The cranial endocast of *Dipnorhynchus sussmilchi* (Sarcopterygii: Dipnoi) and the interrelationships of stem-group lungfishes

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The first virtual cranial endocast of a lungfish from the Early Devonian, *Dipnorhynchus sussmilchi*, is described. *Dipnorhynchus,* only the fourth Devonian lungfish for which a near complete cranial endocast is known, represents a key taxon to help clarify primitive character states. A ventrally-expanded telencephalic cavity is present in the endocast of *Dipnorhynchus* demonstrating that this is the primitive state for the Dipnoi. *Dipnorhynchus* also possesses a utricular recess differentiated from the sacculolagenar pouch like that seen in stratigraphically younger lungfish (*Dipterus, Chirodipterus, Rhinodipterus*). We do not find separate pineal and para-pineal canals in contrast to a reconstruction from previous authors. We conduct the first phylogenetic analysis of Dipnoi based purely on endocast characters, which supports a basal placement of *Dipnorhynchus* within the dipnoan stem group, in agreement with recent analyses. Our analysis demonstrates the value of endocast characters for inferring phylogenetic relationships.

1   **The cranial endocast of *Dipnorhynchus sussmilchi***

2   **(Sarcopterygii: Dipnoi) and the interrelationships of stem-**

3   **group lungfishes**

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20   **ABSTRACT**

21   The first virtual cranial endocast of a lungfish from the Early Devonian, *Dipnorhynchus*

22   *sussmilchi*, is described. *Dipnorhynchus,* only the fourth Devonian lungfish for which a near

23   complete cranial endocast is known, represents a key taxon to help clarify primitive character

24   states. A ventrally-expanded telencephalic cavity is present in the endocast of *Dipnorhynchus*

25   demonstrating that this is the primitive state for the Dipnoi. *Dipnorhynchus* also possesses a

26   utricular recess differentiated from the sacculolagenar pouch like that seen in stratigraphically

27   younger lungfish (*Dipterus, Chirodipterus, Rhinodipterus*). We do not find separate pineal and

28   para-pineal canals in contrast to a reconstruction from previous authors. We conduct the first

29   phylogenetic analysis of Dipnoi based purely on endocast characters, which supports a basal

30   placement of *Dipnorhynchus* within the dipnoan stem group, in agreement with recent analyses.

31 Our analysis demonstrates the value of endocast characters for inferring phylogenetic

32 relationships.

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35 **INTRODUCTION**

36 Lungfish, or dipnoans as they are also known, have origins dating back over 400 million years.

37 Today there are just six extant species, but it was during the Devonian Period that they reached

38 the peak of their success and diversity (Clack et al. 2011). 'Total-group' lungfishes are a well-

39 supported monophyletic group, but early dipnoan phylogeny has long been contentious and

40 remains unresolved (Johanson & Ahlberg 2011). The split between the extant lungfish families is

41 thought to have occurred in the Permian (Heinicke et al. 2009). In general terms this means that

42 'crown-group' lungfishes contains all the living representatives and their last common ancestor

43 (of plausible Permian age), and all of the (both fossil and living) descendants of that ancestor.

44 Thus, 'stem-group' lungfish is equivalent to the total group minus the crown group, and contains

45 all of the Devonian lungfishes. The most basal member known and sister group to all other

46 lungfishes is *Diabolepis* from the Lower Devonian of China (Chang 1995; Chang & Yu 1984),

47 although some authors disagree with this interpretation (Campbell & Barwick 2001). The group

48 is thought to have radiated quickly (Lloyd et al. 2011), and early Devonian lungfishes are known

49 from deposits across China, Russia, Europe, North America and Australia. The Australian fauna

50 from this time is dominated by the robust, short-headed 'dipnorhynchid' taxa, typified by

51 *Dipnorhynchus* itself (Etheridge 1906).

52

53 Material of the Early Devonian genus *Dipnorhynchus* was first described over a century ago, and

54 although the name '*Ganorhynchus*' was originally used, '*Dipnorhynchus*' was erected two

55 decades later for *D. sussmilchi* (Jaekel 1927). *Dipnorhynchus sussmilchi* (Campbell & Barwick

56 1982a) is known from the Taemas – Wee Jasper limestones that occur around Burrinjuck Dam in

57 New South Wales, Australia (see Figure 1), and have been dated as Emsian in age (Thomson &

58 Campbell 1971). Other dipnoan taxa described from the same site include *Dipnorhynchus*

59 *kurikae* (Campbell & Barwick 2000), *Speonesydrion iani* (Campbell & Barwick 1983), and

60 *Cathlorhynchus trismodipterus* (Campbell et al. 2009). Furthermore, there is an additional

61   *Dipnorhynchus* species known from a locality about 200 km south of the Taemas – Wee Jasper

62   limestones, *D. kiandrensis* (Campbell & Barwick 1982b).

63

64   The skull roof and associated cranial material of *D. sussmilchi* was first described in some detail

65   (Hills 1941), and then later elaborated upon (Campbell 1965; Thomson & Campbell 1971).

66   However a thorough investigation of braincase material for the genus did not come until later

67   when Campbell and Barwick (1982a) described the neurocranium and reconstructed the

68   endocranial cavity of *D. sussmilchi*. Later, similar treatment for *D. kurikae* ensued (Campbell &

69   Barwick 2000). Further details regarding the neurocranium and space for the endolymphatic

70   ducts and labyrinth of *D. sussmilchi* shortly followed (Campbell et al. 2000).

71

72   With the increasing accessibility of modern, non-invasive scanning technology such as

73   synchrotron and micro-computed tomography (µCT), along with more sophisticated software

74   packages for data processing and visualization, the field of palaeoneurology seems to be

75   undergoing an upsurge (Walsh et al. 2013). Until relatively recently, researchers had to rely upon

76   fortuitous findings of damaged skulls, or resort to destructive techniques (Stensiö 1963) to

77   examine the internal anatomy of the braincase. These more traditional techniques have been

78   shown to be somewhat limited, especially with respect to fine morphological details (Giles et al.

79   2016). However, today we are quickly increasing the number of taxa for which virtual cranial

80   endocast morphology is known across all vertebrate groups (Balanoff et al. 2015; Falk 2012; Lu

81   et al. 2012), including fishes (Clément & Ahlberg 2010; Dupret et al. 2014; Giles & Friedman

82   2014; Giles et al. 2016; Maisey 2007).

83

84   *Chirodipterus wildungensis* from the Upper Devonian of Germany was the first cranial endocast

85   of a lungfish published (Säve-Söderbergh 1952), although this was drawn from a single damaged

86   specimen and provided only a relatively crude reconstruction. Other examples include a partial

87   endocast of the Late Devonian *Holodipterus* (Pridmore et al. 1994), as well as those of

88   *Dipnorhynchus* (Campbell & Barwick 1982a; Campbell & Barwick 2000). Although the first

89   virtual lungfish endocasts only came recently, they have greatly enriched our knowledge of the

90   field. Not only are these methods non-destructive, but they provide far more comprehensive

91   information about the cranial cavity, and far superior possibilities for visualization. These

92   include the Late Devonian *Rhinodipterus* from Australia (Clement & Ahlberg 2014) and

93   *Dipterus* from the Middle Devonian of Scotland (Challands 2015). Further to this, the brain and

94   endocast of the extant Australian lungfish, *Neoceratodus*, is also known from CT data (Clement

95   et al. 2015), and researchers are developing techniques for reconstructing brains in extinct

96   members (Clement et al. 2016). Not only are cranial endocasts rich sources of morphological

97   data in their own right, they can also give clues as to an animal's brain structure, sensory abilities

98   and inferred behavior.

