A new Lower Triassic ichthyopterygian assemblage from Fossil Hill, Nevada

Neil P Kelley, Ryosuke Motani, Patrick Embree, Michael J Orchard

We report a new ichthyopterygian assemblage from Lower Triassic horizons of the Prida Formation at Fossil Hill in central Nevada. Although fragmentary, the specimens collected so far document a diverse fauna. One partial jaw exhibits isodont dentition with blunt tipped, mesiodistally compressed crowns and striated enamel. These features are shared with the Early Triassic genus *Utatsusaurus* known from coeval deposits in Japan and British Columbia. An additional specimen exhibits a different dentition characterized by relatively small, rounded posterior teeth resembling other Early Triassic ichthyopterygians particularly *Grippia.* This Nevada assemblage marks a southward latitudinal extension for Early Triassic ichthyopterygians along the eastern margin of Panthalassa and indicates repeated circum-oceanic dispersal events in Early Triassic ichthyopterygians.

1   A new Lower Triassic Ichthyopterygian assemblage from Fossil Hill, Nevada

2   NEIL P. KELLEY,*,1,2 RYOSUKE MOTANI,1 PATRICK EMBREE,3 and MICHAEL J.

3   ORCHARD,4 1Department of Earth and Planetary Sciences, University of California, Davis, 1

4   Shields Avenue, Davis, California, 95616, U.S.A., kelleynp@si.edu; rmotani@ucdavis.edu;

5   1Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, PO

6   Box 37012, Washington, DC 20013, USA.; 38834 Central Avenue, Orangevale, CA 95662

7   patembree@aol.com; 4Natural Resources Canada - Geological Survey of Canada, 1500-605

8   Robson St., Vancouver, B.C. V6B 5J3, Canada mike.orchard@canada.ca

9

10

11

12   *Corresponding author

13

14

15

16

17

18

19

20

21

22

23

24 Abstract

25 We report a new ichthyopterygian assemblage from Lower Triassic horizons of the Prida

26 Formation at Fossil Hill in central Nevada. Although fragmentary, the specimens collected so far

27 document a diverse fauna. One partial jaw exhibits isodont dentition with blunt tipped,

28 mesiodistally compressed crowns and striated enamel. These features are shared with the Early

29 Triassic genus *Utatsusaurus* known from coeval deposits in Japan and British Columbia. An

30 additional specimen exhibits a different dentition characterized by relatively small, rounded

31 posterior teeth resembling other Early Triassic ichthyopterygians, particularly *Grippia.* This

32 Nevada assemblage marks a southward latitudinal extension for Early Triassic ichthyopterygians

33 along the eastern margin of Panthalassa and indicates repeated trans-hemispheric dispersal

34 events in Early Triassic ichthyopterygians.

35

36 Main article text

37 Introduction

38 Ichthyosaurs were among the most enduring and successful Mesozoic marine reptile groups,

39 appearing in the Early Triassic and persisting some 150 million years until their extinction in the

40 Late Cretaceous (McGowan and Motani, 2003). The fossil record of early ichthyopterygians (the

41 clade comprising ichthyosaurs and close relatives) includes a variety of morphologically

42 disparate taxa from widespread localities in Asia, North America and the Arctic. Most of these

43 assemblages are broadly contemporaneous, all being late Spathian (late Early Triassic) in age.

44 Recent discoveries in China (Ji et al., 2014, Motani et al., 2015) have extended this record

45 earlier into the Spathian and have shed new light on the phylogenetic and biogeographic origins

46 of the clade. However, the rapid early diversification and trans-hemispheric dispersal history of

47 ichthyopterygians during the Early Triassic remains poorly understood.

48

49 Nevada has been an important source of Triassic marine reptile fossils since the 19th Century

50 producing abundant and well-preserved Middle Triassic (Leidy, 1868; Merriam, 1905, 1908,

51 1910; Sander et al., 1994, 1997; Fröbisch et al., 2006, 2013) and Late Triassic (Camp 1976,

52 1980) ichthyopterygian and sauropterygian fossils. Notably, Early 20th Century field work led by

53 John Merriam and Annie Alexander at the Fossil Hill locality in the Humboldt Range produced

54 several specimens of the ichthyosaur *Cymbospondylus* (Merriam 1908)–previously described by

55 Leidy (1868) on the basis of fragmentary remains–as well as the type specimens of

56 *Omphalosaurus nevadanus* (Merriam, 1906) and *Phalarodon fraasi* (Merriam 1910). Later work

57 by Camp (1976, 1980), Sander et al. (1994, 1997) and others illuminated rich Middle and Late

58 Triassic marine reptile assemblages preserved in Nevada.

59

60 In contrast, knowledge of Early Triassic marine reptile fossils in this region is scant. The only

61 published Early Triassic marine reptile occurrence from Nevada is based on a partial jaw referred

62 to the enigmatic genus *Omphalosaurus* and described as a second species, *O. nettarhynchus*

63 Mazin and Bucher, 1987. This specimen was collected from the Spathian-aged informally

64 designated "lower member" of the Prida Formation in the Humboldt Range, which sits

65 immediately below the well-known Fossil Hill Member of the Prida Formation, famous for its

66 rich marine reptile assemblage including the aforementioned *Cymbospondylus, Phalarodon,* and

67 *Omphalosaurus nevadanus*. Fragmentary, float-derived remains of Early Triassic

68 ichthyopterygians have been reported from Spathian horizons in southeastern Idaho (Massare

69   and Callaway, 1994; Scheyer et al., 2014) roughly 500 km to the northeast of the Fossil Hill

70   locality. Even further to the east, the early sauropterygian *Corosaurus alcovensis* Case, 1936 is

71   known from the Alcova limestone in Wyoming whose Early Triassic age was recently confirmed

72   (Lovelace and Doebbert, 2015).

73

74   Here, we report a new Early Triassic ichthyopterygian assemblage from the lower member of the

75   Prida Formation at the Fossil Hill Locality. These fossils are Spathian (Lower Triassic) in age

76   based on co-occuring conodont and ammonoid faunas and sit stratigraphically below the diverse

77   Middle Triassic marine reptile assemblage from the Fossil Hill Member of the Prida Formation.

78   These occurrences extend the southward latitudinal range of early ichthyopterygians in North

79   America and demonstrate that early in their evolutionary history, multiple ichthyopterygian taxa

80   quickly dispersed around or across wide expanses of ocean and ranged from sub-tropical to high

81   temperate waters on the eastern margin of northern Panthalassa.

