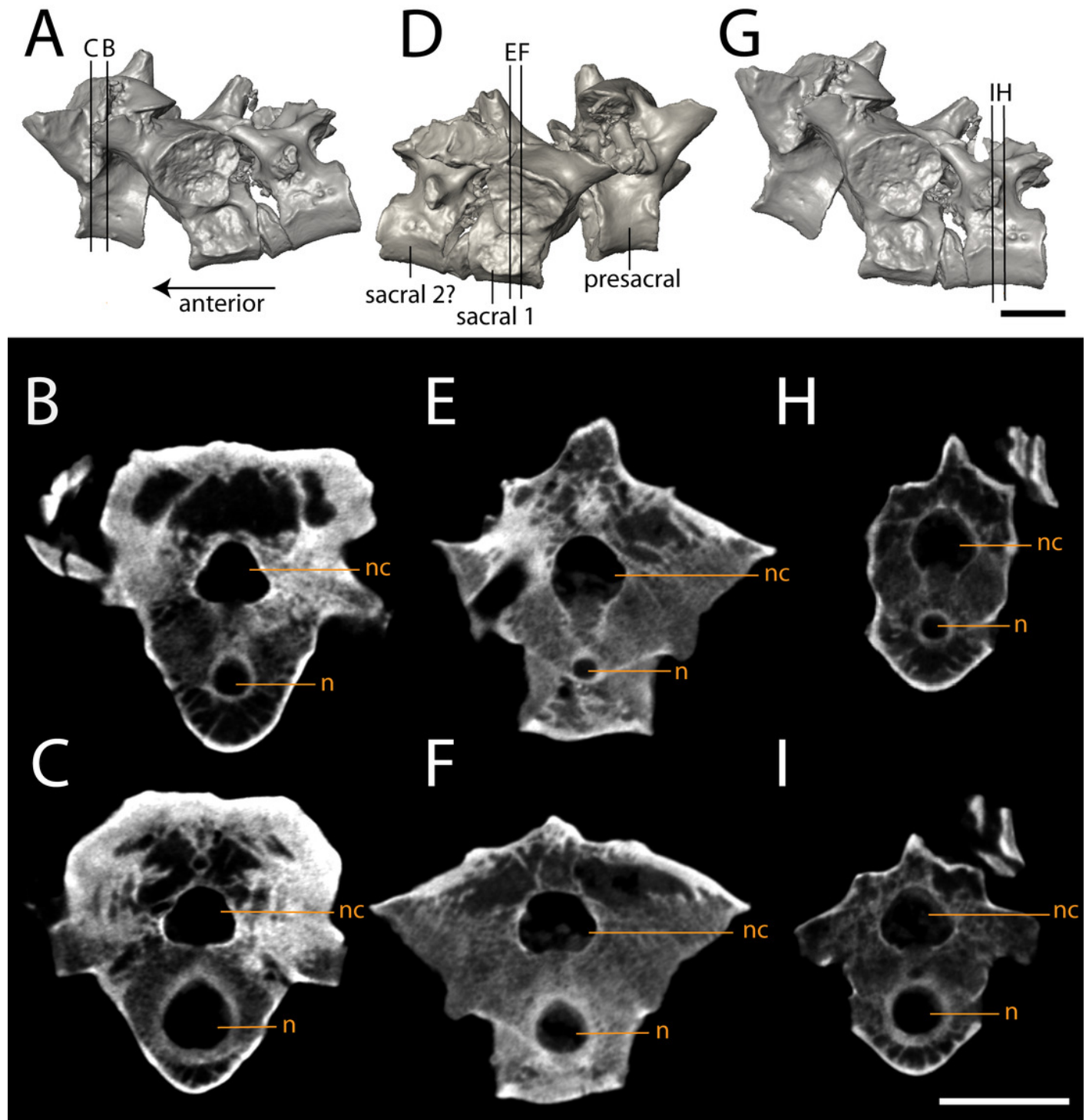
Figure 7

OMNH 74721.

