

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^{1,2,3*}, EMILY J. RAYFIELD¹ and JENNIFER A. CLACK²

5 ¹School of Earth Sciences, University of Bristol, Wills Memorial Building, Queen's Road,
6 Bristol, UK; e-mails: laura.porro@bristol.ac.uk, E.Rayfield@bristol.ac.uk

7 ²Department of Zoology, University of Cambridge, Downing Street, Cambridge, UK; e-mail:
8 jac18@cam.ac.uk

9 ³ *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

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 (μ 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/ μ 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 μ 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 μ 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 adsymphyisial, and medially by the postsymphyisial; 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, μ 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 (=postsplénial)*. 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 μ 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.** μ 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-
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.