

1 Computed tomography, anatomical description and three-dimensional reconstruction of the  
2 lower jaw of *Eusthenopteron foordi* Whiteaves, 1881 from the Upper Devonian of Canada

3

4 by LAURA B. PORRO<sup>1,2,3\*</sup>, EMILY J. RAYFIELD<sup>1</sup> and JENNIFER A. CLACK<sup>2</sup>

5 <sup>1</sup>School of Earth Sciences, University of Bristol, Wills Memorial Building, Queen's Road,  
6 Bristol, UK; e-mails: [laura.porro@bristol.ac.uk](mailto:laura.porro@bristol.ac.uk), [E.Rayfield@bristol.ac.uk](mailto:E.Rayfield@bristol.ac.uk)

7 <sup>2</sup>Department of Zoology, University of Cambridge, Downing Street, Cambridge, UK; e-mail:  
8 [jac18@cam.ac.uk](mailto:jac18@cam.ac.uk)

9 <sup>3</sup> *Current address*: Structure and Motion Laboratory, Department of Comparative Biomedical  
10 Sciences, Royal Veterinary College, University of London, Hatfield, UK; e-mail:  
11 [lporro@rvc.ac.uk](mailto:lporro@rvc.ac.uk)

12

13 \*Corresponding author

14

15 **Abstract:** The cranial anatomy of the iconic early tetrapod *Eusthenopteron foordi* is probably  
16 the best understood of all fossil fishes. In contrast, the anatomy of the lower jaw – crucial for  
17 both phylogenetics and biomechanical analyses – has been only superficially described.

18 Computed tomography data of three *Eusthenopteron* skulls were segmented using  
19 visualization software to digitally separate bone from matrix and individual bones from each  
20 other. Here we present a new description of the lower jaw of *Eusthenopteron* based on micro-  
21 computed tomography data, including: detailed description of sutural morphology and the  
22 mandibular symphysis; confirmed occurrence of pre- and intercoronoid fossae on the dorsal  
23 aspect of the lower jaw; and the arrangement of the submandibular bones. Furthermore, we  
24 identify a novel dermal ossification, the postsymphysial, present on the anteromedial aspect  
25 of the lower jaw in *Eusthenopteron* and describe its distribution in other stem tetrapod taxa.

26 Sutural morphology is used to infer load regimes and, along with overall skull and lower jaw  
27 morphology, suggests that *Eusthenopteron* may have used biting along with suction feeding  
28 to capture and consume large prey. Finally, visualization software was used to repair and  
29 reconstruct the lower jaw, resulting in a three-dimensional digital reconstruction.

30

31 **Key words:** fish, early tetrapod, *Eusthenopteron*, lower jaw, computed tomography, feeding.

32

33 THE iconic lobe-finned fish *Eusthenopteron foordi* (Whiteaves 1881, 1888), from the Upper  
34 Devonian (Frasnian) Escuminac Formation of Miguasha National Park (Quebec, Canada), is  
35 a crucial taxon for understanding the morphology, ecology and evolution of sarcopterygians,  
36 including early tetrapods. Anatomical data from this taxon have been extensively  
37 incorporated into cladistic analyses (Ahlberg and Johanson 1998; Ruta *et al.* 2003; Coates *et*  
38 *al.* 2008), and in studies on limb evolution (Gregory and Raven 1941; Westoll 1943;  
39 Andrews and Westoll 1970; Coates and Clack 1990; Shubin *et al.* 1997; Coates *et al.* 2002;  
40 Boisvert *et al.* 2008; Clack 2009; Shubin *et al.* 2014), ear architecture (Brazeau and Ahlberg  
41 2006) and feeding (Hitchcock, 1995; Anderson *et al.* 2013; Neenan *et al.* 2014).

42 Numerous anatomical descriptions of the skull of *Eusthenopteron foordi* are available  
43 (Bryant 1919; Stensio 1922; Sternberg 1941), including detailed studies by Jarvik that  
44 utilized serial grinding tomography of a well-preserved specimen, SMNH (Swedish Museum  
45 of Natural History, Stockholm, Sweden) P. 222. This painstaking work revealed the anatomy  
46 of the cranial dermal bones, braincase, palatoquadrate, and visceral skeleton, including details  
47 of cranial sutural morphology and the courses of sensory canals, pit-lines, nerves, blood  
48 vessels and visceral muscles (Jarvik 1942, 1944, 1954). As a result of these studies, the

49 cranial anatomy of *Eusthenopteron* is among the best known of all fossil fishes (Cunningham  
50 *et al.* 2014). In contrast, the lower jaw of *Eusthenopteron* has been briefly described (Jarvik  
51 1944, 1980) and only a few drawings from the 530 cross-sections produced by Jarvik were  
52 ever published, providing limited information on sutural contacts in the lower jaw. This lack  
53 of data, particularly of the medial and dorsal aspects of the lower jaw, has hampered attempts  
54 to carry out three-dimensional (3D) mechanical analyses. Furthermore, the arrangement of  
55 the bones of the medial aspect of the lower jaw is important in providing characters for  
56 phylogenetic analyses (Ahlberg and Clack 1998), yet these regions were treated only  
57 superficially by Jarvik (1944, 1980).

58 Computed tomography (CT) and computed microtomography ( $\mu$ CT) are increasingly  
59 being applied to fossils (Cunningham *et al.* 2014). Applications include ‘virtual’ preparation  
60 of fossils (e.g., Abel *et al.* 2012; Porro *et al.* 2015), particularly fragile or very small material  
61 (e.g., Donoghue *et al.* 2006; Porro *et al.* 2011), visualizing internal cavities or bone histology  
62 (e.g., Lautenschlager *et al.* 2012; Rücklin *et al.* 2012), and capturing skeletal morphology for  
63 biomechanical analyses (e.g., Rayfield *et al.* 2001; Pierce *et al.* 2012). In this study, we used  
64 CT/ $\mu$ CT and visualization software, in addition to original fossil material, to produce the first  
65 detailed osteological description and 3D reconstruction of the lower jaw of *Eusthenopteron*.  
66 Among our findings, we describe and name a new dermal ossification – the postsymphysial –  
67 which is a bone found on the anteromedial aspect of the lower jaw in *Eusthenopteron* and  
68 several other stem tetrapods.

#### 69 *Institutional abbreviations*

70 MHNM, Musée d’Histoire naturelle de Miguasha, Miguasha National Park, Nouvelle,  
71 Quebec, Canada; UMZC (CAMZM), University Museum of Zoology Cambridge,  
72 Cambridge, UK.

73

74 **MATERIAL AND METHODS**

75 Three specimens of *Eusthenopteron foordi* were used in this study: MHNM 06-538, which  
76 consists of a nearly complete, minimally deformed skull; UMZC GN.1147, consisting of  
77 mediolaterally crushed cranium and partial right lower jaw; and UMZC GN.792, a nearly  
78 complete, dorsoventrally crushed skull. MHNM 06-538 (Fig. 1A-B) was scanned in 2004 at  
79 the high-resolution CT facility maintained by the Department of Geological Sciences at the  
80 University of Texas (Austin, Texas, USA). The whole specimen was scanned, producing 340  
81 16-bit TIFF images with a resolution of 0.165 mm/pixel and slice thickness of 1 mm.  
82 Additionally, two higher resolution scans of this specimen were carried out – the anterior 56  
83 mm of the specimen (producing 140 slices with a resolution of 0.096 mm/pixel and a slice  
84 thickness of 0.5 mm) and the rear of the skull (producing 250 slices with a resolution of 0.165  
85 mm/pixel and a slice thickness of 0.5 mm). UMZC GN.1147 (Fig. 1C) was scanned in 2013  
86 at the Imaging and Analysis Centre of the Natural History Museum (London, UK) on an X-  
87 Tek HMX-ST  $\mu$ CT 225 scanner (Nikon Metrology, Tring, UK) producing 1926 DICOM  
88 slices with a resolution of 0.0797 mm/voxel. UMZC GN.792 (Fig. 1D-F) was scanned in  
89 2014 in the Cambridge Biotomography Centre (Zoology Department) at the University of  
90 Cambridge on an X-Tek H 225  $\mu$ CT scanner (Nikon Metrology, Tring, UK) scanner  
91 producing 1920 TIFF images with a resolution of 0.0655 mm/voxel.

92 Scans were processed using the 3D visualization software package Avizo 7.1.1 (FEI  
93 Visualization Sciences Group, Mérégnac Cedex, France). Within the segmentation editor,  
94 density thresholding was initially used to separate higher density bone from lower density  
95 matrix. Scans were processed slice-by-slice (interpolating across no more than five slices at a  
96 time) to separate individual bones and sutures (Fig. 2). Sutures occur as low density areas

97 between bones (Appendix S1). Original specimens were used to confirm the location of  
98 sutures and differentiate them from post-mortem damage. Individual bones were isolated and  
99 separately labeled within the segmentation editor and 3D surface models of each element  
100 were created that could be manipulated in isolation in 3D space; the following description is  
101 based on these models.

102         Some limits to the data sets used in the description and reconstruction should be  
103 noted. The ventral margins of the posterior lower jaws of MHMN 06-538 and UMZC  
104 GN.792 are abraded. In contrast, UMZC GN.1147 preserves the ventral margin of the lower  
105 jaw, although the anterior end of the jaw is missing. The 3D reconstruction (Fig. 3)  
106 incorporates: the anterior half of the dentary, first infradentary, second infradentary,  
107 postsymphysial from the right lower jaw of MHMN 06-538; the posterior half of the dentary,  
108 fourth infradentary, adsymphysial, coronoids, prearticular and articular from the left lower  
109 jaw of MHMN 06-538; and the third infradentary from the right lower jaw of UMZC  
110 GN.1147. Scans from UMZC GN.792 were segmented and examined to confirm anatomical  
111 details of the symphyisial region but were not incorporated into the 3D reconstruction. With  
112 the exception of the large anterior teeth, the very small individual dentary teeth were not  
113 segmented in any of the scanned specimens due to their very small size.

114         The left side of MHMN 06-538 is minimally deformed. Thus, the left lower jaw of  
115 this individual was used a 'template' for 3D reconstruction. Surface models of individual  
116 bones from the right side of MHMN 06-538 and from UMZC GN.1147 (see previous  
117 paragraph) were reflected across the sagittal midline and moved into position on the left  
118 lower jaw of MHMN 06-538. Because of differences in specimen size and resolution of CT  
119 scans, surface models from UMZC GN.1147 were scaled by a factor of 1.35 to match the size  
120 of MHMN 06-538. The reflected elements were fitted into place using sutural contacts as  
121 well as fragments of these bones preserved on the left side of MHMN 06-538. Finally, the

122 reconstructed left ramus of the lower jaw was duplicated and reflected across the sagittal  
123 midline to create the right lower jaw ramus. Transformation matrices for all lower jaw bones  
124 from the original data sets to the final 3D reconstruction are available as supporting  
125 information (see Appendix S2).