82   *Institutional Abbreviations*. USNM, National Museum of Natural History, Smithsonian

83   Institution, Washington, D.C., U.S.A.

84

85   Materials and Methods

86   **Geological and Stratigraphic Setting**

87   The new fossils reported here were collected from multiple horizons within the unnamed lower

88   member of the Prida Formation of the Star Peak Group at Fossil Hill, on the eastern flank of the

89   Humboldt Range in Pershing County, Nevada (Fig. 1). The Star Peak Group consists of a

90   sequence of syndepositionally deformed carbonate-dominated units deposited on what was then

91   the western shelf of North America (Nicholls & Silberling, 1977; Wyld, 2000). In the study area,

92   the lower member of the Prida Formation forms the base of the Star Peak Group and sits

93   unconformably atop the Permian/Lower Triassic aged Koipato Group volcanics (Wyld, 2000).

94

95   The lower member of the Prida Formation transitions from siliciclastic sand and conglomerate

96   layers near the contact with the underlying Koipato Group to dark-grey limestone above with

97   intermittent microbialite, conglomerate and chert-dominated beds. The presence of

98   conglomerates and microbialites indicate relatively shallow conditions with a general trend

99   towards deeper water facies characteristic of the overlying Fossil Hill Member (Wyld, 2000).

100   Gastropods and bivalves are abundant in lower layers whereas conodonts and ammonoids are

101   found locally within middle and upper layers of the lower member. Scattered vertebrate fossils

102   occur in multiple horizons within the lower member (Fig. 1), but are most abundant in the middle

103   carbonate layers where they are associated with the conodont *Triassospathodus symmetricus*

104   (Orchard, 1995) and the ammonoid *Prohungarites gutstadti* (Guex et al., 2010) indicating a late

105   Spathian age (Subcolumbites ammonoid biozone). These fossils were collected by the landowner

106   and co-author Patrick Embree, who donated the material to the Smithsonian National Museum of

107   Natural History.

108

109   Results

110   **Systematic Paleontology**

111   Ichthyopterygia Owen, 1840

112   cf. *Utatsusaurus* Shikama, Kamei and Murata, 1978

113   **Diagnosis.** Teeth smaller than marginal dentition present on pterygoid; squamosal not entirely

114   eliminated from supratemporal fenestra by supratemporal; interclavicle cruciform; dorsal margin

115   of external naris formed entirely by nasal; prefrontal shelf prominent; transverse flange of the

116   pterygoid well defined and anterolaterally projecting; supratemporal terrace present; tooth

117   implantation subthecodont, with both dental groove and shallow socket; tooth crowns of middle

118   to posteriorly placed teeth distomesially compressed; humerus as wide proximally as distally;

119   humerus longer than wide; ulnar facet of humerus as wide as radial facet; no more than five

120   phalanges in any digit; posterior dorsal vertebrae cylindrical in outline (from Cuthbertson et al.,

121   2013a; after Motani, 1999; McGowan and Motani, 2003).

122

123   **Referred specimen**. USNM 559349 Partial mandible including teeth. (Fig. 2)

124   **Locality**. Fossil Hill, Humboldt Range, Pershing County, Nevada.

125   **Horizon and age**. Found as surface float within an outcrop of Lower Triassic (upper Spathian)

126   lower member of Prida Formation, Star Peak Group. Based on location and matrix lithology this

127   jaw is inferred to derive from horizon FH1-7 (Fig. 1), which is Spathian based on the occurrence

128   of the ammonoid *Prohungarites gutstadi* (i.e. Subcolumbites Zone of Guex et al., 2010) and

129   conodonts *Triassospathodus symmetricus* (Orchard, 1995) and *Neostrachanognathus* sp.

130   extracted from the matrix.

131

132   **Description**. USNM 559349 is a partial mandible measuring 82 mm long. The jaw fragment

133   preserves portions of the dentary, surangular and splenial. The surfaces of the dentary and

134   surangular are heavily striated and the orientation of these striations differs between the bones.

135   The suture between the dentary and surangular is long and straight, extending across the entire

136   preserved portion of the jaw. In places this suture is indistinct but can be traced by the

137   contrasting surface striation patterns of the dentary and surangular. The splenial can be observed

138   at the broken anterior edge of the fossil where it comprises the medial and ventral portion of the

139   jaw where a thin projection wraps underneath the surangular. A row of irregular weathered

140   depressions follows the approximate course of the suture between the surangular and dentary but

141   it is not clear if these represent natural foramina or are simply artifacts of weathering. Judging

142   from the arrangement of the bones, the fragment likely represents a central-posterior portion of

143   the left mandibular ramus anterior to the coronoid process.

144

145   Thirteen lower teeth are present, along with an additional poorly preserved isolated tooth

146   between the tenth and eleventh in-place teeth, which may be either a disarticulated upper or

147   lower tooth. The teeth are set within alveoli along a continuous groove. No distinct bony septa

148   between alveoli are visible but may be present at the bottom of the dental groove, being

149   concealed in matrix that is very difficult to remove through mechanical preparation. The roots of

150   some teeth are clearly expanded at the base and exhibit plications that are coarser than crown

151   striation. The most anterior tooth is completely exposed anteriorly, revealing its root structure

152   inside the dental groove. It is seen there that the root ceases its expansion once inside the

153   groove, and teeth are embedded to both the labial wall and the base of the groove. A narrow gap

154   emerges between the lingual wall and the root toward the dentigerous margin. Tooth

155   implantation is likely subthecodont (*sensu* Motani, 1997a), although histological study is

156   necessary to firmly establish this. The root cross-section is much wider than long, as reported for

157   *Utatsusaurus hataii* (Motani, 1996).

158

159   Teeth are isodont and conical with striated crowns. Tooth roots are extensively exposed above

160   the alveolar margin such that they account for half or more of the exposed height of each tooth.

161 Tooth crowns are distinguished from these exposed roots by a distinct margin, with most crowns

162 slightly constricted at their base. Some crowns exhibit slightly higher convexity of their anterior

163 surface relative to the posterior surface given them a slightly recurved appearance. The teeth are

164 also recurved lingually toward the tip, as clearly seen in the most anterior tooth (Fig 2B). This

165 curvature closely resembles what was described for *Utatsusaurus hataii* (Motani, 1996:Fig. 3;

166 Cuthbertson et al., 2013a:Fig 7C, D). The tips of the teeth are relatively blunt. Tooth crowns are

167 approximately 3.6 mm tall and 2 mm in mesiodistal diameter. Spacing between teeth ranges from

168 3 mm to 6 mm, more widely spaced teeth may have replacement teeth between them. One 10

169 mm gap along the tooth row likely represents at least one missing tooth. Several teeth are broken,

170 either at the root or the crown, revealing a pulp cavity without evidence of infolding of the

171 dentine.