99

100   We expand on this growing body of work by investigating the cranial endocast of

101   *Dipnorhynchus sussmilchi* from the Early Devonian of Australia as revealed from tomographic

102   data. Our work represents the oldest, and only the fourth lungfish taxon endocast investigated,

103   and is the currently the only example from the Early Devonian. The data from *Dipnorhynchus*

104   contributes to uncovering how the lungfish brain has evolved through time, and also provides

105   valuable data in resolving early dipnoan phylogeny.

106

107

108   **MATERIAL & METHODS**

109   The *Dipnorhynchus sussmilchi* Etheridge (1906) specimen (ANU 18815) is a well-preserved,

110   acid-prepared complete cranium from the Early Devonian (Emsian) Taemas-Wee

111   Jasper/Burrinjuck limestones of New South Wales, Australia (Fig. 1). The specimen is housed at

112   the Australian National University, Canberra, Australia, and was scanned at the High Resolution

113   X-ray Computed Tomography (μCT) facility of the same location (Sakellariou et al. 2004) with a

114   voxel resolution of 30.4 microns. The ANU μCT facility is based on cone beam geometry and

115   has a detector pixel width of 2048 pixels.

116

117   *VGStudio Max*, version 2.2 (Volume Graphics Inc., Germany) was used to achieve three-

118   dimensional segmentation and modeling of the cranial endocast through a combination of

119   manual segmentation and thresholding. The resulting endocast model was smoothed by a factor

120   of three prior to export.

121

122   We assembled our character matrix of 20 characters and 10 taxa in *Mesquite 3.01* (see

123   Supplementary Information for full details). Characters 1-13 were taken from previous analyses

124   (Friedman 2007; Giles et al. 2015), however 14-20 are new characters identified through the

125   course of this study. The parsimony analysis was conducted using the heuristic search algorithm

126   in *PAUP v4.0b10* (Swofford 2001) using stepwise addition, 10,000 random addition sequence

127   replicates holding five trees at each step, with tree bisection and reconnection (TBR) enabled,

128   and automatically increasing maxtrees by 100. The Late Devonian coelacanth *Diplocercides* was

129   designated as the outgroup. Bootstrap values were then calculated using 1000 random replicates

130   of the heuristic search in PAUP, again with TBR enabled for 10 replicates.

131

132

133   **DESCRIPTION**

134   The skull measures 24 mm across the quadrates at its widest point, and with a height of 20 mm

135   from the base of the quadrate to the top of the skull roof. The scan data extends from the tip of

136   the snout to the mid-point of the labyrinth region. The endocast itself (Figs 2-5) measures 13.5

137   mm across the widest points of the horizontal semicircular canals, and 26 mm from the anterior-

138   most point of the nasal capsules to the junction between the posterior and anterior semicircular

139   canals. Unfortunately the occipital region of the specimen is not included in the scan.

140   Proportionally the nasal capsules are the longest structures of the endocast being approximately

141   25% of the total endocast length. The metencephalic and telencephalic regions account for 10-

142   15% the endocast length, the diencephalic <10% and the mesencephalic cavity, at ~5% the total

143   endocast length, is the smallest component of the endocast.

144

145   *Nasal capsules*

146   The nasal capsules are large, oblong structures with a convex dorsal surface. The medial edges of

147   the nasal capsules are not parallel, instead they converge anteromedially at an angle of 45

148   degrees. Unlike Thomson and Campbell (1971) we do not recognise an anterior nasal opening

149   for a nostril present, but there is a canal exiting the capsules in their posterolateral corners. This

150   most likely housed the profundus nerve. We see no evidence of threefold sub-divisions as

151   reconstructed for this taxon by Thomson and Campbell (1971, Fig 29).

152

153 ***Forebrain***

154 *Telencephalic region*

155 The canals for the olfactory nerves (n.I) are expanded at their anterior extent where they join the

156 nasal capsules, and a canal likely for either the median or lateral nasal vein, exits in a posterior

157 direction just behind the nasal capsules. The olfactory tracts are broad and diverge from each

158 other at 45°, and they are proportionally shorter in *Dipnorhynchys* than in *Dipterus* or

159 *Rhinodipterus* (Challands 2015; Clement & Ahlberg 2014). At their junction there are two small

160 rounded expansions visible in each tract that probably housed the olfactory bulbs (Fig. 5). The

161 telencephalic region is mostly flat dorsally, reminiscent of the condition seen in *Youngolepis*

162 (Chang 1982), however there is a strong rise towards the pineal canal posteriorly on the dorsal

163 margin. There is a small yet distinct expansion of the telencephalic ventral edge, mostly obscured

164 behind the large canals for the optic nerves. However, there is no evidence of a distinctive lateral

165 telencephalic expansion like that originally reconstructed in *Dipnorhynchus* (Campbell &

166 Barwick 1982a), nor those seen in *Chirodipterus wildungensis* (Säve-Söderbergh 1952),

167 *Rhinodipterus kimberleyensis* (Clement & Ahlberg 2014), nor extant lungfishes (Clement et al.

168 2015; Northcutt 2011).

169

170 *Diencephalic region*

171 The diencephalic cavity is slightly narrower than the telencephalic region and also about one-

172 third shorter. Two wide, cylindrical anterolaterally-directed canals for the optic nerves (n.II) exit

173 the endocast in a ventral position at the anterior boundary of the diencephalic region. *D.*

174 *sussmilchi* carries a posteroventrally long hypophyseal recess with a number of smaller, well-

175 defined canals entering it. The hypophyseal recesses of *Rhinodipterus* and *Dipterus* do not

176 extend as far ventrally (Challands 2015; Clement & Ahlberg 2014), however these structures in

177 *Youngolepis* (Chang 1982) and *Eusthenopteron* (Stensiö 1963) are of similar proportions to

178 *Dipnorhynchus*. The hypophyseal cavity reconstructed from our scan data differs in a number of

179 aspects from that of Campbell and Barwick (1982, fig 25). As our reconstruction is based

180 directly on a scan of the cavity, whereas Campbell and Barwick's reconstruction was based on

181 inferences from partly visible structures, we believe the differences reflect the limitations of the

182 latter technique. Dorsal to the hypophysis lies a short, rounded hypothalamus oriented posteriorly

183 underneath the cranial cavity (Fig. 2). There are a number of paired canals exiting the

184 hypophysis; the most anterior of these extend far anterior, as far as the optic nerve canals before

185 extending outwards laterally and likely housed the palatine arteries. The posteriorly-directed

186 canals diverge outwards towards the trigeminal nerves and probably contained the internal

187 carotid arteries. It is interesting to note that the canal for the internal carotid does not appear to

188 bifurcate for a branch for the pseudobranchial artery like seen in *Dipterus* (Fig. 10b, Challands,

189 2015) and other stratigraphically younger lungfish. Slightly dorsal to this canal are two small

190 canals interpreted as housing the pituitary veins. Slightly anterior to these canals are two further

191 canals directed in an anterolateral direction that probably housed the ophthalmic arteries. Along

192 the dorsal edge of the diencephalic region lies a broad eminence from which the pineal canal

193 leads upwards towards the circular pineal gland in the skull roof. The pineal gland is situated

194 further anterior than that originally drawn for *Dipnorhynchus* (Campbell & Barwick 1982a). We

195 find no obvious evidence of a parapineal gland (*contra* Campbell and Barwick 1982a), however

196 there are a number of miniscule canals leaving from along the midline towards the skull roof

197 dorsally in this area.