126

## 127 **RESULTS**

### 128 *Anatomical description of the lower jaw*

129 The complete left lower jaw of MHMN 06-538 measures 234 mm in length; the cranium of  
130 this specimen measures 216 mm from premaxilla to the median extrascapular (in dorsal  
131 projection). The preserved portion of the lower jaw of UMZC GN.1147 measures 111 mm  
132 from the tip of the retroarticular process to the preserved tip of the anterior coronoid fang.  
133 The lower jaws of UMZC GN.792 are not visible externally. The length of the cranium  
134 between the premaxilla and median extrascapular is 88 mm; thus, this specimen is  
135 substantially smaller than either MHMN 06-538 or UMZC GN.1147.

136 The lateral aspect of the lower jaw is made up of the dentary and four infradentaries  
137 (Fig. 3A); the medial aspect is made up of the first infradentary, prearticular, adsymphysial,  
138 postsymphysial, three coronoids and articular (Fig. 3B). The lower jaw is dorsoventrally  
139 tallest at the level of the posterior tip of the dentary and tapers anteriorly and posteriorly. The  
140 ventral margin of the lower jaw is gently curved while the dorsal margin is relatively straight;  
141 *Eusthenopteron* lacks the upturned anterior lower jaw exhibited by *Acanthostega* (Clack,  
142 2003; Porro *et al.* 2015). The coronoid fangs and dorsolateral edges of the three coronoid  
143 bones are visible in lateral view above the dorsal margin of the dentary (Fig. 3A). The  
144 Meckelian fenestra is located at the ventromedial margin of the lower jaw. It extends from the

145 first infradentary – prearticular contact to the fourth infradentary – articular contact, and was  
146 either filled by Meckelian bone (Jarvik 1954, 1980) or intermittently closed by point contacts  
147 between the infradentaries and the prearticular (Fig. 3D).

148         In dorsal view, the lateral and medial margins of the lower jaw are parallel along most  
149 of its length (Fig. 3C). There are three openings in the dorsal surface of the anterior lower jaw  
150 in *Eusthenopteron* – one precoronoid fossa and two intercoronoid fossae. These fossae are  
151 primitive features within stem tetrapods (Jeffery 2003). The precoronoid fossa is present in  
152 porolepiforms (except *Duffichthys*), “osteolepiforms” (including the Tristichopteridae) and  
153 elpistostegids (Ahlberg 1992; Lebedev, 1995; Long *et al.* 1997; Ahlberg and Clack 1998;  
154 Ahlberg *et al.* 2000). It occurs in basal rhizodonts but is lost in derived forms (Vorobyeva  
155 and Obrucheveva 1977; Jeffery 2003; Brazeau 2005). The precoronoid fossa is convergently  
156 lost in most of the digitated tetrapods - including *Elginerpeton*, *Densignathus*, *Metaxygnathus*  
157 and *Acanthostega* (Ahlberg and Clack 1998; Daeschler 2000; Porro *et al.* 2015) – but  
158 retained in the elginerpetontids *Obruchevichthys* and *Webererpeton* (Clément and Lebedev,  
159 2014). The precoronoid fossa of *Eusthenopteron* (clearly visible in CT scans of MHMN 06-  
160 538 and UMZC GN.792; Fig. 2A, E; Appendix S1B) is bordered posteriorly by the anterior  
161 coronoid, laterally by the anterior coronoid and dentary, anteriorly by the dentary, Meckelian  
162 bone and adsymphyseal, and medially by the postsymphyseal; it accommodated the vomerine  
163 fangs when the jaws were closed. An intercoronoid fossa is present between the anterior and  
164 middle coronoids of *Eusthenopteron*, with a second, smaller intercoronoid fossa between the  
165 middle and posterior coronoids (visible in CT scans of MHMN 06-538 and UMZC GN.1147;  
166 Fig. 2A, D; Appendix S1A). The intercoronoid fossae have a similar phylogenetic  
167 distribution as the precoronoid fossa. These openings accommodate the enlarged fangs of the  
168 palatine and ectopterygoid when the jaws were closed. The elongate mandibular adductor

169 fossa occupies the posterior third of the lower jaw and is bounded by the dentary, surangular,  
170 posterior coronoid, prearticular and articular.

171

172 *Meckelian bone*. The intramandibular canal of some stem tetrapods is partly lined by  
173 endochondral Meckelian bone, forming the floor of the pre- and intercoronoid fossae and  
174 occupying the gap (Meckelian fenestra) between the prearticular and the infradentaries on the  
175 ventromedial aspect of the lower jaw. Posteriorly, the Meckelian ossification forms the  
176 articular; anteriorly, it fills the intramandibular canal and contributes to the symphyseal  
177 surface in some taxa. Such a symphyseal contribution is commonly referred to as the  
178 mentomeckelian ossification or mentomandibular rib. The Meckelian element is ossified  
179 along its entire length and exposed at the symphysis in porolepiforms (Ahlberg 1992), most  
180 “osteolepiforms” (Lebedev 1995; Long *et al.* 1997; Ahlberg and Clack 1998) and  
181 elpistostegids (Ahlberg and Clack 1998; Ahlberg *et al.* 2000). It is ossified in *Elginerpeton*,  
182 *Obruchevichthys*, *Densignathus*, *Ventastega*, *Metaxygnathus*, *Ymeria* and *Ichthyostega* but it  
183 does not floor the dorsal fossae or contribute to the symphysis (Ahlberg 1995, 2005; Ahlberg  
184 and Clack 1998; Daeschler 2000; Clack *et al.* 2012; Clément and Lebedev, 2014); it does  
185 appear to contribute to the symphysis in *Webererpeton* (Clément and Lebedev, 2014). The  
186 Meckelian element is completely unossified in rhizodonts (except the basal taxon  
187 *Letognathus*) and only the articular is ossified in *Acanthostega* (Jeffery 2003; Brazeau 2005;  
188 Porro *et al.* 2015).

189 Previous descriptions of the lower jaw of *Eusthenopteron foordi* (Jarvik 1944; Clack  
190 2012) report a core of Meckelian bone (the ceratomandibular of Jarvik [1954]) surrounded by  
191 a sleeve of dermal bone. Isolated drawings from Jarvik’s serial grinding series (Jarvik 1954,  
192 1980) suggest that the Meckelian bone is a slender rod restricted to the ventromedial margin

193 of the intramandibular canal between the prearticular and infradentary bones, expanding and  
194 ossifying fully at the anterior and posterior ends of the lower jaw (Jarvik 1980). Meckelian  
195 bone is difficult to visualize in CT scans as its density is similar to that of the surrounding  
196 matrix: it appears to be intermittent in the middle portion of the lower jaws of MHMN 06-538  
197 and UMZC GN.1147. Wisps of higher density material are visible in the mandibular adductor  
198 fossae of MHMN 06-538; anteriorly, these fragments first appear in the medioventral corner  
199 of the intramandibular canal, gradually filling the adductor fossa and grading into the  
200 articular posteriorly. We suggest that these higher density fragments represent ossified  
201 fragments of Meckelian bone in the middle and posterior lower jaw. The articular is  
202 completely ossified.

203 Scans of UMZC GN.792 demonstrate that the Meckelian bone is limited to the  
204 ventromedial corner of the intramandibular canal at the midpoint of the precoronoid fossa.  
205 Anterior to this point, the Meckelian bone expands to fill the intramandibular canal; however,  
206 it does not appear to be exposed at the symphysis. The morphology of symphyisial region of  
207 the lower jaw of *Eusthenopteron* is covered in detail in the Discussion.

208

209 *Dentary*. The dentary is long and narrow in lateral view, being tallest anteriorly, featuring  
210 nearly parallel dorsal and ventral margins along most of its length, and tapering to a point  
211 posteriorly (Fig. 3A). In dorsal view (Figs 2A and 3C), the dentary is transversely narrow,  
212 widening anteriorly as described by Jarvik (1980) to form a medial shelf that articulates with  
213 the adsymphyisial and postsymphyisial and contributes to the anterior margin of the  
214 precoronoid fossa. In ventral view (Fig. 3D), the anterior end of the dentary expands towards  
215 the midline so that its ventromedial margin contributes to the symphysis. In transverse

216 section, the dentary is mediolaterally thin and laterally bowed; the dorsal margin is thickened  
217 but lacks the medial shelf exhibited by *Acanthostega* (Porro *et al.* 2015).

218         Among stem tetrapods, enlarged dentary teeth near the symphysis are referred to as  
219 tusks while enlarged coronoid teeth are referred to as fangs (Jeffery 2003; Brazeau 2005; but  
220 note alternative definitions proposed by Bolt and Lombard, 2001). Dentary tusks are absent  
221 in porolepiforms but are present in all known rhizodonts (Johanson and Ahlberg 2001).  
222 Enlarged dentary teeth near the symphysis occur in the “osteolepiforms” *Gogonasus* and  
223 *Medoevia* (Lebedev 1995; Long *et al.* 1997); however, Ahlberg and Clack (1998) do not  
224 classify these as tusks. Derived tristichopterids, elpistostegids and digitated tetrapods exhibit  
225 tusks (Schultze and Arsenault 1985; Ahlberg and Johanson 1997; Ahlberg and Clack 1998;  
226 Daeschler 2000; Ahlberg *et al.* 2000; Johanson and Ahlberg 2001; Clack *et al.* 2012; Clément  
227 and Lebedev, 2014). Unlike rhizodonts, in which the marginal tooth row labial to the tusk is  
228 interrupted to form a diastema (Brazeau 2005), the dentary tusks of other tetrapodomorphs lie  
229 lingual to a marginal tooth row that continues uninterrupted to the symphysis, with the  
230 possible exception of *Obruchevichthys* (Clément and Lebedev, 2014). The dentary teeth of  
231 *Eusthenopteron* increase in size anteriorly, with the first two teeth being larger and more  
232 strongly recurved than succeeding teeth (Jarvik 1944); however, these are not considered  
233 tusks by most authors (Ahlberg and Clack 1998; Johanson and Ahlberg 2001), which are  
234 thought to be absent in basal tristichopterids .