172

173 **Remarks**. The tooth morphology observed in this specimen closely resembles that described for

174 *Utatsusaurus hataii* from the Lower Triassic Osawa Formation of Kitakami, Japan (Shikama et

175 al., 1978). Most notably, the teeth curve lingually and slightly posteriorly toward the tip, which is

176 a feature that is uniquely known in *Utatsusaurus* among basal ichthyopterygians. Other shared

177 features include: isodont dentition, tall exposed roots, blunt conical striated crowns, a slightly

178 constricted base of some crowns, and an absence of infolding in the pulp cavity. Each of these

179 features is observed in the holotype of *Utatsusaurus hataii* (IGPS 95941) (Motani, 1996) and

180 most are reported in a referred specimen (UHR 30691) (Cuthbertson et al., 2013a). No other

181 Early Triassic or later ichthyopterygian exhibits this suite of dental characters.

182

183   The teeth of this specimen do diverge from *Utatsusaurus hataii* in their much larger size. The

184   maximum tooth exposed height in this specimen is 11 mm, whereas the maximum crown height

185   and width are 4.5 mm and 2.3 mm respectively (Table 1), compared with 3.3 mm, 1.7 mm and

186   0.9 mm for the same measurements of teeth in the holotype of *Utatsusaurus hataii* (Motani,

187   1996). However, the holotype represents a juvenile (Motani, 1997c), so the size difference may

188   partly be explained as ontogenetic variation. A referred specimen (UHR 30691) is somewhat

189   larger than the holotype, however, the teeth of this specimen are still considerably smaller than

190   those of USNM 559349. Despite this difference in size, the overall shape of the teeth in each of

191   these specimens is very similar. Motani (1996) reported "crown shape index" values–calculated

192   as crown height divided by average basal diameter of the tooth crown (Massare, 1987)–ranging

193   between 0.9 and 3.1 with an average value of 1.9 in the type specimen of *Utatsusaurus hataii,*

194   while these values range from 1.3 to 2.3 with an average of 1.8 in USNM 559349. Likewise, the

195   "crown ratio"–calculated as crown height divided by total exposed tooth height–averages 0.51 in

196   IGPS 95941 and 0.43 in USNM 559349.

197

198   The overall arrangement of bones in the fragmentary mandible is consistent with that observed in

199   the *Utatsusaurus* holotype (IGPS 94941) and the referred specimen (UHR 30691), notably the

200   long, straight contact between the dentary and surangular. The suture between the surangular and

201   dentary is well developed in IGPS 94941 but indistinct in the larger UHR 30691, possibly a

202   consequence of differing ontogenetic stages, or differential weathering, between these two

203   specimens. USNM 559349 approaches UHR 30691 in that the suture between the dentary and

204   surangular is somewhat obscured, but its approximate course can be traced by a contrast in bone

205   texture and an irregular row of weathered pits. This might suggest a relatively mature individual,

206   as has been proposed for IGPS 9494, but this is highly speculative given the incomplete nature of

207   the material.

208

209   A partial skull from the Lower Triassic Vega Phroso Member of the Sulphur Mountain

210   Formation from British Columbia, Canada was referred to *Utatsusaurus* sp. by Nicholls and

211   Brinkman (1993), based largely on the presence of the same dental features detailed above. The

212   teeth of the British Columbia specimen are similar in size to those of the Nevada specimen

213   described here (Nicholls & Brinkman, 1993) and distinctly larger than those found in the

214   holotype of *Utatsusaurus hataii* from Japan (Motani, 1996). It is therefore possible that these

215   larger-toothed specimens from the eastern margin of Panthalassa (Nevada, British Columbia)

216   represent a form allied with but distinct from *Utatsusaurus hataii*; however more complete

217   material is needed before this can be confirmed. Recently, Cuthbertson et al. (2014) described

218   another partial skull from the Vega Phroso Member, which they also referred to *Utatsusaurus*

219   sp., although they concluded that the material originally referred to this genus by Nicholls and

220   Brinkman (1993) was non-diagnostic at the genus level. Unfortunately this recently described

221   material lacks a lower jaw or teeth and cannot be compared to USNM 559349.

222

223   Ichthyopterygia Owen, 1840

224   cf. Grippiidae Wiman, 1929

225   **Definition**. The last common ancestor of *Grippia longirostris* and *Gulosaurus helmi*, and all its

226   descendants (Ji et al., 2015).

227   **Diagnosis**. Maxilla with multiple tooth rows; posterior tooth crown rounded; supratemporal-

228   postorbital contact present; proximal manual phalanges not closely packed proximo-distally

229   (from Ji et al., 2015).

230

231   **Referred specimen**. USNM 559350 Partial maxilla including teeth. (Fig. 3)

232   **Locality**. Fossil Hill, Humboldt Range, Pershing County, Nevada.

233   **Horizon and Age**. Collected from FH1-5 (Fig. 1) horizon which is Spathian in age based on the

234   occurrence of the ammonoid *Prohungarites gutstadi* (Guex et al., 2010) and conodonts including

235   *Triassospathodus* and *Neostrachanognathus*. This horizon is also characterized by distinctive

236   spherical structures originally interpreted as microbial (i.e. 'oncoids') but more recently

237   suggested to represent sponge "reefs" (Brayard et al., 2011; see further discussion below).

238   **Description**. USNM 559350 (Fig. 3) is a partial maxilla measuring 20 mm and bearing five teeth

239   exposed in medial view. The teeth are robust cones exhibiting a trend of posteriorly increasing

240   basal diameter, whereas the crown height remains constant giving the posteriormost preserved

241   tooth a distinctly rounded shape. There is a distinct constriction below the crown separating it

242   from the root below, however the constriction is very slight in the anteriormost tooth. The

243   anteriormost crown height and width are 1.7 mm and 1.2 mm respectively; in the second

244   posteriormost tooth, which is better preserved than the posteriormost tooth, crown height and

245   width are 1.3 mm and 2.1 mm. The tooth enamel appears smooth and polished with little

246   indication of striation; however, this could be attributed to tooth wear. Faint plication is visible

247   on some roots. Although some teeth are abraded, none expose the pulp cavity clearly enough to

248   determine presence or absence of infolded dentine.

249

250   In medial view the teeth are attached to the lingual wall of the maxilla, representing pleurodont

251   tooth attachment. An expanded bone of attachment conceals the bases of the two posteriormost

252   teeth, suggesting subleurodont attachement, a modified form of pleurodont attachment (Motani,

253   1997a), in at least the posterior region of the maxillary tooth row. While only a single row of

254   teeth is observed, a shallow depression on the lingual margin of the tooth row immediately

255   anterior to the second posteriormost tooth could represent the attachment facet of a missing

256   tooth. If this were the case it might possibly represent a second row immediately lingual to the

257   preserved teeth. Wide spacing between the four anteriormost teeth would easily accommodate an

258   additional offset tooth row as observed in the maxillary dentition of *Grippia* (Motani, 1997b) and

259   *Gulosaurus* (Cuthbertson et al., 2013b).