A, anterior view, **B,** posterior view, **C,** dorsal view, **D,** ventralview, **E,** proximal view, and **F,** distal view. Scale bar equals 1 cm.
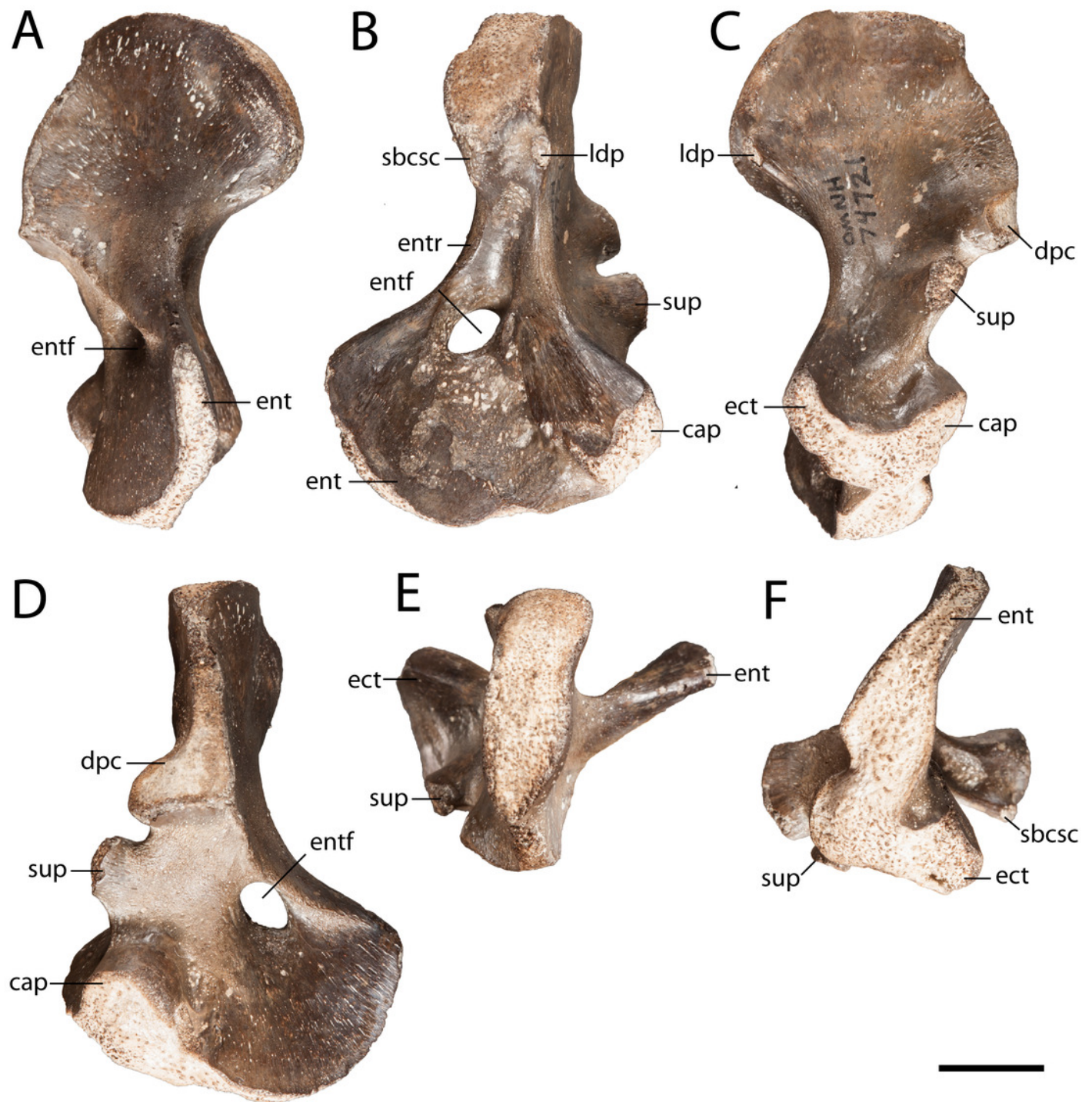
Figure 8

Hindlimb elements of *Seymouria*.