235         The anteromedial edge of the anterior dentary contributes to the symphysis,  
236 approaching its opposite in a loose, vertical contact (Figs 2F and 3D). The symphyseal pit  
237 described by Jarvik (1980) cannot be discerned in CT scans. The dorsomedial tip of the  
238 dentary is “capped” by a small, dermal element, the adsymphyseal (Fig. 2A, E). Posteriorly,  
239 the ventromedial margin of the dentary contacts the ventral margin of the postsymphyseal in  
240 an anteroposteriorly long and transversely narrow butt joint (Fig. 2A, E); the medial aspect of

241 the dentary is separated from the lateral aspect of the postsymphysial by the Meckelian bone  
242 (anteriorly) and the precoronoid fossa (posteriorly). The first infradentary wedges between  
243 the dentary and postsymphysial, separating these elements at the level of the anterior tip of  
244 the anterior coronoid. The ventral margin of the dentary contacts the lateral margin of the first  
245 infradentary. Scans of MHMN 06-538 and UMZC GN.792 reveal that this contact is either a  
246 butt joint or that the first infradentary externally overlaps the dentary in a short scarf, *contra*  
247 illustrations and descriptions by Jarvik (1944, 1980) that suggest that the ventral margin of  
248 the dentary overlaps the first infradentary. The ventral margin of the dentary overlaps (often  
249 to a considerable extent) the dorsal margins of second, third and fourth infradentaries. The  
250 medial aspect of the dentary broadly contacts the lateral aspects of the three coronoid bones  
251 (Figs 2A and 3C); faint interdigitations are present, as depicted by Jarvik (1954). The  
252 posterior tip of the dentary contributes to the lateral margin of the mandibular adductor fossa  
253 (Figs 2A and 3C). The dentary reaches the midpoint of the surangular in UMZC GN.1147  
254 (Fig. 2C) but extends nearly to the jaw joint in MHMN 06-538 (Fig. 2A).

255

256 *First infradentary (=splenial)*. The first infradentary is the shortest of the series and forms the  
257 anteroventral margin of the lower jaw in lateral and medial views (Fig. 3A-B). The first  
258 infradentary is shaped like an inverted “Y” in transverse section; the short stem of the “Y” is  
259 directed dorsolaterally, contacting the dentary and externally overlapping the second  
260 infradentary. As in *Acanthostega* (Porro *et al.* 2015), one arm of the “Y” is dorsomedially-  
261 directed; it meets the ventral margins of the postsymphysial and prearticular in rounded butt  
262 joints. As in all stem tetrapods less crownward than elpistostegids, this dorsomedial arm is  
263 not developed into a medial lamina (Ahlberg and Clack 1998). The other arm of the “Y” is  
264 directed ventromedially, forming a flange that contributes to the mandibular symphysis by  
265 either under- or overlapping its counterpart across the midline (Figs 2F and 3D) – see section

266 titled “Mandibular symphysis of *Eusthenopteron*” in the Discussion for more details. The  
267 surface between the arms of the “Y” is deeply concave; anteriorly this may have  
268 accommodated a ligament pit, as suggested for *Acanthostega* (Ahlberg and Clack 1998; Porro  
269 *et al.* 2015). Posterior to the contact between the first infradentaries, this concave depression  
270 articulates with the rounded lateral margins of the first and second branchiostegal rays (Fig.  
271 2B-C; Appendix S1C).

272         The morphology and sutural contacts of the posterior margin of the first infradentary  
273 is variable among the specimens included in this study. In both lower jaws of MHMN 06-  
274 538, the dorsomedial and ventromedial laminae (arms of the “Y”) of the first infradentary  
275 bifurcate into dorsal and ventral processes; the ventral process is short and terminates as a  
276 rounded tip that underlaps the second infradentary. The dorsal process is longer and is  
277 applied to the ventral margin of the prearticular. The notch between the dorsal and ventral  
278 processes is rounded and forms the anterior and dorsal margins of a small opening that is  
279 bounded posteroventrally by the second infradentary. The right lower jaw of UMZC GN.792  
280 is badly abraded at this level; however,  $\mu$ CT scans of the left lower jaw of this specimen  
281 suggest a similar morphology as exhibited by MHMN 06-538. The shape and sutural contacts  
282 of the posterior margin of the first infradentary of UMZC GN.1147 are different – the  
283 dorsomedial and ventromedial laminae of the first infradentary do not bifurcate. Instead, the  
284 posterior margin of the first infradentary is rounded and externally laps the second  
285 infradentary (Fig. 2D). This deviation may be due to strong mediolateral compression of this  
286 specimen.

287

288 *Second infradentary (=postsplenial)*. The second infradentary is anteroposteriorly longer than  
289 the first infradentary (Fig. 3A). It is tallest at its midsection and tapers anterodorsally and

290 posteroventrally. It is mediolaterally thin in cross-section and bowed ventrolaterally. The  
291 anterior tip of the second infradentary inserts between the dentary and first infradentary,  
292 being overlapped by both bones in scarf joints. The dorsomedial aspect of the second  
293 infradentary contacts the ventrolateral aspect of the anterior and middle coronoids in a  
294 smooth, curving contact. Scans of UMZC GN.1147 demonstrate that the ventral margin of  
295 the second infradentary is grooved and articulates with the lateral margins of the second,  
296 third, and fourth branchiostegal rays (Fig. 2C). The dorsal margin of the second infradentary  
297 overlaps the ventral margin of the third infradentary in a scarf joint that is anterodorsally-  
298 oriented in lateral view (Figs 2C and 3A). The second infradentary terminates posteriorly as a  
299 rounded tip underlapping the third infradentary. Scans of the UMZC GN.1147 reveal that the  
300 ventral margin of the second infradentary makes weak point contacts with the ventral margin  
301 of the prearticular.

302

303 *Third infradentary (=angular)*. The third infradentary is similar in shape to the second  
304 infradentary, being tallest at its midsection and tapering anteriorly and posteriorly, and is  
305 gently laterally bowed in cross-section. The central portion of this bone is missing in MHMN  
306 06-538 and its ventral margin is severely abraded on both sides of UMZC GN.792. In  
307 contrast, it is broken longitudinally but otherwise well-preserved in UMZC GN.1147 (Fig.  
308 2C), and most of the following description is based on this specimen. The ventral margin of  
309 the third infradentary features a groove along its length, continuous with the groove along the  
310 ventral margins of the first and second infradentary. This groove articulates with the lateral  
311 margins of the fifth, sixth and seventh branchiostegal rays (Fig. 2C). There are small point  
312 contacts between the ventral margin of the third infradentary and the prearticular. Scans of  
313 UMZC GN.1147 reveal discontinuous patches of a material with a density unlike that of  
314 either bone or matrix associated with gaps between these two bones. These patches most

315 likely represent Meckelian bone, as depicted by Jarvik (1980, figs 76 and 84) in his drawings.  
316 The posterodorsal margin of the third infradentary overlaps the ventral margin of the fourth  
317 infradentary in a short scarf (Figs. 2C and 3A). The dorsomedial aspect of the third  
318 infradentary broadly contacts the ventrolateral surfaces of the middle and posterior coronoids.  
319

320 *Fourth infradentary (=surangular)*. The fourth infradentary makes up the posterolateral  
321 portion of the lower jaw (Figs 2C and 3A) and contributes to the lateral margin of the  
322 mandibular adductor fossa (Figs 2A and 3C). It features a curved ventral margin and nearly  
323 straight dorsal margin, and is tallest posterior to the tip of dentary. It is gently laterally bowed  
324 in cross-section with a thickened dorsal margin. The anterior tip of the fourth infradentary  
325 inserts between and is overlapped by the dentary and third infradentary. Its medial surface  
326 makes a short contact with the lateral surface of the posterior coronoid. There is an oblique  
327 ridge, directed anterodorsally, on the lateral surface of the fourth infradentary, dorsal to a row  
328 of sensory pores (=oral canal of Jarvik [1944]) and in line with the posterior tip of the  
329 dentary. This ridge is clearly visible in MHMN 06-538 (Fig. 3A) and UMZC GN.1147 (Fig.  
330 2C), and divides the lateral aspect of this bone into a larger, ventral surface which is highly  
331 ornamented and a small, dorsolaterally-directed surface that is laterally overlapped by the  
332 quadratojugal when the mouth is closed, as exhibited by various rhizodonts and *Gogonasus*  
333 (Long *et al.* 1997; Brazeau 2005). In UMZC GN.1147 and the left lower jaw of MHMN 06-  
334 538, the anterior half of the ventral margin of the fourth infradentary is grooved to receive the  
335 lateral margin of the eighth branchiostegal ray (Fig. 2B-C). It is possible that the upper lip  
336 forming this groove (continuous from the first through fourth infradentaries) supported the  
337 Meckelian element, as suggested for rhizodonts (Brazeau 2005). The thickened posterior half  
338 of the ventral margin of the fourth infradentary rises steeply towards the tip of the  
339 retroarticular process and does not feature a groove. The fourth infradentary laterally overlaps

340 the articular and wraps partially around its posterior aspect; it does not contribute to the jaw  
341 joint except by a lip that restricts lateral movement of the quadrate. The posterior tip  
342 (retroarticular process) of the fourth infradentary is short and thickened, and may have served  
343 as an attachment site for a muscle or ligament. The ventral margin of the fourth infradentary  
344 contacts the ventral margin of the prearticular. Posteriorly, this contact is a strong butt joint;  
345 anteriorly, the elements separate and the articular or patches of Meckelian bone are visible  
346 between the fourth infradentary and prearticular (Fig. 3D).

347

348 *Adsymphysial*. The adsymphysial (also known as the parasymphysial plate) of  
349 *Eusthenopteron* is a small, disc-shaped bone with a rounded anterior edge and a very short,  
350 tapering posteromedial process. It is visible in  $\mu$ CT scans of UMZC GN.792 (Fig. 2E), in  
351 which it caps the dorsomedial tip of the dentary, the dorsal surface of the Meckelian bone and  
352 the dorsal margin of the postsymphysial. Scans of MHMN 06-538 reveal a small element on  
353 both sides of the head that loosely contacts the dorsal aspect of the dentary anteriorly but has  
354 disarticulated posteriorly (Fig. 2A). No adsymphysial teeth or denticles can be resolved in  
355 scans of either UMZC GN.792 or MHMN 06-538.