198

199 ***Midbrain***

200 *Mesencephalon*

201 The mesencephalic cavity is the shortest region of the endocast and is as narrow as the

202 diencephalic cavity. On the lateral face of the endocast are two small paired canals exiting in

203 anterolateral directions (Fig. 2); the ventrally lower one would have housed the oculomotor nerve

204 (n.III), and the dorsally higher one the trochlear nerve (n.IV). The ventral and dorsal edges of the

205 mesencephalic cavity are fairly flat, about twice as high as the telencephalic region.

206

207 ***Hindbrain***

208 *Metencephalic and Myelencephalic cavities*

209 The metencephalic region extends from the bifurcating canals for the trigeminal nerves (n.V) to

210 a poorly defined region posterior to the canals for the auditory nerves (n.VIII), although a

211 distinct boundary can-not be determined. The canal for the ophthalmic nerve (n.V_1) extends

212 anterolaterally, while the combined canal for maxillary and mandibular nerves (n.$V_{2\&3}$) is

213 broader and extends in a posterolateral direction. Slightly posterodorsal to this, the canal for the

214 facial nerve (n. VII) extends laterally. There is a further canal anterior to and slightly ventral to

215   the utricular recess that could have housed the abducens (n. VI) nerve (Fig. 4). Unlike Campbell

216   and Barwick, we have not been able to identify the canals for the auditory (n. VIII) nerves from

217   the data (Fig. 2). The anterior portion of the metencephalic region is of similar width to the

218   preceding mesencephalon, thought it widens laterally slightly towards its posterior extent. The

219   ventral margin is straight but the dorsal surface is gently curved to form a convex margin

220   forming the deepest brain region. There are no prominent supraotic cavities like those seen in

221   *Rhinodipterus* present (Clement & Ahlberg 2014). Very little can be said concerning the

222   myelencephalic region as most of this is missing from the scan, however it appears to have a

223   slightly lower dorsal margin than the metencephalic region but is of similar width.

224

225   ***Labyrinth region***

226   Although the labyrinth region is incomplete, we can still observe a number of salient features.

227   The anterior semicircular canals stand much higher than the dorsal extent of the hindbrain and

228   *Dipnorhynchus* presumably possessed a relatively tall superior sinus. There is a large ampulla on

229   the anterior semicircular canal, and although its full extent can not be determined, the

230   sacculagenar pouch appears to have been large. The utricular recess is only moderately

231   expanded. This is in contrast with more derived lungfishes such as *Rhinodipterus* (Clement &

232   Ahlberg 2014), *Chirodipterus* (Säve-Söderbergh 1952), and *Dipterus* (Challands 2015), although

233   we note it is more expanded than the reconstruction by Campbell and Barwick (1982a, fig. 25).

234

235

236   **PHYLOGENETIC ANALYSIS**

237   The phylogenetic analysis implemented herein focuses solely on characters identifiable from

238   cranial endocasts, and is far from comprehensive. The approach of Friedman (2007) in using the

239   whole neurocranial complex can include a greater wealth of data than our analysis. However

240   great care must be taken so as not to score the same character twice, once described from the

241   neurocranium and once as an endocast feature. Indeed, the results of the phylogenetic analysis

242   are preliminary, but it is our hope that with increasingly accessible scanning technology and a

243   greater number of specimens examined that our character matrix will demonstrate the efficacy of

244   endocast characters in their own right and serve as a framework for future analyses and new data,

245 and allow workers to infer phylogeny from endocasts in cases where associated neurocranial data

246 is not adequately provided.

247

248 The comparative endocast data used in our analysis was taken from the literature (Challands

249 2015; Chang 1982; Clement & Ahlberg 2014; Clement et al. 2015; Holland 2014; Lu et al. 2016;

250 Säve-Söderbergh 1952; Stensiö 1963). Although only small, the results of our analysis (Fig. 6)

251 focusing on cranial endocast characters mostly reflect the hypotheses of relationships seen in

252 other recent phylogenetic analyses of lungfishes and other Devonian sarcopterygians (Challands

253 2015; Clement 2012; Lu et al. 2016; Qiao & Zhu 2009).

254

255 The maximum parsimony analysis produced a strict consensus tree with a score of 34 steps, and

256 a consistency index (CI) and retention index (RI) of 0.68, homoplasy index (HI) of 0.32, and a

257 rescaled consistency index (RCI) of 0.46. *Qingmenodus* is the most basal taxon above the

258 outgroup *Diplocercides*. The tetrapodomorphs *Gogonasus* and *Eusthenopteron* form a clade as

259 sister group to the lungfish total group (Dipnomorpha). *Youngolepis* is the most basal taxon in

260 the Dipnomorpha, with *Dipnorhynchus* the most basal of the Dipnoi. *Dipterus, Chirodipterus*

261 and *Rhinodipterus* are more derived occupying successive branches, with *Neoceratodus*

262 comprising a crownward position (Fig. 6).

263

264

265 **DISCUSSION**

266 **a) The *Dipnorhynchus sussmilchi* endocast**

267 The first reconstruction of the cranial endocast of *Dipnorhynchus* was drawn directly from

268 broken specimens and inferring internal morphology without the aid of scanning technology

269 (Campbell & Barwick 1982a), similar to the method used for *Chirodipterus wildungensis* (Säve-

270 Söderbergh 1952). In comparison with that reconstruction, we largely agree with most characters

271 including the placement of the cranial canals and general proportions of brain regions. However

272 the most striking point of difference is that there is no large recess for a separate para-pineal

273 canal visible in our scan data (*contra* Campbell & Barwick 1982, fig 25). There is a large,

274 obvious space for the pineal canal (Fig. 1b), but our specimen of *Dipnorhynchus sussmilchi*

275 appears to lack any separate para-pineal canal. Furthermore, the position of the pineal gland is

276   placed further anteriorly in our reconstruction compared to that of Campbell and Barwick (1982),

277   at the level of the optic nerve canals rather than at the level of n. IV; this is more in line with the

278   generalized gnathostome condition. There are, however, a number of minute canals exiting the

279   cranial cavity dorsally in this dorsal region of the forebrain that may have been related to the

280   pineal organ.