A, photograph of ROMVP 80915 and ROMVP 80917 in posterior view; **B,** the same in ventral view; **C,** digital rendering of ROMVP 80916 in posterior view; **D,** the same in anterior view; **E,** the same in dorsal view; **F,** the same in ventral view; **G,** the same in proximal view; **H,** the same in distal view. Scale bar equals 1 cm.
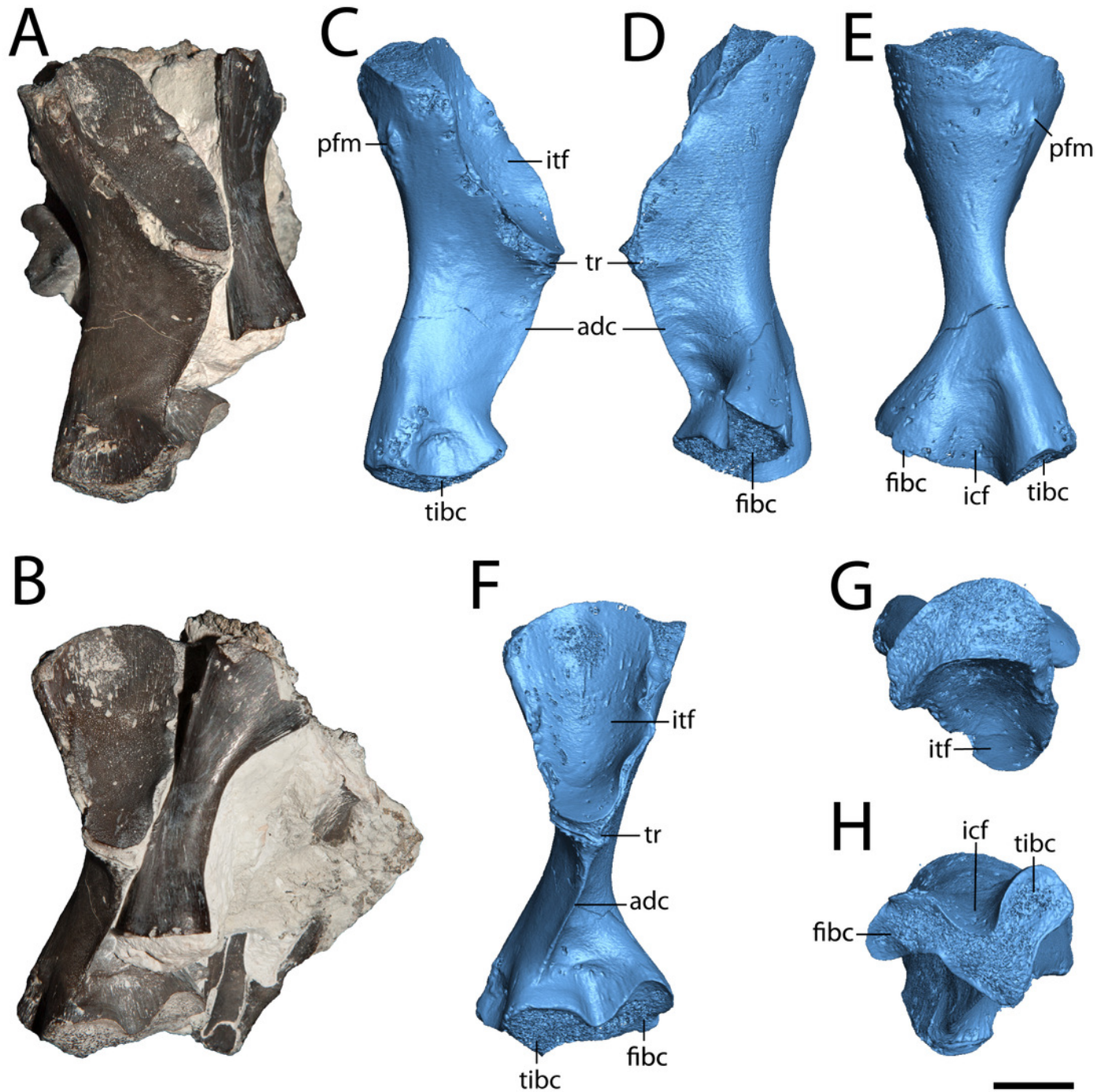
Figure 9

Partial femora of *Seymouria*.

A-F, ROMVP 80916 and **G-L,** ROMVP 81200 in anterior, posterior, dorsal, ventral, proximal, and distal views. Scale bar equals 1 cm.

Figure 10

Histological section of a partial femur (ROMVP 80916) of *Seymouria*.