356 The morphology and dentition of the adsymphysial poses a coding problem among  
357 stem tetrapods (Clack *et al.* 2012). It is small, rests on the dentary and Meckelian element,  
358 and does not contact the anterior coronoid in most porolepiforms and derived rhizodonts  
359 (Ahlberg 1992). In contrast, the adsymphysial is elongate and sutures to the anterior coronoid  
360 in the basal rhizodonts *Gooloogongia* and *Letognathus* (Johanson and Ahlberg 2001; Brazeau  
361 2005). The “osteolepiforms” *Gogonasmus* and *Medoevia* feature an elongate adsymphysial that  
362 caps the Meckelian bone and contacts the anterior coronoid (Lebedev 1995; Long *et al.* 1997;  
363 Ahlberg and Clack 1998) while tristchopterids and elpistostegids feature a small

364 adsymphyial that rests on the dentary, Meckelian bone and/or postsymphyial, fails to  
365 contact the anterior coronoid and is frequently detached and lost, leaving only an attachment  
366 scar (Ahlberg and Johanson 1997; Ahlberg and Clack 1998; Ahlberg *et al.* 2000; Johanson  
367 and Ahlberg 2001). In all “osteolepiforms” and elpistostegids, the adsymphyial is lightly  
368 denticulated. In contrast, more derived tetrapodomorphs feature an elongate adsymphyial  
369 that sutures to the anterior coronoid and bears an organized tooth row, usually including  
370 fangs (Ahlberg and Clack 1998; Daeschler 2000; Clack *et al.* 2012; Clément and Lebedev,  
371 2014; Porro *et al.* 2015).

372

373 *Postsymphyial.* Jarvik (1980) described the prearticular of *Eusthenopteron* as comprising  
374 two separate bones – the “prearticular” and the denticulated “prearticular dental plate”. As  
375 noted by Ahlberg and Clack (1998), this terminology is highly confusing as the “prearticular  
376 dental plate” is, in fact, the true prearticular. Jarvik’s “prearticular” is a slender, curving bone  
377 that is present in all three *Eusthenopteron* specimens included in this study (although only its  
378 posterior half is preserved in UMZC GN.1147). It is dorsoventrally tallest anteriorly and  
379 tapers to a point posteriorly, forming the medial margin of the precoronoid fossa and the  
380 medial wall of the anterior intramandibular canal (Figs 2A, E and 3B, C). In cross-section it  
381 is mediolaterally thin, and its tapering posterior tip underlies the anterior tip of the true  
382 prearticular in an anteroposteriorly long contact that is undulating in cross-section. We  
383 identify this element as a novel dermal ossification in the lower jaw of *Eusthenopteron*,  
384 which we call the postsymphyial. In addition to its contacts with the dentary, first  
385 infradentary and adsymphyial (previously described), the lateral margin of the  
386 postsymphyial overlaps the medial edge of the anterior coronoid in a short scarf joint. The  
387 anterior portion of the postsymphyial forms part of the mandibular symphysis, approaching  
388 its counterpart across the midline in a loose, vertical butt contact.

389           The size of the postsymphysial and its surrounding contacts rule out the possibility  
390 that it represents a portion of the adsymphysial. Scans reveal that the element is higher  
391 density than either the matrix or the Meckelian bone within the intramandibular canal; its  
392 density is similar to that of other dermal bones of the lower jaw. Along with its external  
393 appearance, the element is clearly dermal (not endochondral) bone, and is therefore not part  
394 of the Meckelian ossification. Ahlberg and Clack (1998) noted that the postsymphysial might  
395 represent a separate ossification, but chose to adhere to conventional terminology and  
396 referred to this element as an anterior process of the prearticular. Scans of all three  
397 *Eusthenopteron* specimens demonstrate a clear, unambiguous sutural contact with the  
398 prearticular; thus, this element is not simply an anterior extension of the prearticular.

399           Primitively, the postsymphysial is absent and the Meckelian ossification is developed  
400 into a mentomandibular rib that is exposed at the symphysis and forms the medial margin of  
401 the precoronoid fossa. This is the condition in porolepiforms, the basal rhizodont *Letognathus*  
402 and the “osteolepiform” *Gogonasus* (Ahlberg 1992; Long *et al.* 1997; Brazeau 2005). Long *et*  
403 *al.* (1997) note that there is no forward extension of the prearticular in *Gogonasus* as in  
404 *Medoevia*. Ahlberg and Clack (1998) identify a raised, denticulated field with distinct edges  
405 as the “prearticular dental plate” in *Gogonasus* but the anterior edge of the prearticular is a  
406 very short distance in front of this field and there is no anterior process (and no  
407 postsymphysial) in this taxon. In contrast, the “osteolepiform” *Medoevia* features a  
408 “prearticular anterior process” that contacts the anterior coronoid (medially), the first  
409 infradentary (ventrally) and the Meckelian bone (medially), and is clearly distinct from the  
410 shagreen-covered main body of the prearticular (Lebedev 1995). It is likely that this  
411 “prearticular anterior process” represents the postsymphysial in this taxon, although CT scans  
412 would be necessary to confirm such a diagnosis. An anterior process of the prearticular also  
413 occurs in tristichopterids and elpistostegids, including *Panderichthys* (Ahlberg and Clack

414 1998), and may represent the postsymphysial. The postsymphysial is not present in later  
415 tetrapods such as *Densignathus*, *Ventastega*, *Metaxygnathus*, *Acanthostega*, *Ymeria* or  
416 *Ichthyostega*, as the medial lamina of the first infradentary (upper arm of the “Y”) expands  
417 dorsally to contact the dentary, adsymphysial and prearticular (Ahlberg and Clack 1998;  
418 Daeschler 2000; Clack *et al.* 2012; Porro *et al.* 2015). Therefore, we identify the  
419 postsymphysial as a novel ossification that occurs in *Eusthenopteron* and may be present in  
420 other “osteolepiforms”, tristichopterids and elpistostegids. Scans of individual taxa within  
421 these groups would be necessary to unambiguously support or refute the presence of this  
422 ossification.

423

424 *Prearticular*. The dominant bone of the medial aspect of the lower jaw, the prearticular (Figs  
425 2A, D and 3B) is tallest at the anterior margin of the mandibular adductor fossa, tapering to a  
426 fine point anteriorly and a rounded margin posteriorly. The ventral margin of the prearticular  
427 is smoothly curved along its entire length; the dorsal margin is gently curved anterior to the  
428 mandibular adductor fossa and more deeply embayed posteriorly. In transverse section, the  
429 bone is mediolaterally thin with a thickened, outwardly (laterally) turned dorsal margin. It is  
430 medially bowed along most of its length, although it becomes vertical at its contact with the  
431 articular. Scans demonstrate that the anterior tip of the prearticular twists about its long axis,  
432 overlying the posterior tip of the postsymphysial. The prearticular contacts the first  
433 infradentary in a rounded butt joint in *Eusthenopteron*; similar contact between the  
434 prearticular and first infradentary occurs in most “osteolepiforms” (Lebedev 1995; Ahlberg  
435 and Johanson 1997; Ahlberg and Clack 1998). In contrast, the ventral margin of the  
436 prearticular rests on the Meckelian ossification and does not reach the first infradentary in  
437 porolepiforms or *Gogonasus* (Ahlberg 1992; Long *et al.* 1997). The laterally turned dorsal  
438 margin of the prearticular overlaps the medial shelves of the coronoids and forms the medial

439 margin of the mandibular adductor fossa. The prearticular is broadly applied to the medial  
440 aspect of the articular. The medial surface of the posterior prearticular of MHMN 06-538 and  
441 UMZC GN.1147 bears a shallow, anteroposteriorly elongated depression that may mark a  
442 muscle attachment site. This depression is bounded dorsally by a longitudinal ridge (Figs 2D  
443 and 3B, E); a similar ridge occurs on the prearticular of *Medoevia* (Lebedev 1995). The  
444 ventral margin of the prearticular weakly contacts the ventral margins of the second and third  
445 infradentaries; however, it is joined more firmly to the posterior part of the fourth  
446 infradentary.

447

448 *Anterior coronoid.* The anterior coronoid (Figs 2 and 3C) of *Eusthenopteron* is  
449 anteroposteriorly short and dorsoventrally expanded. It is tallest at its midsection and tapers  
450 anteriorly and posteriorly. The anterior and posterior portions of the bone are thin vertical  
451 sheets in transverse section; the central portion (which bears the enlarged fangs) is shaped  
452 like an inverted “L” in cross-section. The lateral surface of the vertical lamina contacts the  
453 medial aspect of the dentary, with a small area contacting the dorsomedial aspect of the  
454 second infradentary. The edge of the medial shelf fits under the lateral margins of the  
455 postsymphysial and prearticular. The anterior margin of the anterior coronoid forms the  
456 lateral and posterior margins of the precoronoid fossa; the posterior edge of the anterior  
457 coronoid forms the anterior margin of the first intercoronoid fossa. The number of fangs (and  
458 replacement pits) borne on the coronoids varies among and within individuals, presumably as  
459 a result of different stages of tooth replacement; such variability in the number of fangs is  
460 also noted in *Gogonasus* (Long *et al.* 1997). The right anterior coronoids of UMZC GN.1147  
461 (preserved portion) and MHMN 06-538 bear a single large fang, with a smaller tooth visible  
462 in MHMN 06-538 within a replacement pit posterior to the large fang. The left anterior  
463 coronoid of MHMN 06-538 and both anterior coronoids of UMZC GN.792 bear two large

464 fangs. The posterior tip of the anterior coronoid touches the anterior tip of the middle  
465 coronoid in UMZC GN.1147; there is no contact between these two elements in MHMN 06-  
466 538 or UMZC GN.792. The anterior process of the coronoid does not contact the  
467 adsymphyseal plate in *Eusthenopteron*, as is typical for tristichopterids (see previous  
468 discussion in “Adsymphyseal” section).

469

470 *Middle coronoid.* The middle coronoid (Figs 2 and 3C) is slightly shorter than the anterior  
471 coronoid. Its cross-sectional geometry resembles that of the anterior coronoid. Its anterior and  
472 posterior margins are more rounded than those of the anterior coronoid, the medial shelf is  
473 overlapped by the dorsal margin of the prearticular and the lateral aspect of the vertical  
474 lamina contacts the medial surfaces of the dentary and second and third infradentaries. The  
475 right middle coronoid of UMZC GN.1147 bears a large fang and a smaller, anterior tooth  
476 within a replacement pit; both middle coronoids of MHMN 06-538 bear two fangs. The  
477 anterior margin of the middle coronoid forms the posterior edge of the first intercoronoid  
478 fossa; the posterior margin of this bone forms the anterior edge of the second intercoronoid  
479 fossa. The posterolateral tip of the middle coronoid weakly contacts the anterior tip of the  
480 posterior coronoid.