281

282   Another significant difference was the lack of any noticeable lateral expansion in the

283   telencephalic region in contrast to that shown by Campbell and Barwick (1982). Instead the

284   narrow forebrain appears similar to that of the Early Devonian dipnomorph, *Youngolepis* (Chang

285   1982, fig. 19) in this respect though the presence of a small ventral expansion in *Dipnorhynchus*

286   is more reminiscent of the condition seen in *Dipterus* (Challands 2015). Similarly, Campbell and

287   Barwick (1982) did not reconstruct an utricular recess outwardly differentiated from the

288   sacculolagenar pouch. However, we find a differentiated sacculolagenar – utricular recess from

289   our data. The condition is more similar to that reconstructed for *Dipnorhynchus kurikae* by the

290   same authors (Campbell & Barwick 2000, fig. 4).

291

292   New characters that can be identified in our scan data include the size and shape of the nasal

293   capsules, the position of the nasal vein (Fig. 1), as well as details concerning the canals exiting

294   the hypophysis. We were able to distinguish and trace the course of the canals for the palatine,

295   ophthalmic and internal carotid arteries, as well as the canal for the pituitary vein (Figs. 3, 4).

296

297   The results of the phylogenetic analysis do support the use of endocast characters in analyses,

298   either in isolation or in conjunction with other morphological characters. Although virtual

299   palaeoneurology is still its infancy, especially with respect to fishes, cranial endocasts show great

300   potential with which to support hypotheses of phylogeny.

301

302

303   **b) Comparison with other Dipnoi**

304   In Figure 6 the updated endocast of *Dipnorhynchus* is compared with that of other Devonian

305   lungfishes from which a complete cranial endocast is known, as well as the Early Devonian

306   dipnomorph, *Youngolepis,* two tetrapodomorph taxa (*Gogonasus* and *Eusthenopteron*) and

307   *Diplocercides* the coelacanth. In the forebrain, the slight ventral expansion of the telencephalic

308   region in *Dipnorhynchus sussmilchi* contrasts with the more pronounced expansion in the

309   stratigraphically younger *Chirodipterus wildungensis* and *Rhinodipterus kimberleyensis*. This

310   trend and its implications have already been discussed (Clement & Ahlberg 2014). It was

311   proposed that this trend of increasing size of the telencephalic region might correlate with an

312   increased reliance on olfaction in lungfishes over time. Two slight bulges at the base of the

313   olfactory nerves (see Fig. 4) suggest that the olfactory bulbs were sessile rather than pedunculate.

314   Relatedly, we believe that the identification of the olfactory bulbs in *Rhinodipterus* may have

315   been originally overlooked; a slight bulge in telencephalic region just posterior of the olfactory

316   canals could represent these (Clement and Ahlberg 2014, fig. 2) as is the condition interpreted in

317   *Dipterus* also (Challands 2015).

318

319   Posterior of the pineal recess in *Dipnorhynchus* and *Dipterus* (but apparently lacking in

320   *Chirodipterus*) lies a small bulge on the dorsal surface of the hindbrain region of the endocast.

321   Challands (2015, fig. 9) tentatively identified this as the space for the optic lobes in *Dipterus*.

322   Campbell and Barwick (1982) reconstructed a single dorsally oriented canal in this region, but

323   we again could not locate such a canal in the tomographic data. Unfortunately this region of the

324   skull was damaged in *Rhinodipterus* so its presence or absence cannot be accurately determined

325   for this taxon.

326

327   As previously discussed (Challands 2015; Clement & Ahlberg 2014), Devonian lungfishes show

328   a trend of increasing size of the utricular recess relative to the sacculolagena, and that of

329   *Dipnorhynchus* remains small and relatively undifferentiated in comparison to the later taxa. Not

330   surprisingly, it closely resembles that of *Dipnorhynchus kurikae* (Campbell and Barwick 2000,

331   fig. 5). Moreover, *Dipterus* and *Rhinodipterus* both possess a small notch demarcating the

332   lagenar and saccular portions of the labyrinth region, while this is absent in *Chirodipterus* and

333   extant lungfishes (Clement and Ahlberg 2014, fig. 4). All of the lungfish, as well as *Youngolepis*,

334   *Gogonasus* and *Eusthenopteron* possess a high superior sinus that extends dorsally above the

335   endocranial roof.

336

337 Overall the updated endocast of *Dipnorhynchus* closely resembles that of *Youngolepis* in

338 possessing a ventrally-extensive hypophyseal recess, and in lacking any telencephalic lateral

339 expansion. However the emergence of a differentiated utricular recess, ventral expansion of the

340 telencephalon (albeit only slight) and a combined anterodorsally-oriented para-pineal gland

341 resembles those of stratigraphically younger lungfish. These features lend support to the

342 primitive placement of *Dipnorhynchus* within the Dipnoi more basally than other lungfish for

343 which the endocranial anatomy is known.

344

345 **c) Evolutionary significance**

346 The cranial endocast of *Dipnorhynchus* exhibits conditions typical for primitive sarcopterygians.

347 A small utricular recess is shared with *Youngolepis, Eusthenopteron, Diplocercides* and

348 *Qingmenodus* implying that the expansion of the utricular recess is a derived dipnoan condition

349 (synapomorphy). On the other hand, *Dipnorhynchus* demonstrates retention of derived characters

350 first observed in the tetrapodomorphs *Eusthenopteron* and *Gogonasus* (Fig. 6) and early

351 actinopterygians (Giles et al. 2016): that is, a sinus superior that extends above the roof of the

352 rhombencephalon and clear segregation of the utricular recess from the sacculus.

353

354 Of further note is the proportion of the hindbrain, the rhombencephalon, relative to other

355 Devonian sarcopterygians. *Dipnorhynchus* and all subsequent dipnoans demonstrate a shortening

356 of the distance between the hypophyseal recess and rhombencephalon, a state more akin to basal

357 actinopterygians such as *Mimipiscis* (Giles & Friedman 2014). As such, this character appears to

358 be a synapomorphy for the Dipnoi, convergent with the condition in Actinopterygii (Giles et al.

359 2016), the shortening likely related to the loss of the intracranial joint. Lu et al. (2016) noted that

360 the rhombencephalon in Devonian sarcopterygians is generally well-developed to the anterior,

361 with the facial nerve (n.VII) being located well behind the trigeminal complex and anterior to the

362 labyrinth. They tentatively attributed this expansion to an increased demand for functional

363 sensitivity processed in this region of the brain (e.g. motor control in the pons and cerebellum),

364 which if correct, has reverted to the primitive actinopterygian condition in the first appearance of

365 the Dipnoi. Other morphological correlates with well-developed facial functional sensitivity are,

366 however, still present in the Dipnoi such as in *Dipterus* where Challands (2015) noted the

367 extensive innervation in the rostral region by the facial nerve (n.VII) as well as the lateral line by

368   the same nerve complex. Such patterns illustrate the complexities involved in simply attributing

369   endocast volume to increased functional processing for a certain region of the brain. Inferring

370   functional evolutionary trajectories from endocast volumes, especially where demarcation

371   between regions is to a certain extent subjective, is, at best, speculative unless the nervous and

372   functional systems are considered as a whole.