A, full cross-section near the minimum diaphyseal circumference; **B,** close-up of the cortical bone showing five lines of arrested growth (LAGs); **C,** close-up under cross-polarized light of the remodelled bone interface between the cortical bone and the medullary cavity. Note that part C is from a different thin section than in part A and thus an inset magnification box is not marked. Scale bars equal to 1 mm (A); 250 µm (B-C).
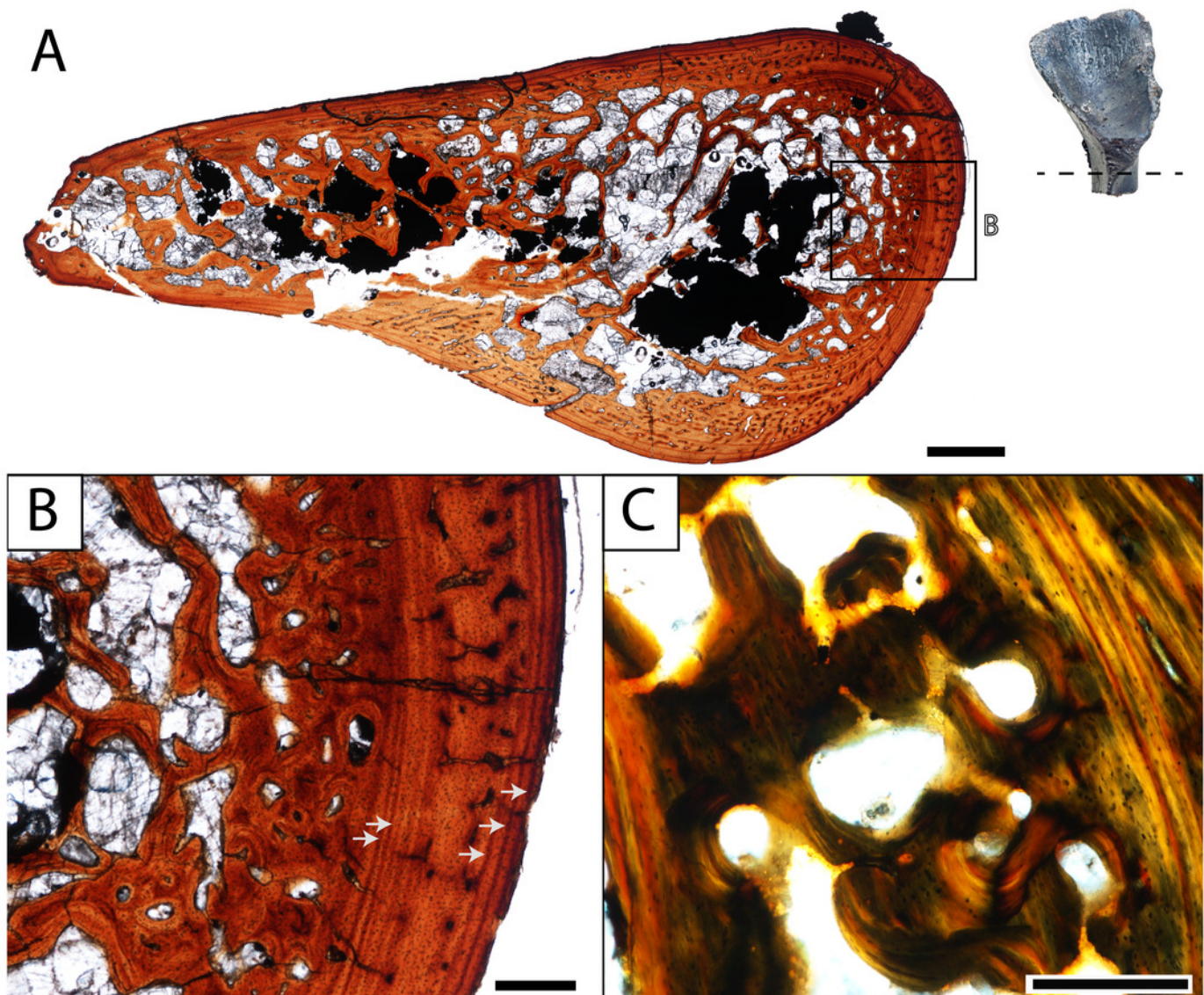
Figure 11

Histological section of a partial femur (ROMVP 81200) of *Seymouria*.