481

482 *Posterior coronoid.* The posterior coronoid of *Eusthenopteron* (Figs 2 and 3C) is twice the  
483 length of the anterior and middle coronoids. It resembles the other coronoids in cross-  
484 sectional geometry and in its medial contact with the prearticular. The vertical lamina  
485 laterally contacts the medial aspects of the dentary and third infradentary; the tapered  
486 posterior tip laterally contacts the fourth infradentary and contributes to the lateral margin of  
487 the mandibular adductor fossa. The posterior coronoid bears two sets of enlarged fangs,

488 situated on either side of a deep concavity in the center of the bone that accommodated the  
489 posterior set of enlarged ectopterygoid fangs. The possession of two sets of fangs on the  
490 posterior coronoid is a derived condition unique to tristichopterids (Ahlberg and Clack 1998).  
491 The posterior coronoids on both sides of MHMN 06-538 feature two large fangs anterior and  
492 one fang posterior to the concavity; the right posterior coronoid of UMZC GN.1147 features  
493 one large fang anterior and two smaller teeth posterior to the concavity, with no visible  
494 replacement pits.

495

496 *Articular.* Scans show that the articular of *Eusthenopteron* is shaped like an inverted triangle  
497 in transverse section. In dorsal view, the articular is widest at the level of the jaw joint and  
498 tapers anteromedially to a fine point lying against the prearticular, as in *Gogonasus* (Long *et*  
499 *al.* 1997). This process reaches the anterior limit of the mandibular adductor fossa in MHMN  
500 06-538 but is substantially shorter in UMZC GN.1147. The articular is extensively  
501 overlapped by the fourth infradentary (laterally) and prearticular (medially). High-resolution  
502 CT scans of the posterior portion of MHMN 06-538 reveal the detailed morphology of the  
503 articular for the first time. Posteriorly, the articular expands laterally to form the posterior  
504 wall of the mandibular adductor fossa, which is strongly concave dorsally and anteriorly. The  
505 dorsal margin of this concavity is drawn up into a strong ridge that is U-shaped in dorsal  
506 view. This ridge defines the posterior margin of the adductor fossa and the anterior margin of  
507 the jaw joint. The jaw joint surface faces posterodorsally and is concave in lateral view; in  
508 dorsal view, it is mediolaterally wider than it is anteroposteriorly long. It bears a low, central  
509 eminence that separates the joint surface into lateral and medial faces (Jarvik 1980). Posterior  
510 to the jaw joint, the articular terminates as a transversely oriented, thickened ridge (which  
511 looks like a rounded point in lateral view). The ridges of the articular limited anterior and  
512 posterior movements of the lower jaw against the quadrate; additionally, the posterior ridge

513 may have served as a muscle attachment site (Jarvik 1980). A pair of canals anterior to the  
514 joint surface described by Jarvik (1980) cannot be discerned in CT scans. Because the fourth  
515 infradentary wraps around the posterior margin of the articular, there is no comma-shaped  
516 scar on the ventral aspect of the articular as reported in *Gogonasus* (Long *et al.* 1997) or by  
517 Jarvik (1980) in *Eusthenopteron*.

518

### 519 *The submandibular bones*

520 Closely associated with the bones of the lower jaw are the submandibular bones (Fig. 2B-C),  
521 which supported elements of the gill cover (Jarvik, 1944) and played a role in operating the  
522 pump mechanism by which *Eusthenopteron* and other “osteolepiforms” ventilated their gills  
523 (Long *et al.* 1997; Clack 2012; Schoch 2014). These bones were described by Jarvik (1944,  
524 1980) but CT scans of MHMN 06-538 and UMZC GN.1147 reveal new details of their  
525 contacts with each other and the infradentary series. There are eight marginal bones that lie  
526 medial to lower jaws, which are referred to here as branchiostegal rays (note that the large  
527 posterior element is referred to as the submandibulobranchiostegal plate by Jarvik [1980]).  
528 Branchiostegal rays 1-7 are ovoid or rectangular in shape, being anteroposteriorly elongate  
529 and mediolaterally narrow. Branchiostegal ray 8 is over twice the length of the anterior  
530 branchiostegal rays and transversely expanded; in ventral view, it is roughly triangular in  
531 shape with the apex directed medially. The substantially larger size of the posterior  
532 branchiostegal ray also occurs in *Gogonasus* (Long *et al.* 1997) and *Medoevia* (Lebedev  
533 1995). In cross-section, these marginal bones are thickest at their rounded, lateral margins  
534 and taper medially to a fine point.

535         Between these marginal bones, *Eusthenopteron* exhibits a pair of large, triangular  
536 principal gular plates and a single, unpaired, diamond-shaped median gular. Like the

537 marginal bones, the principal gulars are thickest laterally and taper medially to a fine point in  
538 cross-section. The median gular, which is partially preserved in UMZC GN.1147, is thickest  
539 in its center and thins laterally. Anteriorly, the median gular becomes triangular in cross-  
540 section with the apex forming a ventrally-directed keel that inserts between the first  
541 branchiostegal rays. As illustrated by Jarvik (1944, 1980), the posterolateral margins of the  
542 median gular ventrally lap the anteromedial margins of the principal gulars, which exhibit a  
543 distinct overlap surface. The principal gulars also exhibit overlap surfaces along their lateral  
544 margins, which correspond to the medial margins of the branchiostegal rays. The medial  
545 margins of the principal gulars approach each other at the midline, and the right principal  
546 gular underlaps its counterpart anteriorly in MHMN 06-538; however, this may be due to  
547 deformation.

548         The medial margins of branchiostegal rays 2-8 underlap the principal gular plate;  
549 branchiostegal rays 1 and 2 underlap the lateral margin of the median gular plate; a similar  
550 arrangement between the branchiostegal rays and gulars is reported in *Gogonasus* (Long *et*  
551 *al.* 1997). The posterior margin of each branchiostegal ray ventrally laps the anterior margin  
552 of the succeeding branchiostegal ray, as illustrated by Jarvik (1944, 1980). The rounded  
553 lateral margins of the branchiostegal rays are not underlapped by the infradentaries as  
554 described by Jarvik (1944, 1980) but articulate with a continuous groove (previously  
555 described) along the ventromedial margins of the infradentaries. The morphology of this  
556 contact may have permitted the branchiostegal rays to rotate against the lower jaws during  
557 buccal expansion associated with ventilation of the gills or suction feeding.

558         During the early evolution of tetrapods, the operculogular series (including the  
559 submandibular bones) is reduced and eventually lost: *Panderichthys* retains a full set of  
560 operculogular bones, although these are reduced in anteroposterior length compared to  
561 *Eusthenopteron* (Clack 2012); *Tiktaalik* features submandibulars and gulars but the status of

562 the opercular bones is indeterminate (Daeschler et al. 2006); and the operculogular series is  
563 entirely absent in *Acanthostega*. This progressive loss of the submandibular bones is mirrored  
564 by the reduction and loss of the opercular series and transformation of the hyomandibula into  
565 the stapes; all of these components worked to maintain a tight connection between and ensure  
566 coordinated movements of the skull and gill skeleton during ventilation (Jarvik 1954). These  
567 trends are thought to reflect a reduced reliance on gills for breathing or suction feeding  
568 (Clack 2012).

569

### 570 *3D Reconstruction of the Eusthenopteron lower jaw*

571 The lateral aspect of the 3D model (Fig. 3A) closely resembles previous reconstructions  
572 (Jarvik 1944, Jarvik 1980): the infradentaries and tips of the coronoid fangs are visible in  
573 external view, the sutures between the infradentaries are anterodorsally-directed, and the  
574 second infradentary is the longest in the series. In contrast, there are notable differences  
575 between previous reconstructions and the 3D model in medial view (Fig. 3B). The  
576 symphyseal pit, illustrated by Jarvik (1944, 1980), is not present; instead, the elongate  
577 postsymphyseal forms a substantial part of the mandibular symphysis. Although absent from  
578 earlier descriptions, Jarvik (1980) later figured and described a small “parasymphyseal dental  
579 plate” between the dentary, prearticular and Meckelian bone. Scans reveal that such an  
580 element, the adsymphyseal, is present at the anteromedial tip of the lower jaw between the  
581 dentary and postsymphyseal, capping the Meckelian bone (Fig. 3B-C). The posterodorsal  
582 margin of the prearticular is more deeply embayed than depicted by Jarvik (1944, 1980),  
583 exposing the articular and medial aspect of the surangular in medial view. The dorsal aspect  
584 of the lower jaw of *Eusthenopteron* has never been reconstructed and CT scans confirm the  
585 presence of the precoronoid fossa and two intercoronoid fossae. Finally, the ventral aspect of

586 the 3D reconstruction demonstrates the intermittent contacts between the prearticular and  
587 infradentaries, with the Meckelian bone occupying gaps between these elements.

588

## 589 **DISCUSSION**

### 590 *Mandibular symphysis*

591 The mandibular symphysis of *Eusthenopteron* has been previously described and figured  
592 (Jarvik 1944, 1980); however, CT scans reveal numerous new details. The symphyseal region  
593 of MHMN 06-538 is broken and rich in high-density precipitates, creating scanning artifacts;  
594 scans of UMZC GN.792 are clearer and provide much of the information presented below.

595 Jarvik (1944) states that the Meckelian bone is exposed at the mandibular symphysis  
596 at the bottom of the symphyseal pit, a feature roofed by the anteromedial extension of the  
597 dentary. Evidence from CT scans suggests the symphyseal pit is absent and that Meckelian  
598 bone fills the anterior portion of the intramandibular canal but is not exposed at the  
599 mandibular symphysis in either MHMN 06-538 or UMZC GN.792. Instead, the symphysis is  
600 formed by the dentary, postsymphyseal and first infradentary, and the intramandibular canal  
601 does not open into the symphysis in *Eusthenopteron* as in *Acanthostega* (Porro *et al.* 2015).  
602 The anterior intramandibular canal is bounded by the dentary (laterally and dorsally),  
603 adsymphyseal (dorsally), first infradentary (laterally and ventrally), and postsymphyseal  
604 (medially), and opens posteriorly into the precoronoid fossa (Fig. 3C).

605 In both MHMN 06-538 and UMZC GN.792, the dorsoventrally expanded and  
606 flattened medial surface of the postsymphyseal closely approaches but does not directly  
607 contact its counterpart across the midline at the symphysis. Likewise, the flat medioventral

608 surface of the dentary approaches but does not contact its opposite, and presumably both of  
609 these elements were joined across the symphysis by strong ligaments.

610 Scans reveal that the medioventral flange of the left first infradentary of UMZC  
611 GN.792 extensively underlaps the right first infradentary across the symphysis (Fig. 2F). The  
612 most anterior portion of the left infradentary of MHMN 06-538 is broken; however, it also  
613 appears that the left first infradentary underlapped its counterpart in this specimen. This  
614 asymmetrical contact between the first infradentaries was described and figured by Jarvik  
615 (1944) and is not a result of postmortem deformation but genuine symphyseal morphology.  
616 As the only bone-bone contact at the mandibular symphysis of *Eusthenopteron*, the first  
617 infradentaries would have been subjected to high stress as force was transferred across the  
618 symphysis, particularly during unilateral biting.