373

374

375   **CONCLUDING REMARKS**

376   Here we present the oldest lungfish cranial endocast known, that of *Dipnorhynchus sussmilchi*,

377   from the Early Devonian of Australia, as reconstructed from tomographic data. The virtual

378   endocast presented herein largely confirms the previous depiction of that by Campbell and

379   Barwick (1982a) however there exist a number of differences of note. These include the lack of a

380   separate para-pineal gland, and similarly the lack of any lateral expansion of the telencephalon.

381   However the presence of a small, but differentiated utricular recess, and new details of the canals

382   exiting the ventrally-extensive hypophysis are revealed.

383

384   As only the fourth Devonian lungfish endocast known, *Dipnorhynchus* represents a significant

385   contribution to the field of vertebrate palaeoneurology. However, to be able to draw more useful

386   conclusions concerning dipnoan phylogeny or function we must continue to expand our

387   knowledge base. Neurocrania (and consequently their associated cranial endocasts) are

388   morphologically complex and phylogenetically informative structures, as has already been well

389   illustrated for lungfishes (Friedman 2007). We present the first character matrix based solely on

390   endocast characters for lungfishes. The analysis supports a basal placement of *Dipnorhynchus*

391   within the dipnoan stem group in agreement with other recent phylogenetic analyses

392   demonstrating the robustness of endocasts alone in creating instructive phylogenetic hypotheses.

393

394

399   Campbell (formerly of Australian National University, Australia) is thanked for discussions

400   concerning dipnoan palaeoneurology.

401

402

403   **FIGURE CAPTIONS**

404   **Figure 1. Map showing localities yielding Early Devonian dipnorhynchid taxa in south-**

405   **eastern Australia.**

406

407   **Figure 2. *Dipnorhynchus sussmilchi* cranial endocast in lateral view.** A, virtual

408   reconstruction; and B, schematic illustration of ANU 18815; C, reproduction of *D. sussmilchi*

409   endocast from Campbell and Barwick (1982, fig. 25a).

410

411   **Figure 3. *Dipnorhynchus sussmilchi* cranial endocast in dorsal view.** A, virtual

412   reconstruction; and B, schematic illustration.

413

414   **Figure 4. *Dipnorhynchus sussmilchi* cranial endocast in ventral view.** A, virtual

415   reconstruction; and B, schematic illustration.

416

417   **Figure 5. *Dipnorhynchus sussmilchi* cranial endocast in anterolateral view.** A, virtual

418   reconstruction; and B, schematic illustration.

419

420   **Figure 6. Phylogenetic relationships as interpreted from cranial endocast morphology.** A,

421   the Late Devonian coelacanth *Diplocercides kayseri* (from Stensiö 1963, fig. 45); B, the Early

422   Devonian onychodont *Qingmenodus yui* (from Lu et al. 2016, fig. 2); the Late Devonian

423   tetrapodomorphs C, *Gogonasus andrewsae* (from Holland 2014, figs. 22,23); and D,

424   *Eusthenopteron foordi* (Stensiö 1963, fig. 50); E, the Early Devonian dipnomorph *Youngolepis*

425   *praecursor* (from Chang 1982, fig. 19); F, the Early Devonian dipnoan *Dipnorhynchus*

426   *sussmilchi* (ANU 18815); G, the Middle Devonian dipnoan *Dipterus valenciennesi* (from

427   Challands 2015, fig. 9); the Late Devonian dipnoans H, *Chirodipterus wildungensis* (from Säve-

428   Söderbergh 1952, fig. 9); and I, *Rhinodipterus kimberleyensis* (WAM 09.6.149); J, the extant

429   Australian lungfish *Neoceratodus forsteri* (from Clement et al. 2015, fig. 6).

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542

Figure 1

Map showing localities yielding Early Devonian dipnorhynchid taxa in south-eastern Australia.
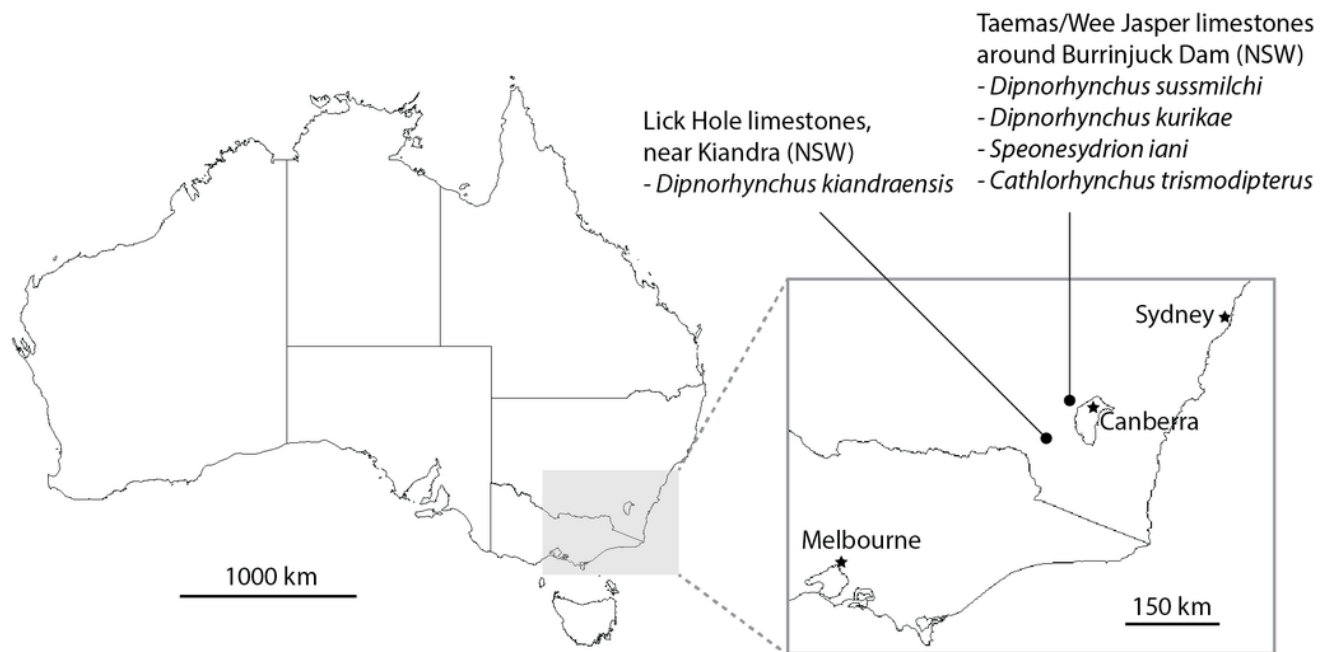
Figure 2

Dipnorhynchus sussmilchi cranial endocast in lateral view

A, virtual reconstruction; and B, schematic illustration of ANU 18815; C, reproduction of *D. sussmilchi* endocast from Campbell and Barwick (1982, fig. 25a).