260

261   **Remarks**. Among Early Triassic ichthyopterygians, small, robust teeth, similar to those reported

262   here, are typical of the posterior dentition of *Grippia* (Motani, 1997b). Rounded teeth are also

263   observed in the Early Triassic genus *Chaohusaurus* (Motani & You, 1998) and, to a lesser

264   extent, *Gulosaurus* (Cuthbertson et al. 2013b). *Grippia* was previously reported from the Lower

265   Triassic Vega Phroso Member of the Sulphur Mountain Formation in British Columbia

266   (Brinkman et al., 1992). This specimen was later redescribed as a distinct taxon, *Gulosaurus*

267   *helmi* (Cuthbertson et al., 2013b) and found to be sister taxon to *Grippia longirostris*. Similarly,

268   recent work by Ji et al. (2015), established a new clade Grippioidea including *Grippia*,

269   *Gulosaurus, Utatsusaurus,* and *Parvinatator,* although the precise relationships among these taxa

270   varied somewhat depending on taxon and character inclusion. The enigmatic marine reptile

271   *Omphalosaurus nettarhynchus* (Mazin & Bucher, 1987), previously reported from Spathian

272   lower member of the Prida Formation, also possesses rounded dentition, but is distinct from this

273   specimen by its much larger size and in exhibiting a broad pavement of rounded teeth on the

274   mandible.

275

276   Alternatively, this specimen may have some affinity with *Chaohusaurus*, an Early Triassic

277   ichthyopterygian from China in which some specimens also show distinctly rounded posterior

278   dentition (Motani & You, 1998). However the posterior teeth of *Chaohusaurus* are generally

279   smaller and more tightly packed than in USNM 559350, averaging approximately ten teeth over

280   20 mm rather than the five teeth observed over the same distance in this specimen.

281   *Chaohusaurus* was previously regarded as a grippidian partly on the basis of possessing multiple

282   maxillary tooth rows and rounded posterior dentition (Motani, 1999). However, more recent

283   analyses (Cuthbertson et al. 2013b, Ji et al., 2015) do not support this placement.

284

285   The crown shape index in USNM 559350 ranges from 1.0-2.1 and averages 1.4 (Table 1),

286   similar to the average shape index reported for the maxillary dentition of *Grippia*, 1.4 (Motani,

287   1997b) and *Gulosaurus* 1.64 (Cuthbertson et al. 2013b). Thus, the rounded dentition observed in

288   USNM 559350 is strongly suggestive of an affinity with some other Early Triassic

289   ichthyopterygians but more precise placement will require more complete skeletal material.

290

291   Discussion

292   Despite the fragmentary nature of the remains described here, their resemblance with the

293   distinctive dentitions of other Early Triassic ichthyopterygians allows tentative interpretations to

294   be made. The presence of *Utatsusaurus*-like and *Grippia* or *Chaohusaurus* -like forms suggests

295   similarity with the Lower Triassic Vega-Phroso assemblage from the Wapiti Lake region of

296   British Columbia, from which *Utatsusaurus* (Nicholls & Brinkman, 1993; Cuthbertson et al.,

297   2014) and grippidians (Brinkman et al., 1992; Cuthbertson et al., 2013b) have also been reported.

298   However, the type locality of *Utatsusaurus* is in the Osawa Formation of Japan (Shikama et al.,

299   1978), whereas the type localities of *Grippia* and *Chaohusaurus* are in the Vikinghøgda

300   Formation (= "Sticky Keep Formation" of older references) of Spitsbergen (Wiman, 1929, 1933;

301   Hounslow et al., 2008) and the Nanlinghu Formation of Anhui Province, China (Young & Dong,

302   1972), respectively. Thus, Early Triassic ichthyopterygian taxa were widely distributed around

303   the margins of northern Panthalassa (Cuthbertson et al., 2013b).

304

305   This broad distribution early in their evolutionary history, from numerous Late Spathian

306   (Subcolumbites Zone) localities of broadly coeval age (Scheyer et al., 2014), has made it

307   difficult to pinpoint the biogeographic origins of the group. However, recent work in China has

308   extended the biostratigraphic range of ichthyopterygians to the underlying Procolumbites Zone

309   (Motani et al., 2014; Ji et al., 2014). Furthermore, the occurrence of diverse and endemic

310   hupehsuchians, widely regarded as the ichthyopterygian sister-group, and the plesiomorphic

311   ichthyosauromorph *Cartorhynchus* (Motani et al., 2015) are consistent with an origin of

312   ichthyopterygians near the south China block in equatorial western Panthalassa.

313

314   The inferred nearshore lifestyle of most Early Triassic ichthyopterygians has led others to

315   propose that these early marine reptiles dispersed along coastlines or across transient

316   epicontinental corridors (Cuthbertson et al., 2013b). However, there is little geological evidence

317   for such corridors in the Early Triassic, which was a time of relatively low global sea level

318   (Miller et al., 2005). Furthermore the absence of Early Triassic ichthyopterygian fossils in

319   Western Tethys is surprising under this scenario. Conversely, the biogeographic histories of

320   other aquatic–and even terrestrial–reptile groups are marked by occasional transoceanic dispersal

321   events (Rocha et al., 2006; Velez-Juarbe et al., 2007), and such events could explain the

322   distribution of Early Triassic ichthyopteryians on opposite shores of Panthalassa.

323   Brayard et al. (2009) identified trans-Panthalassan distribution patterns in Spathian

324   ammonoids, identifying similar ammonoid faunas in Nevada, Kitakami and British Columbia,

325   which they attributed to oceanographic currents. The occurrence of some Early Triassic marine

326   reptile taxa (e.g. *Utatsusaurus*) on both the eastern and western margins of of Panthalassa might

327   reflect sporadic crossing of deep ocean basins by these lineages, potentially facilitated by the

328   same ocean currents that mediated transoceanic dispersals of contemporaneous marine

329   invertebrates (Fig. 4). The wide distribution of Early Triassic sauropterygians, including the

330   South China Block (Jiang et al., 2014) and western margin of North America (Storrs, 1991;

331   Lovelace & Doebbert, 2015) on opposite shores of Panthalassa indicates to a similar dispersal

332   history in the early members of that marine reptile clade. Isolated terranes such as South

333   Kitakami, South Primoyre and Chulitna could have served as stepping-stones for shallow marine

334   taxa. Dispersal along coastlines around the northern margins of Panthalassa remains an

335   alternative scenario that could explain the broad distribution of some Early Triassic

336   ichthyopterygians, with pronounced global warmth in the Early Triassic mediating limiting

337   climatic conditions at high latitudes (Sun et al., 2012). However, the apparent absence of

338   ichthyopterygian fossils from high latitudes on the western margin of northern Panthalassa

339   remains a puzzle under this scenario.