619 A longitudinal row of four symphyseal dermal bones or ossicles occur between the  
620 anterior and anteroventral tips of the dentary (but not the first infradentary) in UMZC  
621 GN.792 (Fig. 2F), externally lapping the symphysis as described by Jarvik (1944, 1980).

622

### 623 *Sutural morphology in the lower jaw of Eusthenopteron*

624 Skulls are made up of individual bones joined by collagen fibres at sutures, which assume a  
625 number of forms: butt joints that meet at flat edges; overlapping scarf joints; and convoluted  
626 interdigitations. Experimental and modelling studies have suggested that sutures perform a  
627 functional role by modifying and absorbing strain during feeding and other behaviours, and  
628 particular sutural shapes have been linked to specific loading regimes. Butt joints are  
629 associated with tension or bending, interdigitations are associated with compression, and  
630 scarf joints have been associated with torsion, shear, or both compression and tension (Bolt,

631 1974; Herring and Mucci 1991; Busbey 1995; Rafferty and Herring 1999; Herring and Teng  
632 2000; Markey *et al.* 2006; Markey and Marshall 2007a). By correlating sutural morphology  
633 in the skull roof with *in vivo* strain orientations and feeding mode in living *Polypterus*,  
634 Markey and Marshall (2007b) inferred that *Eusthenopteron* used suction feeding (not biting)  
635 to capture and ingest prey.

636         Jarvik (1944, 1980) illustrated sutural contacts on the lateral aspect of the lower jaw  
637 of *Eusthenopteron*. Evidence from CT scans largely agrees with Jarvik's illustrations -  
638 anterior bones overlap posterior bones in the infradentary series and the dentary extensively  
639 overlaps the second, third and fourth infradentaries (Fig. 4A). Contrary to Jarvik's  
640 illustrations, the dorsal margin of the first infradentary meets the dentary in a butt joint. Scarf  
641 joints are the most common suture type in the lower jaw, while butt joints occur at the  
642 anterior end and ventral margin of the lower jaw and interdigitations are only found between  
643 the dentary and the coronoids. The bones of the dorsal margin of the lower jaw (dentary,  
644 coronoids and prearticular) are strongly joined through broad overlaps and interdigitations  
645 (Fig. 4D); CT scans also reveal the contact between the coronoids and second, third and  
646 fourth infradentaries for the first time. In contrast, the ventral margin of the lower jaw is  
647 weakly sutured (Fig. 4C), particularly in its mid-section, with the second, third and fourth  
648 infradentaries contacting the prearticular only intermittently. However, the slender rod of  
649 Meckelian bone wedged between the prearticular and infradentaries presumably filled any  
650 gaps and strengthened the ventral margin of the lower jaw.

651         Extensive scarf joints, as well as the box-like cross-sectional geometry of the lower  
652 jaw of *Eusthenopteron*, are well-adapted to resisting a loading regime involving torsion, shear  
653 and bending. The coronoids, which bear the largest teeth, meet the dentary at interdigitated  
654 contacts. This sutural morphology suggests resistance to laterally-directed forces on the  
655 coronoid fangs, such as those generated by prey attempting to escape. If *Eusthenopteron*

656 employed suction to capture and ingest prey as suggested by Markey and Marshall (2007b),  
657 the elongate coronoid fangs may have functioned as “place holders” during capture of prey  
658 too large to ingest in a single suction feeding event (see Conclusions below).

659         The first infradentary contacts dorsal elements (dentary, postsymphysial, and  
660 prearticular) via butt joints, which are presumably adapted to resist tension. As noted above,  
661 the contact between the left and right first infradentaries is the strongest of the mandibular  
662 symphysis (the only bone-bone contact at the symphysis), with connections between  
663 opposing postsymphysials and dentaries being ligamentous. As force transfer (from the  
664 balancing- to working-side) during unilateral biting would have occurred primarily through  
665 the first infradentaries, butt joints may have allowed some ‘give’ between these bones and the  
666 dentaries and postsymphysials that were more loosely joined at the symphysis. Similar  
667 deformation at the symphysis during biting has been suggested for rhizodonts (Jeffery 2003),  
668 although the longitudinal intramandibular hinge of rhizodonts is absent in *Eusthenopteron*.

669

## 670 **CONCLUSIONS**

671 In this article we provide the first comprehensive description of the lower jaw of  
672 *Eusthenopteron foordi*, including new information on sutural morphology, the mandibular  
673 symphysis, the jaw joint and the arrangement and contacts of the submandibular bones.  
674 Additionally, we have identified a novel ossification, the postsymphysial, which occurs on  
675 the anteromedial aspect of the lower jaw in *Eusthenopteron* and other “osteolepiform”,  
676 tristichopterid and elpistostegid taxa. Data from CT scans and visualization software were  
677 used to create a 3D digital reconstruction of the lower jaw and sutural morphology was used  
678 to predict load regime and feeding behavior in this iconic fossil taxon.

679           Suction, which relies on rapid expansion of the oropharyngeal cavity, is the primary  
680 feeding mechanism in fishes and many other aquatic vertebrates, being used to capture prey  
681 and during intraoral transport (Westneat 2006). Biting fishes are defined as species that  
682 depend on forceful contact of the oral jaws with the prey during acquisition (Alfaro *et al.*  
683 2001). Changes in skull morphology, muscle activity patterns and behaviour accompany the  
684 transition from suction feeding to biting (Alfaro *et al.* 2001): biting fish have more robust  
685 skulls, better developed adductor muscles (Alfaro *et al.* 2001; Van Wassenbergh *et al.* 2004,  
686 2007) and produce higher forces rather than faster jaw movements (Westneat 2004).  
687 Although the “optimal” design for a biter and a suction feeder are different, modifications to  
688 increase bite performance do not necessarily reduce the ability to use suction (Van  
689 Wassenbergh *et al.* 2007). Many species effectively combine suction and biting to position  
690 prey (Alfaro *et al.* 2001) and all biters retain the ability to generate suction for intraoral  
691 transport (Westneat 2006). Biters often take larger prey than suction feeders, and biting may  
692 represent a strategy to overcome dietary restrictions imposed by maximum gape size  
693 (Westneat 2006).

694           Suction has been inferred as the feeding mechanism used by *Eusthenopteron* based on  
695 various aspects of skull morphology. Hitchcock (1995) suggested that the anterior vertebrae  
696 and posterior aspect of the skull in *Eusthenopteron* accommodated powerful epaxial muscles  
697 that raised the cranium and opened the opercula. According to Hitchcock’s model, this action  
698 forced the quadrate forward, causing depression of the lower jaw. At the same time,  
699 contraction of the sternohyoideus muscle acted on the hyobranchial apparatus to ventrally  
700 expand the oral cavity while mobile joints between the palatoquadrate, braincase and cheek  
701 region allowed lateral expansion of oral cavity. This model placed greater emphasis on the  
702 role of suction during feeding in *Eusthenopteron* and less reliance on biting. More recently,  
703 the sutural morphology of the skull roof has also been used to support suction-feeding in

704 *Eusthenopteron* (Markey and Marshall 2007b). Other anatomical features, such as the well-  
705 developed operculogular series and small marginal teeth, support suction feeding in this  
706 taxon.

707         In contrast, the extensive scarf joints and enlarged coronoid and palatal fangs of  
708 *Eusthenopteron* suggest that biting was used to some extent during prey capture. The  
709 coronoid/palatal fangs of *Eusthenopteron* superficially resemble the long, sharp dentary teeth  
710 of the pike (*Esox lucius*). Pike primarily employ suction to capture and ingest prey; however,  
711 during the capture of very large prey, the teeth are used as ‘place holders’ during successive  
712 suction events that draw prey through the buccal cavity and into the pharynx (LBP personal  
713 observations). Fish that employ both biting and suction feature enlarged jaw adductor  
714 muscles and reinforced articulations of the suspensorium with the neurocranium, which limit  
715 lateral expansion of the buccal cavity; these taxa compensate by larger and faster ventral  
716 expansion of the buccal cavity by depression of the hyoid and branchiostegal rays (Van  
717 Wassenbergh *et al.* 2004, 2007). Examination of the skulls of both *Gogonasus* and  
718 *Eusthenopteron* by Long *et al.* (1997) suggests that any movements between the braincase,  
719 palatoquadrate and cheek region of these taxa were minor, if even possible (*contra*  
720 Hitchcock, 1995); this suggests that lateral expansion of the oral cavity was limited. On the  
721 other hand, the well-developed hyoid skeleton of *Eusthenopteron* (Jarvik 1954) coupled with  
722 the potential for rotation of the branchiostegal rays against the infradentaries supports the  
723 idea that *Eusthenopteron* may have combined suction feeding (generated primarily by ventral  
724 expansion of the oral cavity) with biting, possibly to permit the capture of larger prey.  
725 Morphological adaptations associated with this feeding mode may have set the stage for the  
726 evolution of biting as the primary mode of prey capture in later tetrapods.

727

728 *Acknowledgements.* This work was funded by a Marie Curie International Incoming Research  
729 Fellowship to LBP (“Tetrapods Rising”, 300161). Many thanks to Marius Arsenault  
730 (Miguasha National Park, Québec, Canada) and Tim Rowe (Department of Geological  
731 Sciences, University of Texas at Austin, TX, USA) for CT scans of MHMN 06-538 and to  
732 Sylvain Desbiens (MHMN) and Mathew Lowe (UMZC) for access to specimens. CT-  
733 scanning was carried out by Matthew Colbert and Richard Ketcham (UTCT, Department of  
734 Geological Sciences, University of Texas at Austin, TX, USA) and Dan Sykes (Imaging and  
735 Analysis Centre, Natural History Museum, London, UK). Alejandra Sánchez-Eróstegui and  
736 Jean-Luc Garnier (FEI Visualization Sciences Group, Mérignac Cédex, France) provided  
737 technical support for Avizo. Specimens were photographed by Russell Stebbings (UMZC).  
738 Sincere thanks to our colleagues Professor Per Ahlberg (Uppsala University, Sweden), who  
739 provided valuable observations and insights into sarcopterygian and early tetrapod anatomy,  
740 and Tim Smithson (University of Cambridge), for his observations on symphyseal  
741 morphology and the submandibular bones.