*Note: Auto Gamma Correction was used for the image. This only affects the reviewing manuscript. See original source image if needed for review.
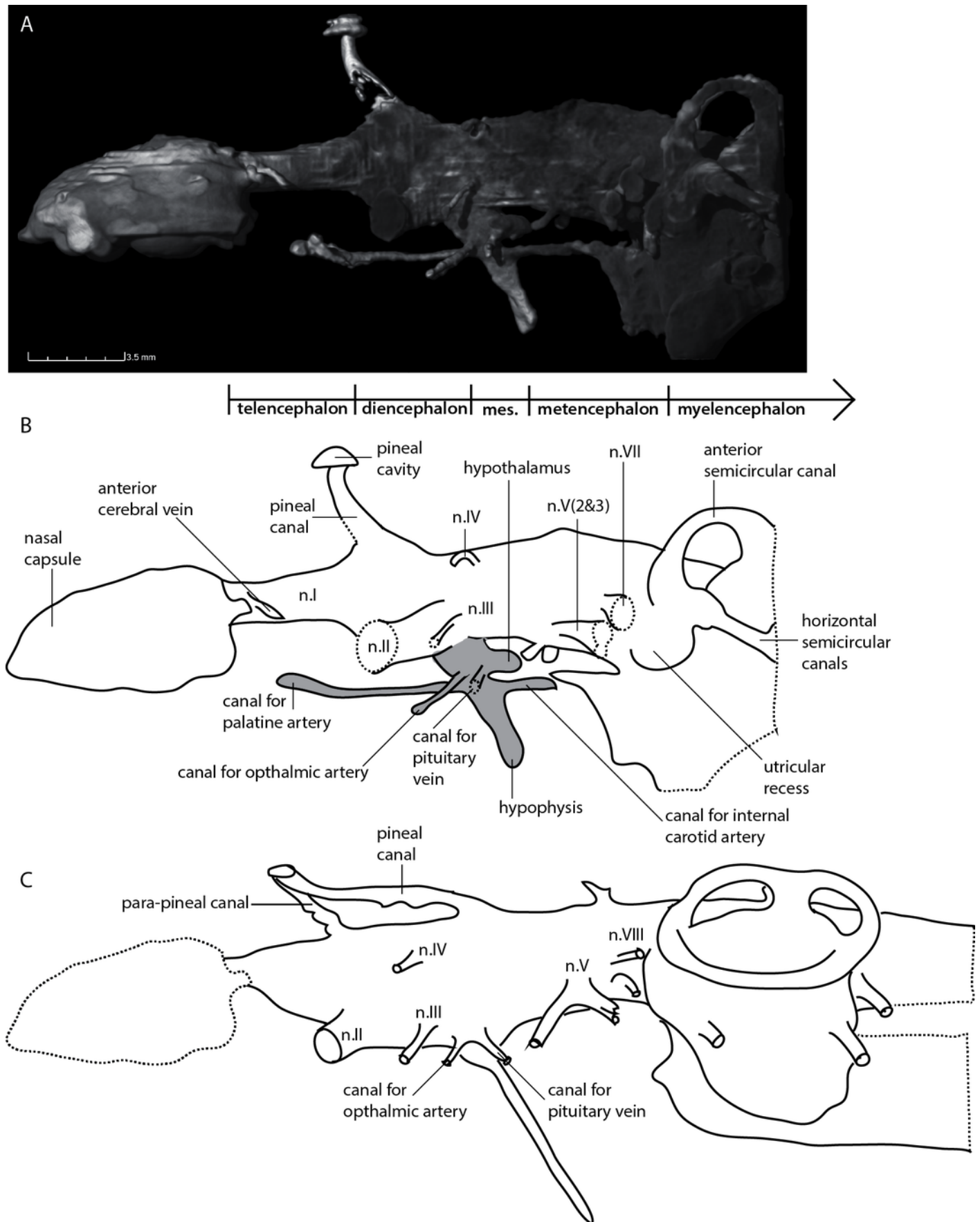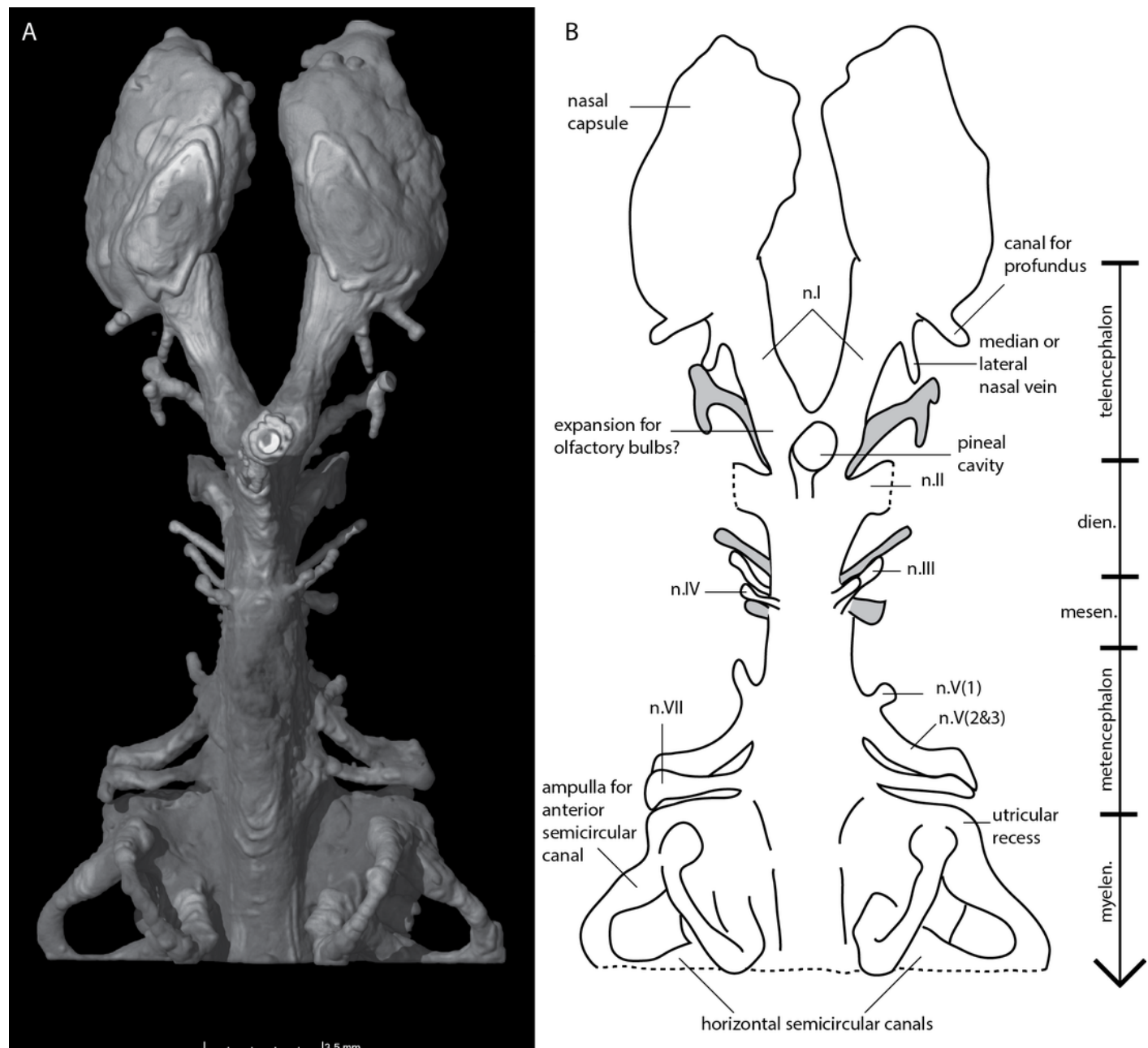
telencephalon | diencephalon | mes. | metencephalon | myelencephalon