340

341   Intriguingly, the oldest marine reptile bearing horizons at Fossil Hill are associated with a

342   prominent limestone marker bed bearing distinctive spherical structures ~1–2 cm in diameter

343   (Fig. 5). We initially interpreted these structures as microbial 'oncoids.' Widespread

344   microbialite-dominated facies are characteristic of Lower Triassic strata globally, including in

345   the western United States (Pruss & Bottjer, 2004; Baud et al., 2007), and are interpreted as a

346   byproduct of the end-Permian mass extinction and subsequent delayed biotic recovery of

347   metazoan reefs (Pruss et al., 2004). A similar association between the basal sauropterygian

348   *Corosaurus* and stromatolites in the Lower Triassic Alcova limestone has been reported

349   previously (Storrs, 1991). More recently, similar spheroidal structures from the Humboldt Range

350   and other localities in western North America have been interpreted as 'transient sponge reefs'

351   (Brayard et al., 2011). Thus, the diversification and dispersal of Early Triassic marine reptiles

352   was apparently well underway at the end of the Early Triassic (Scheyer et al., 2014) despite some

353   lingering signs of continued environmental stress preserved in the same strata. Future work at

354   this new locality, and elsewhere, may help to clarify the role that large-scale environmental

355   changes played in shaping the early evolutionary history of Mesozoic marine reptiles.

356

357   Acknowledgements

362

363   References

364   Baud,A., Richoz, S., and Pruss, S. 2007. The Lower Triassic anachronistic carbonate facies in

365   space and time. *Global and Planetary Change*, 55:81–89.

366   DOI:10.1016/j.gloplacha.2006.06.008

367   Brayard, A., Escarguel, G., Bucher, H., and Brühwiler, T. 2009. Smithian and Spathian (Early

368   Triassic) ammonoid assemblages from terranes: paleoceanographic and paleogeographic

369   implications. Journal of Asian Earth Sciences, 36:420–433.

370   DOI:10.1016/j.jseaes.2008.05.004

371   Brayard, A., Vennin, E., Olivier, N., Bylund, K. G., Jenks, J., Stephen, D. A., Bucher H.,

372   Hofmann, R., Goudemand, and N., Escarguel, G. 2011. Transient metazoan reefs in the

373   aftermath of the end-Permian mass extinction. Nature Geoscience, 4:693–697.

374   DOI:10.1038/ngeo1264

375   Brinkman, D. B., Xijin, Z. H. A. O., and Nicholls, E. L. 1992. A primitive ichthyosaur from the

376   Lower Triassic of British Columbia, Canada. Palaeontology, 35:465–474.

377   Camp, C. L. 1976. Vorläufige Mitteilung über große Ichthyosaurier aus der oberen Trias von

378   Nevada. Sitzungsberichte der Österreichischen Akademie der Wissenschaften,

379   Mathematisch-naturwissenschaftliche Klasse, Abteilung I,185:125–134.

380   Camp, C. L. 1980. Large ichthyosaurs from the Upper Triassic of Nevada. Palaeontographica

381   Abteilung A 170:139–200.

382   Case, E. C. 1936. A nothosaur from the Triassic of Wyoming. University of Michigan

383   Contributions from the Museum of Paleontology 5:1–36.

384   Cuthbertson, R. S., Russell, A. P., and Anderson, J. S. 2013a. Reinterpretation of the cranial

385   morphology of *Utatsusaurus hataii* (Ichthyopterygia) (Osawa Formation, Lower Triassic,

386   Miyagi, Japan) and its systematic implications. Journal of Vertebrate

387   Paleontology, 33:817–830. DOI:10.1080/02724634.2013.756495

388   Cuthbertson, R. S., Russell, A. P., and Anderson, J. S. 2013b. Cranial morphology and

389   relationships of a new grippidian (Ichthyopterygia) from the Vega-Phroso Siltstone

390   Member (Lower Triassic) of British Columbia, Canada. Journal of Vertebrate

391   Paleontology, 33:831–847. DOI:10.1080/02724634.2013.755989

392   Cuthbertson, R. S., Russell, A., and Anderson, J. 2014. The first substantive evidence of

393   *Utatsusaurus* (Ichthyopterygia) from the Sulphur Mountain Formation (Lower–Middle

394   Triassic) of British Columbia, Canada: a skull roof description with comparison to other

395   early taxa. Canadian Journal of Earth Sciences, 51:180–185. DOI: 10.1139/cjes-2013-

396   0185

397   Fröbisch, N. B., Sander, P., and Rieppel, O. 2006. A new species of *Cymbospondylus* (Diapsida,

398   Ichthyosauria) from the Middle Triassic of Nevada and a re-evaluation of the skull

399   osteology of the genus. Zoological Journal of the Linnean Society, 147:515–538. DOI:

400   10.1111/j.1096-3642.2006.00225.x

401   Fröbisch, N. B., Fröbisch, J., Sander, P. M., Schmitz, L., and Rieppel, O. 2013. Macropredatory

402   ichthyosaur from the Middle Triassic and the origin of modern trophic

403   networks. Proceedings of the National Academy of Sciences, 110:1393–1397. DOI:

404   10.1073/pnas.1216750110

405   Guex, J., Hungerbühler, A., Jenks, J.F., O'Dogherty, L., Atudorei, V.,Taylor, D.G., Bucher, H.

406   and Bartolini, A. 2010. Spathian (Lower Triassic) ammonoids from western USA (Idaho,

407   California, Utah and Nevada). Mémoires de Géologie (Lausanne*)*, 49.

408   Hounslow, M. W., Peters, C., Mørk, A., Weitschat, W., and Vigran, J. O. 2008.

409   Biomagnetostratigraphy of the Vikinghøgda Formation, Svalbard (Arctic Norway), and

410   the geomagnetic polarity timescale for the Lower Triassic.Geological Society of America

411   Bulletin, 120:1305–1325. DOI: 10.1130/B26103.1

412   Ji, C., Jiang, D., Motani, R., Rieppel, O., Hao, W., and Sun, Z. 2015. Phylogeny of the

413   Ichthyopterygia incorporating the recent discoveries from South China. Journal of

414   Vertebrate Paleontology. e1025956 DOI: 10.1080/02724634.2015.1025956

415   Ji, C, C. Zhang, D. Jiang, H. Bucher, R. Motani, and A. Tintori 2014. Ammonoid age control of

416   the Early Triassic marine reptile from Chaohu. Paleoworld. Available online 8 December

417   2014. DOI: 10.1016/j.palwor.2014.11.009

418   Jiang, D., Motani, R., Tintori A., Rieppel O., Chen G., Huang J., Zhang R., Sun, Z. and Ji, C.

419   2014. The Early Triassic Eosauropterygian *Majiashanosaurus discocoracoidis*, Gen. Et