742 *Author contributions.* LBP, EJR and JAC conceived of and designed the research. LBP  
743 collected and processed CT data and constructed the three-dimensional model. LBP, EJR and  
744 JAC interpreted CT data. LBP drafted the manuscript. All three authors read and commented  
745 on the manuscript.

746

## 747 **SUPPORTING INFORMATION**

748 Additional supporting information are available in the [Dryad Digital Repository]:

749 doi:10.5061/dryad.t9q11

750 **Appendix S1.**  $\mu$ CT sections through the three specimens (left) with black line indicating  
751 position on corresponding 3D surfaces (right). A, Transverse section through the left first  
752 intercoronoid fossa of MHMN 06-538. B, Transverse section through the right precoronoid  
753 fossa of UMZC GN.792. C, Transverse section through the anterior lower jaw of UMZC  
754 GN.1147.

755 **Appendix S2.** Transformation matrices for three-dimensional surface models of individual  
756 bones of the lower jaw of *Eusthenopteron foordi*.

757

## 758 REFERENCES

759 ABEL, R. L., LAURINI, C. R. and RICHTER, M. 2012. A palaeobiologist's guide to  
760 'virtual' micro-CT preparation. *Palaeontologia Electronica*, **15**. [http://palaeo-  
761 electronica.org/content/issue-2-2012-technical-articles/233-micro-ct-workflow](http://palaeo-<br/>761 electronica.org/content/issue-2-2012-technical-articles/233-micro-ct-workflow).

762 AHLBERG, P. E. 1992. A new holoptychid porolepiform fish from the Upper Frasnian of  
763 Elgin, Scotland. *Palaeontology*, **35**, 813-828.

764 \_\_\_\_ 1995. *Elginerpeton pancheni* and the earliest tetrapod clade. *Nature*, **373**, 420-425.

765 \_\_\_\_ and CLACK J. A. 1998. Lower jaws, lower tetrapods – a review based on the Devonian  
766 genus *Acanthostega*. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **89**, 11-  
767 46.

768 \_\_\_\_ and JOHANSON, Z. 1997. Second tristichopterid (Sarcopterygii, Osteolepiformes) from  
769 the Upper Devonian of Canowindra, New South Wales, Australia and phylogeny of the  
770 Tristichopteridae. *Journal of Vertebrate Paleontology*, **17**, 653-673.

771 \_\_\_\_ \_\_\_\_ 1998. Osteolepiforms and the ancestry of tetrapods. *Nature*, **395**, 792-794.

- 772 \_\_\_ LUKŠEVIČS E. and MARK-KURIK, E. 2000. A near-tetrapod from the Baltic Middle  
773 Devonian. *Palaeontology*, **43**, 533-548.
- 774 \_\_\_ FRIEDMAN M. and BLOM, H. 2005. New light on the earliest known tetrapod jaw.  
775 *Journal of Vertebrate Paleontology*, **25**, 720-724.
- 776 ALFARO, M. E., JANOVETZ, J. and WESTNEAT, M. W. 2001. Motor control across  
777 trophic strategies: muscle activity of biting and suction feeding fishes. *American Zoologist*,  
778 **41**, 1266-1279.
- 779 ANDERSON, P. S. L., FRIEDMAN, M. and RUTA, M. 2013. Late to the table:  
780 diversification of tetrapod mandibular biomechanics lagged behind the evolution of  
781 terrestriality. *Integrative and Comparative Biology*, **53**, 197-208.
- 782 ANDREWS, S. M. and WESTOLL, T. S. 1970. The postcranial skeleton of *Eusthenopteron*  
783 *foordi* Whiteaves. *Transactions of the Royal Society of Edinburgh*, **68**, 207-329.
- 784 BOISVERT, C. A., MARK-KURIK, E. and AHLBERG, P. E. 2008. The pectoral fin of  
785 *Panderichthys* and the origin of digits. *Nature*, **456**, 636-638.
- 786 BOLT, J. R. 1974. Evolution and functional interpretations of some suture patterns in  
787 Paleozoic labyrinthodont amphi-boans and other lower tetrapods. *Journal of Paleontology*, **48**,  
788 434-458.
- 789 BOLT, J. R. and LOMBARD, R. E. 2001. The mandible of the primitive tetrapod  
790 *Greererpeton* and the early evolution of the tetrapod lower jaw. *Journal of Paleontology*, **75**,  
791 1016-1042.

- 792 BRAZEAU, M. D. 2005. A new genus of rhizodontid (Sarcopterygii, Tetrapodomorpha)  
793 from the Lower Carboniferous Horton Bluff Formation of Nova Scotia, and the evolution of  
794 the lower jaws in this group. *Canadian Journal of Earth Sciences*, **42**, 1481-1499.
- 795 \_\_\_ and AHLBERG, P. E. 2006. Tetrapod-like middle ear architecture in a Devonian fish.  
796 *Nature*, **439**, 318-321.
- 797 BRYANT, W. L. 1919. On the structure of *Eusthenopteron*. *Bulletin of the Buffalo Society of*  
798 *Natural History*, **13**, 1-23.
- 799 BUSBEY, A. P. 1995. The structural consequences of skull flattening in crocodylians. 173-  
800 192. In Thomason, J. J. (ed). *Functional morphology in vertebrate paleontology*. Cambridge  
801 University Press, Cambridge, 296 pp .
- 802 CLACK, J. A. 2003. A revised reconstruction of the dermal skull roof of *Acanthostega*  
803 *gunnari*, an early tetrapod from the Late Devonian. *Transactions of the Royal Society of*  
804 *Edinburgh: Earth Sciences*, **93**, 163-165.
- 805 \_\_\_ 2009. The fin to limb transition: new data, interpretations, and hypotheses from  
806 palaeontology and development biology. *Annual Review of Earth and Planetary Sciences*, **37**,  
807 163-179.
- 808 \_\_\_ 2012. *Gaining ground: the origin and evolution of tetrapods, Second Edition*. Indiana  
809 University Press, Bloomington, 544 pp.
- 810 \_\_\_ AHLBERG, P. E., BLOM, H. and FINNEY, S. M. 2012. A new genus of Devonian  
811 tetrapod from northeast Greenland, with new information on the lower jaw of *Ichthyostega*.  
812 *Palaeontology*, **55**, 73-86.

- 813 CLÉMENT, G. and LEBEDEV, O. 2014. Revision of the early tetrapod *Obruchevichthys*  
814 Vorobeya, 1977 from the Frasnian (Upper Devonian) of the North-western East European  
815 platform. *Paleontological Journal*, **48**, 1082-1091.
- 816 COATES, M. I. and CLACK, J. A. 1990. Polydactyly in the earliest known tetrapod limbs.  
817 *Nature*, **347**, 66-69.
- 818 \_\_\_ JEFFERY, J. E. and RUTA, M. 2002. Fins to limbs: what the fossils say. *Evolution and*  
819 *Development*, **4**, 390-401.
- 820 \_\_\_ RUTA, M. and FRIEDMAN, M. 2008. Ever since Owen: changing perspectives on the  
821 early evolution of tetrapods. *Annual Review of Ecology, Evolution, and Systematics*, **39**, 571-  
822 592.
- 823 CUNNINGHAM, J. A., RAHMAN, I. A., LAUTENSCHLAGER, S., RAYFIELD, E. J. and  
824 DONOGHUE, P. C. J. 2014. A virtual world of paleontology. *Trends in Ecology and*  
825 *Evolution*, **29**, 347-357.
- 826 DAESCHLER, E. B. 2000. Early tetrapod jaws from the Late Devonian of Pennsylvania,  
827 USA. *Journal of Paleontology*, **74**, 301-308.
- 828 \_\_\_ SHUBIN, N. H. and JENKINS, F. A. 2006. A Devonian tetrapod-like fish and the  
829 evolution of the tetrapod body plan. *Nature*, **440**, 757-763.
- 830 DONOGHUE, P. C. J., BENGTSON, S., DONG, X., GOSTLING, N. J., HULDTGREN, T.,  
831 CUNNINGHAM, J. A., YIN, C., YUE, Z., PENG, F. and STAMPANONI, M. 2006.  
832 Synchrotron X-ray tomographic microscopy of fossil embryos. *Nature*, **442**, 680-683.
- 833 GREGORY, W. K. and RAVEN, H. C. 1941. Origin of paired fins and limbs. *Annals of the*  
834 *New York Academy of Sciences*, **42**, 273-360.

- 835 HERRING, S. W. and MUCCI, R. J. 1991. *In vivo* strain in cranial sutures: the zygomatic  
836 arch. *Journal of Morphology*, **207**, 225-239.
- 837 \_\_\_ and TENG, S. 2000. Strain in the braincase and its sutures during function. *American*  
838 *Journal of Physical Anthropology*, **112**, 575-593.
- 839 HITCHCOCK, E. C. 1995. A functional interpretation of the anteriormost vertebrae and skull  
840 of *Eusthenopteron*. *Bulletin du Muséum National d'Histoire Naturelle Paris*, **17**, 269-285.
- 841 JARVIK, E. 1942. On the structure of the snout of crossopterygians and lower gnathostomes  
842 in general. *Zoologiska Bidrag Från Uppsala*, **21**, 235-675.
- 843 \_\_\_ 1944. On the dermal bones, sensory canals and pit-lines of the skull in *Eusthenopteron*  
844 *foordi* Whiteaves, with some remarks on *E. save-söderberghi* Jarvik. *Kungliga Svenska*  
845 *Vetenskapsakademiens Handlingar, Third Series*, **21**, 1-48.
- 846 \_\_\_ 1954. On the visceral skeleton in *Eusthenopteron* with a discussion of the parasphenoid  
847 and palatoquadrate in fishes. *Kungliga Svenska Vetenskapsakademiens Handlingar, Fifth*  
848 *Series*, **21**, 1-104.
- 849 \_\_\_ 1980. *Basic structure and evolution of vertebrates*. Academic Press, London, 575 pp.
- 850 JEFFERY, J. E. 2003. Mandibles of rhizodontids: anatomy, function and evolution within the  
851 tetrapod stem-group. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **93**,  
852 255-276.
- 853 JOHANSON, Z. and AHLBERG, P. E. 2001. Devonian rhizodontids and tristichopterids  
854 (Sarcopterygii; Tetrapodomorpha) from East Gondwana. *Transactions of the Royal Society of*  
855 *Edinburgh: Earth Sciences*, **92**, 43-74.