B

- nasal capsule
- anterior cerebral vein
- pineal cavity
- pineal canal
- hypothalamus
- n.IV
- n.VII
- n.V(2&3)
- anterior semicircular canal
- n.I
- n.II
- n.III
- horizontal semicircular canals
- canal for palatine artery
- canal for opthalmic artery
- canal for pituitary vein
- hypophysis
- canal for internal carotid artery
- utricular recess

C

- para-pineal canal
- pineal canal
- n.IV
- n.III
- n.II
- n.V
- n.VIII
- canal for opthalmic artery
- canal for pituitary vein

Figure 3

Dipnorhynchus sussmilchi cranial endocast in dorsal view

A, virtual reconstruction; and B, schematic illustration.

Note: Auto Gamma Correction was used for the image. This only affects the reviewing manuscript. See original source image if needed for review.
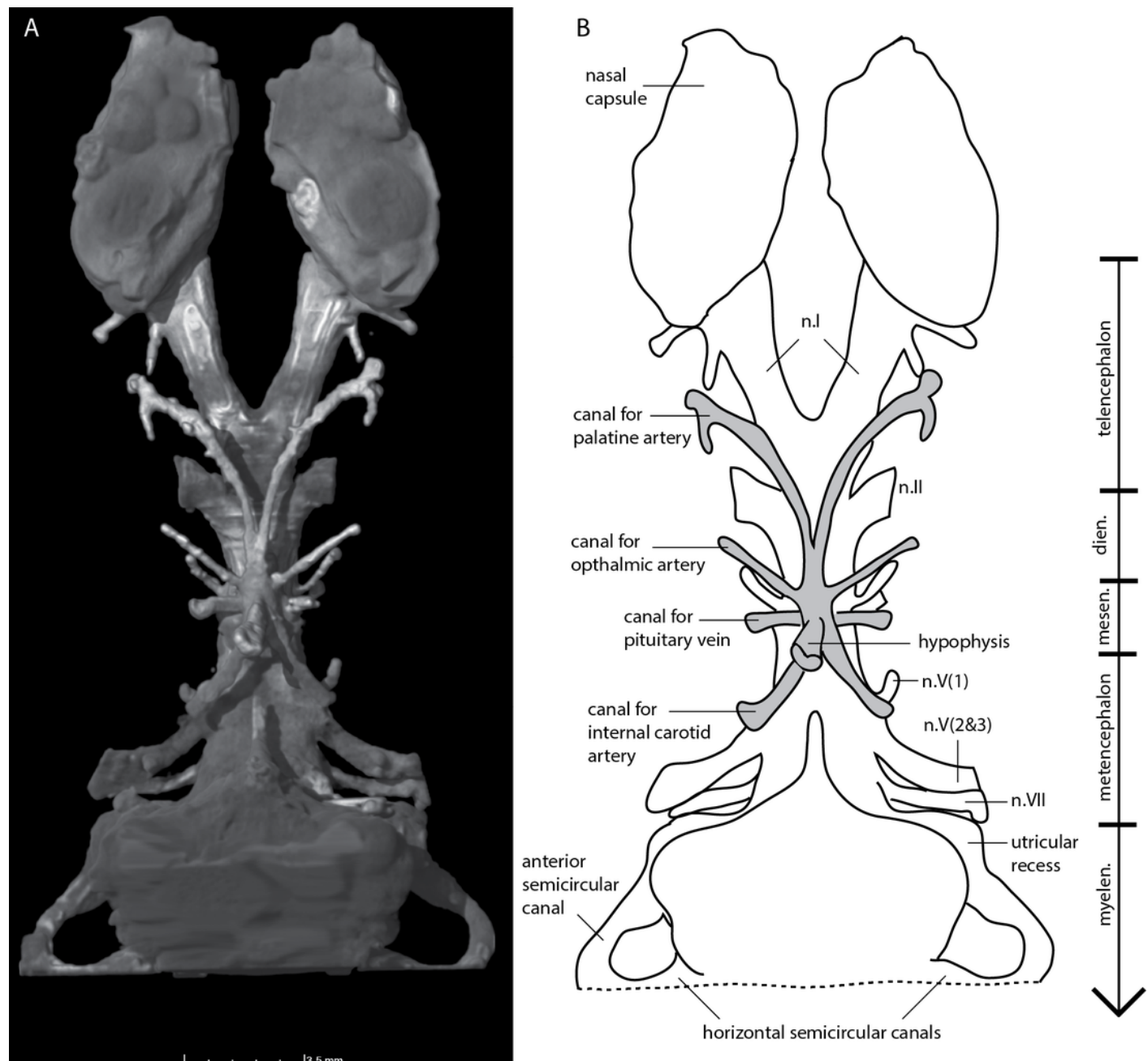
Figure 4

Dipnorhynchus sussmilchi cranial endocast in ventral view

A, virtual reconstruction; and B, schematic illustration.

Note: Auto Gamma Correction was used for the image. This only affects the reviewing manuscript. See original source image if needed for review.