420   Sp. Nov. (Reptilia, Sauropterygia), from Chaohu, Anhui Province, People's Republic of

421   China. Journal of Vertebrate Paleontology, 34(5): 1044-1052. DOI:

422   10.1080/02724634.2014.846264☐

423   Leidy, J. 1868. Notice of some reptilian remains from Nevada. Proceedings of the Academy of

424   Natural Sciences of Philadelphia 109:177–178.

425   Lovelace, D. M., and Doebbert, A. C. 2015. A new age constraint for the Early Triassic Alcova

426   Limestone (Chugwater Group), Wyoming. Palaeogeography, Palaeoclimatology,

427   Palaeoecology, 424:1–5. DOI: 10.1016/j.palaeo.2015.02.009

428   Massare, J. A. (1987). Tooth morphology and prey preference of Mesozoic marine reptiles.

429   Journal of Vertebrate Paleontology, 7:121–137. DOI: 10.1080/02724634.1987.10011647

430   Massare, J. A., and Callaway, J. M. 1994. *Cymbospondylus* (Ichthyosauria: Shastasauridae) from

431   the Lower Triassic Thaynes Formation of southeastern Idaho. Journal of Vertebrate

432   Paleontology, 14:139–141. DOI: 10.1080/02724634.1994.10011545

433 Mazin, J. M., and Bucher, H. 1987. [*Omphalosaurus nettarhynchus*, une nouvelle espèce

434   d'Omphalosauridé (Reptilia, Ichthyopterygia) du Spathien de la Humboldt Range

435   (Nevada, USA)]. Comptes rendus de l'Académie des sciences. Série 2, Mécanique,

436   Physique, Chimie, Sciences de l'univers, Sciences de la Terre, 305:823–828. [French with

437   English Abstract]

438 McGowan, C., and Motani., R. 2003. Part 8. Ichthyopterygia; in H.-D. Sues (ed.), *Handbook of*

439   *Paleoherpetology*. Verlag Dr. Friedrich Pfeil, Munich.

440 Merriam, J. C. 1905. A primitive ichthyosaurian limb from the Middle Triassic of Nevada.

441   University of California Publications. Bulletin of the Department of Geology, 4:33–38.

442 Merriam, J. C. 1906. Preliminary note on a new marine reptile from the Middle Triassic of

443   Nevada. University of California Publications, Bulletin of the Department of Geology

444   5:75–79

445 Merriam, J. C. 1908. Triassic Ichthyosauria, with special reference to the American forms.

446   Memoirs of the University of California 1:1–196

447 Merriam, J. C. 1910. The skull and dentition of a primitive ichthyosaurian from the Middle

448   Triassic. University of California Publications, Bulletin of the Department of Geology

449   5:381–390.

450 Miller, K.G., Kominz, M.A., Browning, J.V., Wright, J.D., Mountain, G.S., Katz, M.E.,

451   Sugarman, P.J., Cramer, B.S., Christie-Blick, N. and Pekar, S.F., 2005. The Phanerozoic

452   record of global sea-level change. Science, 31:1293–1298.

453 Motani, R. 1996. Redescription of the dental features of an Early Triassic ichthyosaur,

454   *Utatsusaurus hataii*. Journal of Vertebrate Paleontology, 16:396–402. DOI:

455   10.1080/02724634.1996.10011329

456   Motani, R. 1997a. Temporal and spatial distribution of tooth implantation in ichthyosaurs; pp.

457   81–103 in Callaway, J. M. and E. L. Nicholls (eds.), Ancient Marine Reptiles. Academic

458   Press, London and New York.

459   Motani, R. 1997b. Redescription of the dentition of *Grippia longirostris* (Ichthyosauria) with a

460   comparison with *Utatsusaurus hataii*. Journal of Vertebrate Paleontology, 17:39–44.

461   DOI: 10.1080/02724634.1997.10010951

462   Motani, R. 1997c. New information on the forefin of *Utatsusaurus hataii* (Ichthyosauria).

463   Journal of Paleontology 71:475–479.

464   Motani, R. 1999. Phylogeny of the Ichthyopterygia. Journal of Vertebrate Paleontology, 19:473–

465   496. DOI: 10.1080/02724634.1999.10011160

466   Motani, R., Jiang, D.Y., Chen, G.B., Tintori, A., Rieppel, O., Ji, C. and Huang, J.D., 2015. A

467   basal ichthyosauriform with a short snout from the Lower Triassic of China. Nature,

468   517:485–488. DOI: 10.1038/nature13866

469   Motani, R. and You, H. 1998. Taxonomy and limb ontogeny *of Chaohusaurus geishanensis*

470   (Ichthyosauria), with a note on the allometric equation. Journal of Vertebrate

471   Paleontology 18:533-540. DOI: 10.1080/02724634.1998.10011080

472   Nicholls, E. L., and Brinkman, D. 1993. A new specimen of *Utatsusaurus* (Reptilia:

473   Ichthyosauria) from the Lower Triassic Sulphur Mountain Formation of British

474   Columbia. Canadian Journal of Earth Sciences, 30:486-490. DOI: 10.1139/e93-037

475   Nicholls, E. L., and Brinkman, D. B. 1995. A new ichthyosaur from the Triassic Sulphur

476   Mountain formation of British Columbia; pp. 521–535 in W. A. S. Sarjeant

477   (ed.), Vertebrate Fossils and the Evolution of Scientific concepts. Gordon and Breach,

478   Switzerland.

479   Nichols, K. M., and Silberling, N. J. 1977. Stratigraphy and depositional history of the Star Peak

480   Group (Triassic), northwestern Nevada (Vol. 178). Geological society of America.

481   Orchard, M.J. 1995. Taxonomy and correlation of Lower Triassic (Spathian) segminate

482   conodonts from Oman and revision of some species of *Neospathodus*. Journal

483   Paleontology, 69: 110-122. DOI: 10.1017/S0022336000026962

484   Owen, R. 1840. Report on British fossil reptiles. Part I. Report of the British Association for the

485   Advancement of Science, Plymouth,9: 43-126.

486   Rocha, S., Carretero, M. A., Vences, M., Glaw, F., and James Harris, D. (2006). Deciphering

487   patterns of transoceanic dispersal: the evolutionary origin and biogeography of coastal

488   lizards (Cryptoblepharus) in the Western Indian Ocean region. Journal of Biogeography,

489   33(1), 13-22. DOI: 10.1111/j.1365-2699.2005.01375.x

490   Pruss, S. B., and Bottjer, D. J. 2004. Late Early Triassic microbial reefs of the western United

491   States: a description and model for their deposition in the aftermath of the end-Permian

492   mass extinction. Palaeogeography, Palaeoclimatology, Palaeoecology, 211:127–137.