A, full cross-section near the minimum diaphyseal circumference; **B,** close-up of the cortical bone showing four lines of arrested growth (LAGs) marked by black arrows; **C,** close-up under cross-polarized light of the remodelled bone interface between the cortical bone and the medullary cavity. Scale bars equal to 1 mm (A); 250 μm (B-C).
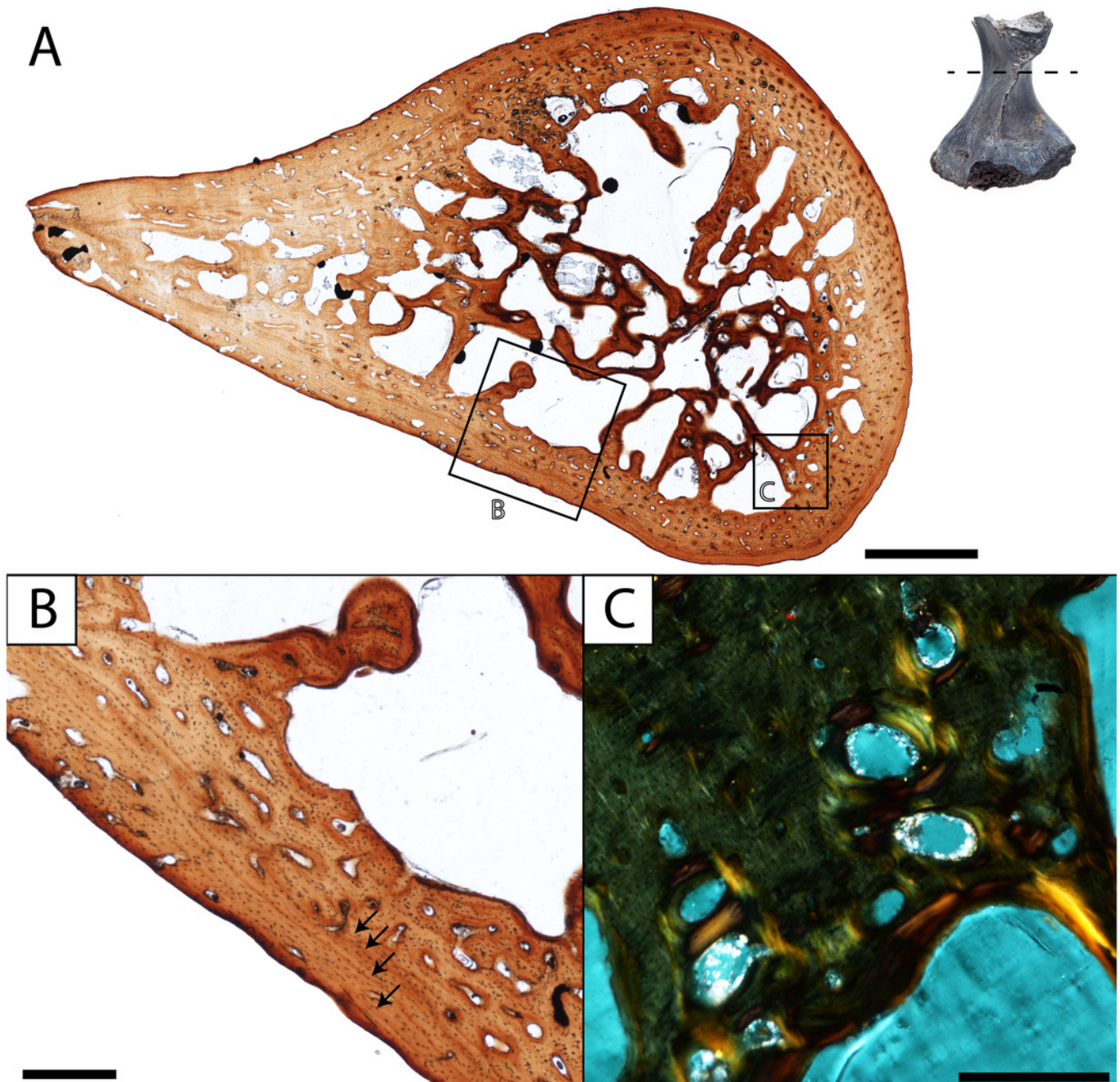
Figure 12

Digital section of a femur (ROMVP 80915) of *Seymouria*.

A, digital rendering showing location of section; **B,** transverse digital section. Scale bar equals 5 mm.