Figure 5

Dipnorhynchus sussmilchi cranial endocast in anterolateral view

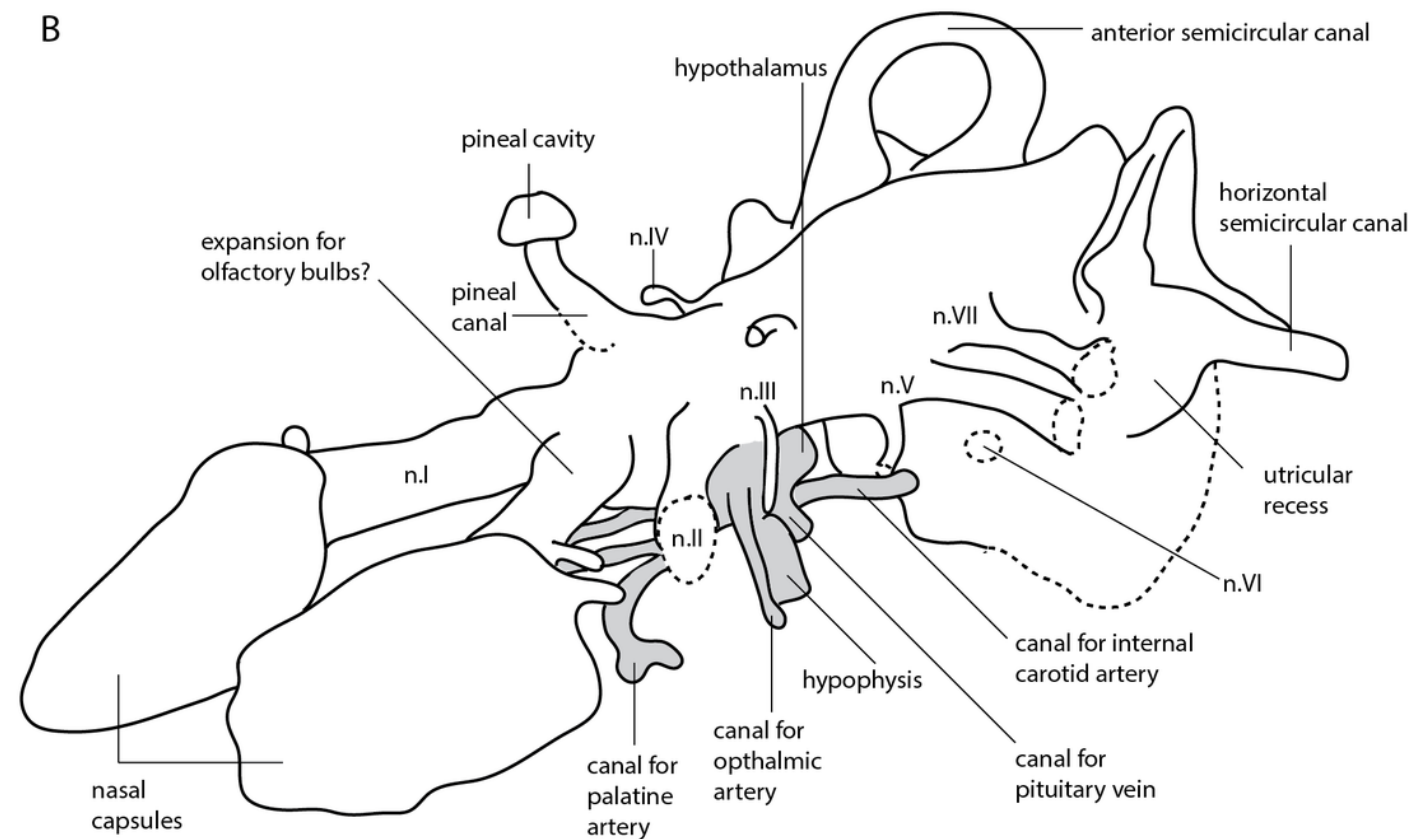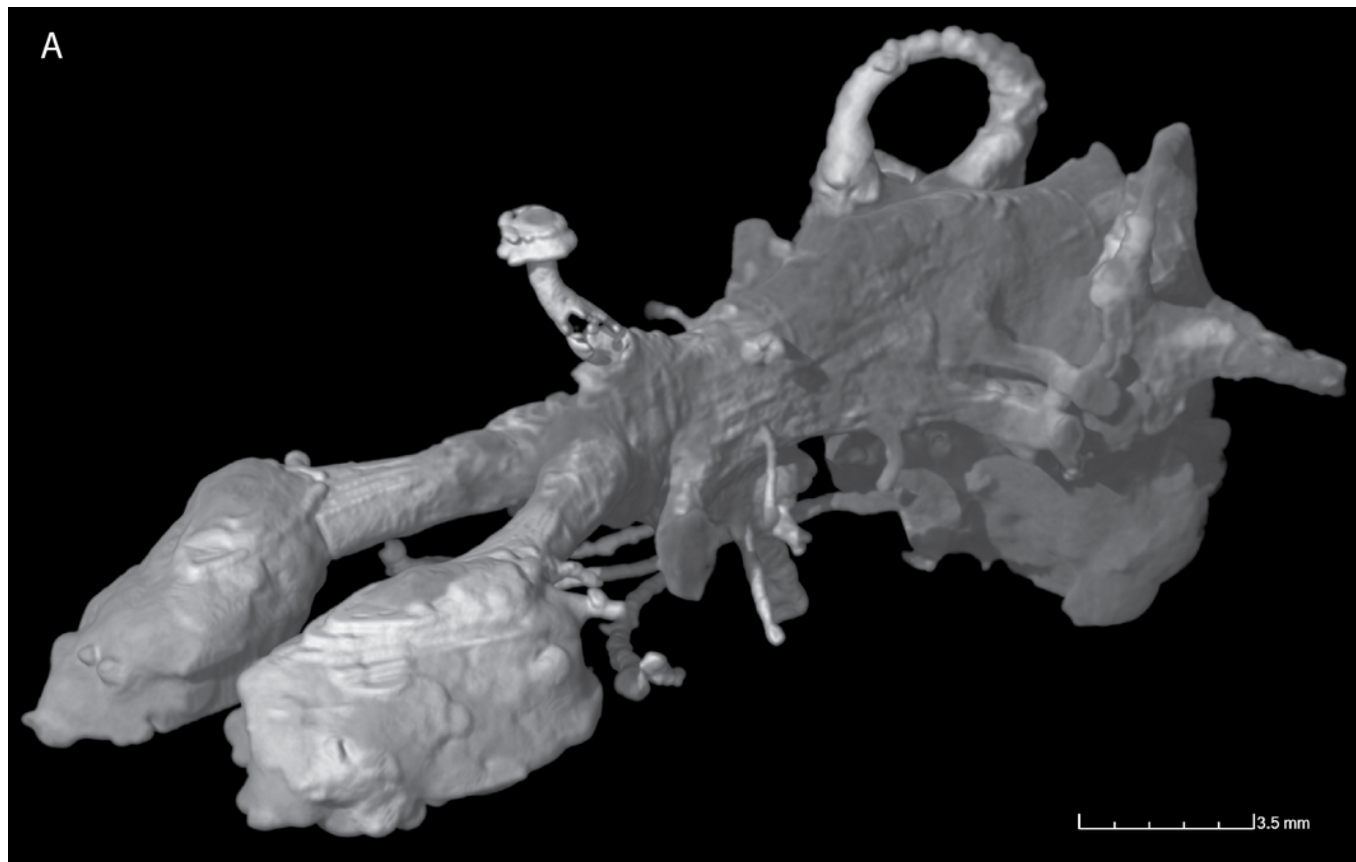A, virtual reconstruction; and B, schematic illustration.

Figure 6

Phylogenetic relationships of selected sarcopterygians as interpreted from cranial endocast morphology.

A, the Late Devonian coelacanth *Diplocercides kayseri* (from Stensiö 1963, fig. 45); B, the Early Devonian onychodont *Qingmenodus yui* (from Lu et al. 2016, fig. 2); the Late Devonian tetrapodomorphs C, *Gogonasus andrewsae* (from Holland 2014, figs. 22,23); and D, *Eusthenopteron foordi* (Stensiö 1963, fig. 50); E, the Early Devonian dipnomorph *Youngolepis praecursor* (from Chang 1982, fig. 19); F, the Early Devonian dipnoan *Dipnorhynchus sussmilchi* (ANU 18815); G, the Middle Devonian dipnoan *Dipterus valenciennesi* (from Challands 2015, fig. 9); the Late Devonian dipnoans H, *Chirodipterus wildungensis* (from Säve-Söderbergh 1952, fig. 9); and I, *Rhinodipterus kimberleyensis* (WAM 09.6.149); J, the extant Australian lungfish *Neoceratodus forsteri* (from Clement et al. 2015, fig. 6).