493   DOI: 10.1016/j.palaeo.2004.05.002

494   Sander, P. M., Rieppel, O. C., and Bucher, H. 1994. New marine vertebrate fauna from the

495   Middle Triassic of Nevada. Journal of Paleontology, 68:676–680. DOI:

496   10.1017/S0022336000026020

497   Sander, P. M., Rieppel, O. C., and Bucher, H. 1997. A new pistosaurid (Reptilia: Sauropterygia)

498   from the Middle Triassic of Nevada and its implications for the origin of the

499   plesiosaurs. Journal of Vertebrate Paleontology, 17:526–533. DOI:

500   10.1080/02724634.1997.10010999

501   Scheyer, T. M., Romano, C., Jenks, J., and Bucher, H. 2014. Early Triassic Marine Biotic

502   Recovery: The Predators' Perspective. PloS one, 9(3). DOI:

503   10.1371/journal.pone.0088987

504   Schmitz, L., Sander, P. M., Storrs, G. W., and Rieppel, O. 2004. New Mixosauridae

505   (Ichthyosauria) from the Middle Triassic of the Augusta Mountains (Nevada, USA) and

506   their implications for mixosaur taxonomy.Palaeontographica, Abteilung A, 270:133-162.

507   DOI: 10.1073/pnas.1216750110

508   Shikama, T., Kamei, T., and Murata, M. 1978. Early Triassic Ichthyosaurus, *Utatsusaurus*

509   *hataii* gen. et sp. nov., from the Kitakami massif, Northeast Japan. Science Reports of the

510   Tohoku University, Sendai, Second Series (Geology), 48:77-97.

511   Silberling, N. J. 1962. Stratigraphic distribution of Middle Triassic Ammonites at Fossil Hill,

512   Humboldt Range, Nevada. Journal of Paleontology, 153-160.

513   Storrs, G. W. 1991. Anatomy and relationships of *Corosaurus alcovensis* (Diapsida:

514   Sauropterygia) and the Triassic Alcova Limestone of Wyoming. Peabody Museum of

515   Natural History, Yale University.

516   Sun, Y., Joachimski, M. M., Wignall, P. B., Yan, C., Chen, Y., Jiang, H., ... & Lai, X. (2012).

517   Lethally hot temperatures during the Early Triassic greenhouse. *Science*, 338: 366–370.
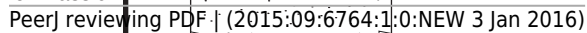
518   Vélez-Juarbe, J., Brochu, C. A., and Santos, H. 2007. A gharial from the Oligocene of Puerto

519   Rico: transoceanic dispersal in the history of a non-marine reptile. Proceedings of the

520   Royal Society B: Biological Sciences, 274:1245-1254. DOI: 10.1098/rspb.2006.0455

521   Wiman, C. 1929. Eine neue Reptilien-Ordnung aus der Trias Spitzbergens. Bulletin of the

522   Geological Institution of the University of Upsala 22: 183-196.

523   Wiman, C. 1933. Uber Grippia longirostris. Nova Acta Regiae Societatis Scientiarum

524   Upsaliensis, ser. 4, 9: 1-19.

525   Wyld, S. J. 2000. Triassic evolution of the arc and backarc of northwestern Nevada, and

526   evidence for extensional tectonism. Special Papers Geological Society of America:185–

527   208.

528   Young, C. C., and Dong, Z. M. 1972. *Chaohusaurus geishanensis* from Anhui

529   Province. Academia Sinica, Institute of Vertebrate Paleontology and Palaeoanthropology,

530   Memoir, 9:11–14.

Figure 1(on next page)

Summarized stratigraphy and regional map

(A) Stratigraphy of the Triassic Prida Formation near Fossil Hill in the Humboldt Range,

Nevada indicating horizons of specimens USNM 559349 and 559350 and conodont samples.

(B) Regional map, modified from Silberling (1962).

Figure A. Stratigraphic column of the Prida Formation, Star Peak Group, showing Lower, Fossil Hill, and Upper Members with ammonite zones, conodont sample locations (FH-1 through FH-40), and key fossiliferous horizons.

Left column labels (top to bottom):
- Ammonite zone
- Ladinian Stage / Upper Member / Subasperum
- Middle Triassic / Anisian Stage / Fossil Hill Member / Occidentalis / Meeki / Rotelliformis / Mimetus / Weitschati
- Star Peak Group / Prida Formation
- Lower Triassic / Spathian Stage / Lower Member / Prohungarites gutstadti
- Kopato Group / Weaver Rhyolite / Permo-Triassic

Bed markers:
- FH-40
- FH-35
- FH-30
- FH-20
- Small faults may exaggerate thickness
- Mostly covered.
- FH-14
- FH1-10
- FH1-9
- FH1-8
- FH1-7 — Inferred horizon of USNM 559349
- FH1-6
- FH1-5 — Distinctive 'oncoid'/sponge horizon USNM 559350
- FH1-4
- FH1-3
- FH1-2
- FH1-1A
- FH1-1
- 10 m

Biostratigraphic boundaries approximate.

Figure B. Location map, Nevada. Shows Humboldt Range, Star Peak, Unionville, Imlay, Fitting, Fossil Hill, Lovelock, U.S. Interstate 80, Nev. Hwy. 50, with 10 km scale bar. Township/Range markers: R. 34 E., R. 35 E., T. 28 N.

Legend: Location of conodont samples

2

Specimen USNM 559349, partial ichthyopterygian jaw cf. *Utatsusaurus*.

(A) Complete specimen, in labial view, anterior to the left. Squares on scale bar equal 5 mm.

(B) Magnified view of anterior dentition, squares on scale bar equal 1 mm.

3

USNM 559350 Partial ichthyopterygian maxilla cf. Grippidia.