A
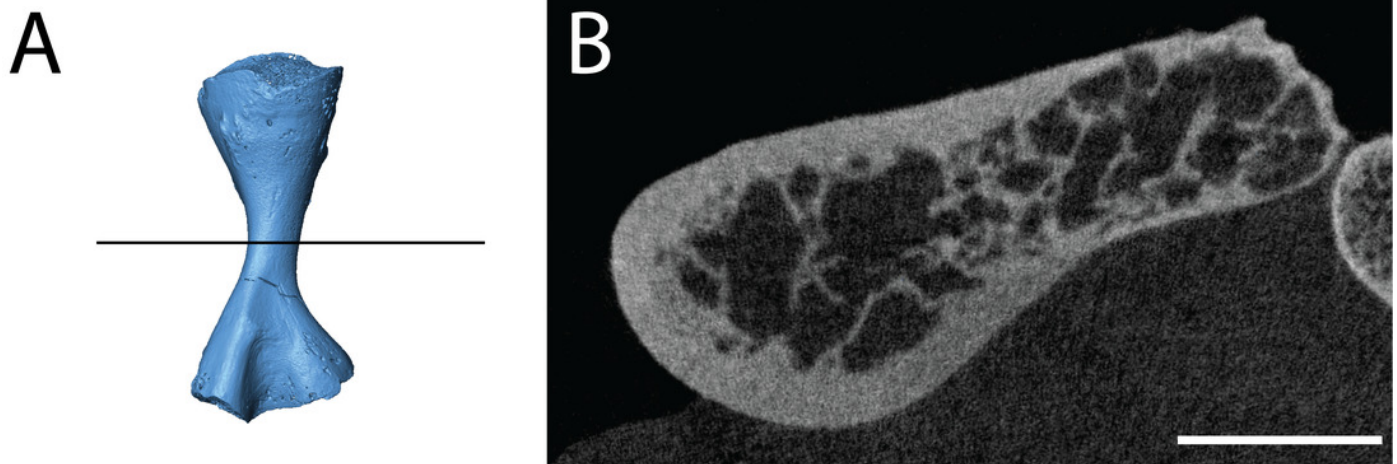
Figure 13

Digital renderings of ROMVP 80917.

A, anterior; **B,** posterior; **C,** medial; **D,** lateral; **E,** proximal; **F,** distal views. Scale bar equals 1 cm.
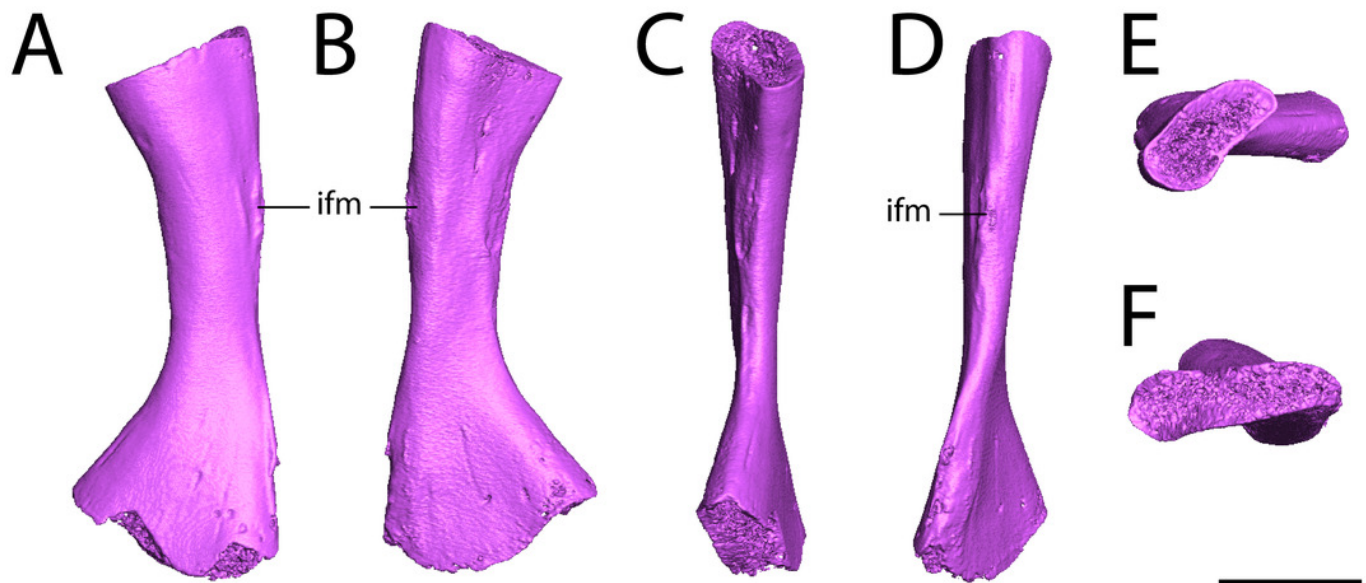
Figure 14

Conceptual phylogeny adapted from Klembara (2011), illustrating the distribution of aquatic and terrestrial taxa among seymouriamorphs.

Blue boxes represent taxa interpreted as being aquatic. Green boxes represent taxa interpreted as terrestrial. Grey boxes represent taxa for which no interpretation has been made. Boxes in pale blue or green containing question marks indicate taxa for which there have been some suggestions regarding the possible ecology of a given ontogenetic stage, but for which there are no known specimens that definitively verify the suggested interpretations.