- 856 LAUTENSCHLAGER, S., RAYFIELD, E. J., ALTANGEREL, P., ZANNO, L. E. and  
857 WITMER, L. M. 2012. Endocranial anatomy of Therizinosauria and its implications for  
858 sensory and cognitive function. *PLOS ONE*, 7, DOI: 10.1371/journal.pone.0052289
- 859 LEBEDEV, O. A. 1995. Morphology of a new osteolepid fish from Russia. *Bulletin du*  
860 *Muséum National d'Histoire Naturelle Paris*, **17**, *Bulletin du Muséum National d'Histoire*  
861 *Naturelle Paris*, **17**, 287-341.
- 862 LONG, J. A., BARWICK, R. E. and CAMPBELL, K. S. W. 1997. Osteology and functional  
863 morphology of the osteolepiform fish *Gogonasus andrewsae* Long 1985, from the Upper  
864 Devonian Gogo Formation, Western Australia. *Records of the Western Australian Museum*,  
865 **Supp. 53**, 1-89.
- 866 MARKEY, M. J. and MARSHALL, C. R. 2007a. Linking form and function of the fibrous  
867 joints in the skull: a new quantification scheme for cranial sutures using the extant fish  
868 *Polypterus endlicherii*. *Journal of Morphology*, **268**, 89-102.
- 869 \_\_\_\_ 2007b. Terrestrial-style feeding in a very early aquatic tetrapod is supported by  
870 evidence from experimental analysis of suture morphology. *Proceedings of the National*  
871 *Academy of Sciences of the United States of America*, **104**, 7134-7138.
- 872 \_\_\_\_ MAIN, R. P. and MARSHALL, C. D. 2006. *In vivo* cranial suture function and suture  
873 morphology in the extant fish *Polypterus*: implications for inferring skull function in living  
874 and fossil fish. *Journal of Experimental Biology*, **209**, 2085-2102.
- 875 NEENAN, J. M., RUTA, M., CLACK, J. A. and RAYFIELD, E. J. 2014. Feeding  
876 biomechanics in *Acanthostega* and across the fish-tetrapod transition. *Proceedings of the*  
877 *Royal Society B*, **281**, 20132689. DOI: 10.1098/rspb.2013.2689

- 878 PIERCE, S. E., CLACK, J. A. and HUTCHINSON, J. R. 2012. Three-dimensional limb joint  
879 mobility in the early tetrapod *Ichthyostega*. *Nature*, **486**, 523-526.
- 880 PORRO, L. B., BUTLER, R. J., BARRETT, P. M., MOORE-FAY, S. and ABEL, R. 2011.  
881 New heterodontosaurid specimens from the Lower Jurassic of southern Africa and the early  
882 ornithischian dinosaur radiation. *Transactions of the Royal Society of*  
883 *Edinburgh: Earth Sciences*, **101**, 351-366.
- 884 \_\_\_\_ RAYFIELD, E. J. and CLACK, J. A. 2015. Descriptive anatomy and three-dimensional  
885 reconstruction of the skull of *Acanthostega gunnari* Jarvik, 1952. *PLOS ONE*, **10(3)**,  
886 e0118882. Doi: 10.1371/journal.pone.0118882.
- 887 RAFFERTY, K. L. and HERRING, S. W. 1999. Craniofacial sutures: morphology, growth,  
888 and *in vivo* masticatory strain. *Journal of Morphology*, **242**, 167-179.
- 889 RAYFIELD, E. J., NORMAN, D. B., HORNER, C.C., HORNER, J. R., SMITH, P. M.,  
890 TOMASON, J. J. and UPCHURCH, P. 2001. Cranial design and function in a large theropod  
891 dinosaur. *Nature*, **409**, 1033-1037.
- 892 RÜCKLIN, M., DONOGHUE, P. C. J., JOHANSON, Z., TRINAJSTIC, K., MARONE, F.  
893 and STAMPANONI, M. 2012. Development of teeth and jaws in the earliest jawed  
894 vertebrates. *Nature*, **491**, 748-751.
- 895 RUTA, M., COATES, M. I. and QUICKE, D. L. J. 2003. Early tetrapod relationships  
896 revisited. *Biological Reviews*, **78**, 251-345.
- 897 SCHOCH, R. R. 2014. *Amphibian Evolution: The Life of Early Land Vertebrates*. John Wiley  
898 and Sons.

- 899 SCHULTZE, H.-P. and ARSENAULT, M. 1985. The panderichthyid fish *Elpistostege*: a  
900 close relative of tetrapods? *Palaeontology*, **28**, 293-309.
- 901 SHUBIN, N., TABIN, C., CARROLL, S. 1997. Fossils, genes and the evolution of animal  
902 limbs. *Nature*, **388**, 639-648.
- 903 \_\_\_\_ DAESCHLER, E. B. and JENKINS, F.A. 2014. Pelvic girdle and fin of *Tiktaalik roseae*.  
904 *Proceedings of the National Academy of Sciences of the United States of America*, **111**, 893-  
905 899.
- 906 STENSIÖ, E. A. 1922. Notes on certain crossopterygians. *Proceedings of the Zoological*  
907 *Society of London*, **92**, 1241-1271.
- 908 STERNBERG, R. M. 1941. Cranial morphology of the Devonian crossopterygian  
909 *Eusthenopteron*. *University of Toronto Studies, Geological Series*, **45**, 1-48.
- 910 VOROBYEVA, E. I. and OBRUCHEVA, H. D. 1977. Rhizodont crossopterygian fishes  
911 (Fam. Rhizodontidae) from the Middle Palaeozoic deposits of the Asian part of the USSR,  
912 89-97. *In Essays on Phylogeny and Systematics of Fossil Agnathans and Fishes*. Nauka,  
913 Moscow. [In Russian]
- 914 WESSENBERGH, S. VAN, HERREL, A., ADRIAENS, D. and AERTS, P. 2004. Effects of  
915 jaw adductor hypertrophy on buccal expansions during feeding of air breathing catfishes  
916 (Teleostei, Clariidae). *Zoomorphology*, **123**, 81-93.
- 917 \_\_\_\_ \_\_\_\_ \_\_\_\_ \_\_\_\_ 2007. No trade-off between biting and suction feeding performance in  
918 clariid catfishes. *Journal of Experimental Biology*, **210**, 27-36.
- 919 WESTNEAT, M. W. 2004. Evolution of levers and linkages in the feeding mechanisms of  
920 fish. *Integrative and Comparative Biology*, **44**, 378-389.

- 921 \_\_\_\_ 2006. Skull biomechanics and suction feeding in fishes. *In* LAUDER, G. V. and  
 922 SHADWICK, R. E. (eds). *Fish Biomechanics, Fish Physiology Series*, **23**, 29-75.
- 923 WESTOLL, T. S. 1943. The origin of the primitive tetrapod limb. *Proceedings of the Royal*  
 924 *Society B*, **131**, 373-393.
- 925 WHITEAVES, J. F. 1881. On some remarkable fishes from the Devonian rocks of  
 926 Scaumenac Bay, in the Province of Quebec. *Annals and Magazine of Natural History, Series*  
 927 *5*, **8**, 159-162.
- 928 \_\_\_\_ 1888. Illustrations of the fossil fishes of the Devonian rocks of Canada. Part II.  
 929 *Transactions and Proceedings of the Royal Society of Canada*, **6**, 77-96.

930

931 **EXPLANATIONS OF FIGURES AND TABLES**

932 **FIG. 1.** Photographs of original *Eusthenopteron foordi* specimens used in this study. A, Left  
 933 lateral view of MHMN 06-538. B, Right lateral view of MHMN 06-538. C, Right lateral  
 934 view of UMZC GN.1147. D, Dorsal view of UMZC GN.792. E, Ventral view of UMZC  
 935 GN.792. F, Close up of mandibular symphysis (inset shown in E). Scale bars equal 50 mm  
 936 (A-B), 20 mm (C– E), and 10 mm (F).

937 **FIG. 2.** Surface models of *Eusthenopteron foordi* specimens prior to retrodeformation. A,  
 938 Dorsal view of MHMN 06-538, showing only the bones of the lower jaw. B, Ventral view of  
 939 MHMN 06-538 showing the submandibular bones (opaque) and bones of the lower jaw  
 940 (transparent). C, Right lateral view of UMZC GN.1147 showing the right lower jaw and  
 941 submandibular bones. D, Medial view of UMZC GN.1147 showing the right lower jaw  
 942 bones. E, Dorsal view of the anterior end of UMZC GN.792. F, Ventral view of the anterior  
 943 end of UMZC GN.792. Individual bones are shown in various colours. Anatomical

944 abbreviations: ad, adsymphysial; ar, articular; br1 – br8, branchiostegal rays 1 through 8; co1,  
 945 anterior coronoid; co2, middle coronoid; co3, posterior coronoid; d, dentary; gu, principal  
 946 gular; ic1, first intercoronoid fossa; ic2, second intercoronoid fossa; if1, first infradentary; if2,  
 947 second infradentary; if3, third infradentary; if4, fourth infradentary; mc, Meckelian bone; mg,  
 948 median gular; os, symphyseal dermal ossicles; pa, prearticular; pf, precoronoid fossa; ps,  
 949 postsymphysial.

950 **FIG. 3.** Three-dimensional reconstruction of the lower jaw of *Eusthenopteron foordi*. Right  
 951 lateral (A) and right medial (B) views of the right lower jaw ramus; dorsal (C), ventral (D)  
 952 and oblique (E) views of the lower jaw. Individual bones are shown in various colours.  
 953 Anatomical abbreviations: ad, adsymphysial; af, mandibular adductor fossa; ar, articular; co1,  
 954 anterior coronoid; co2, middle coronoid; co3, posterior coronoid; d, dentary; ic1, first  
 955 intercoronoid fossa; ic2, second intercoronoid fossa; if1, first infradentary; if2, second  
 956 infradentary; if3, third infradentary; if4, fourth infradentary; mc, Meckelian bone; pa,  
 957 prearticular; pf, precoronoid fossa; ps, postsymphysial.

958 **FIG. 4.** Suture maps of the lower jaw of *Eusthenopteron foordi*. Right lower jaw ramus in  
 959 lateral (A), medial (B), ventral (C) and dorsal (D) views. Heavy solid lines indicate butt  
 960 joints; medium shading indicates scarf joints and the direction (but not the extent) of  
 961 underlap; cross-hatches indicate interdigitated sutures. Some sutures (such as those between  
 962 the coronoids and dentary) are a combination of suture types. The adsymphysial is not shown  
 963 as it is loosely attached to the dentary and postsymphysial. Black shading indicates openings  
 964 in the lower jaw. Dark shading at the anterior end of the jaw (C and D) indicates the  
 965 symphysis; dark shading in the middle and posterior sections of the lower jaw (C) indicates  
 966 the Meckelian bone visible between the infradentaries and the prearticular. The articular is  
 967 overlapped by all surrounding elements and is shown in light shading.