A) Partial maxilla in lingual view, anterior to the left. Squares on scale bar equal 1 mm. White arrow indicates possible attachment facet for tooth in second lingual tooth row. B) Magnified view of dentition.
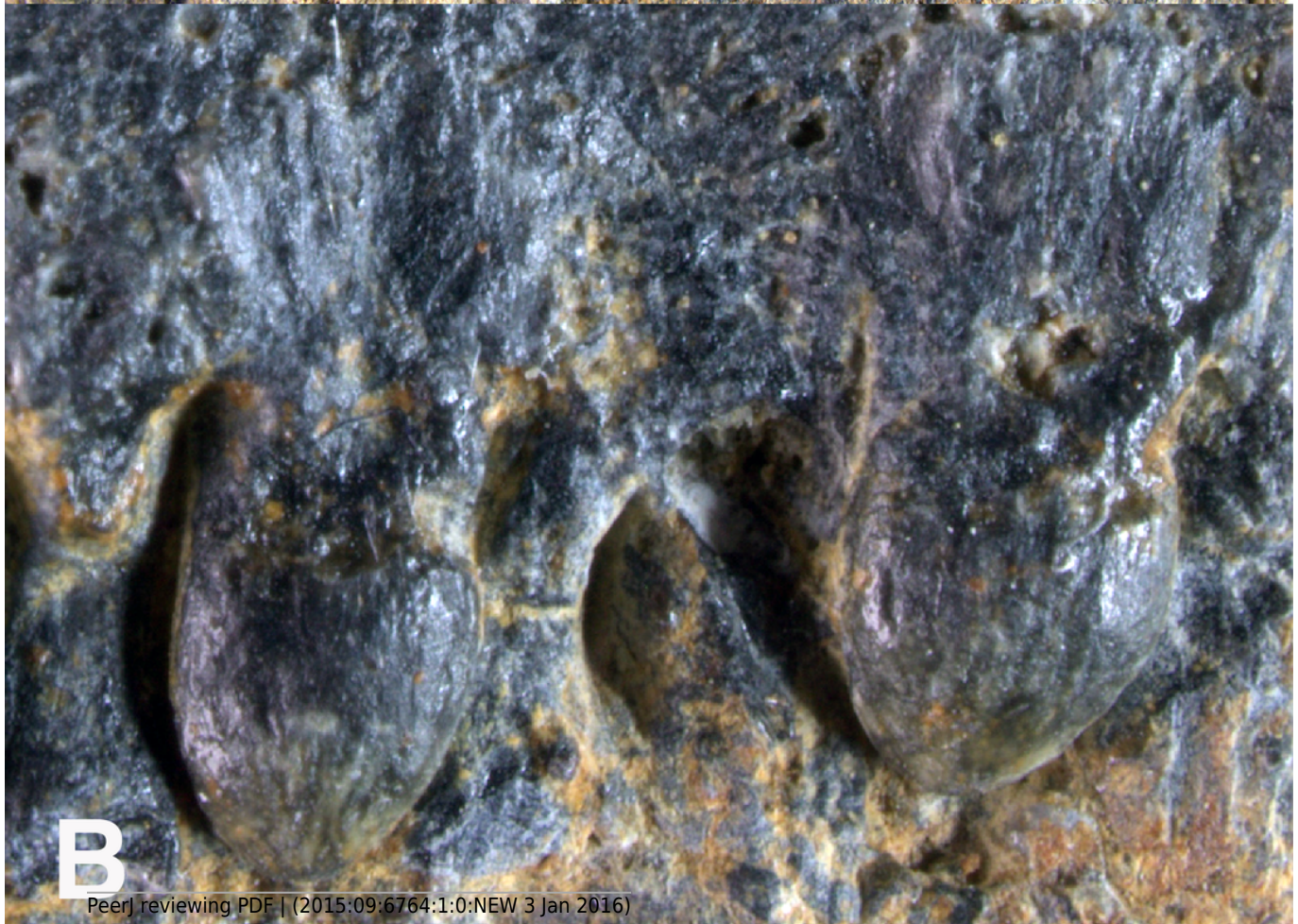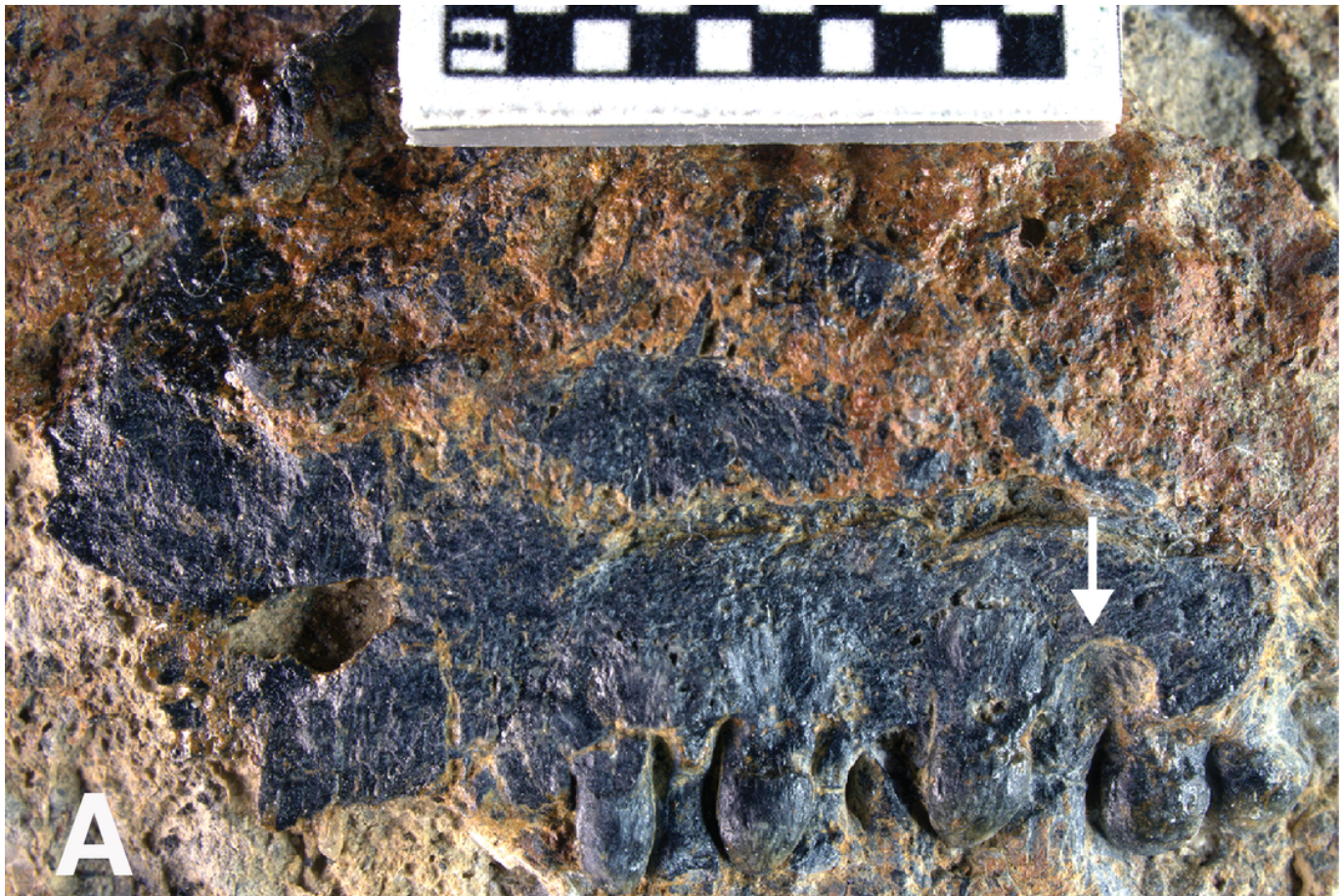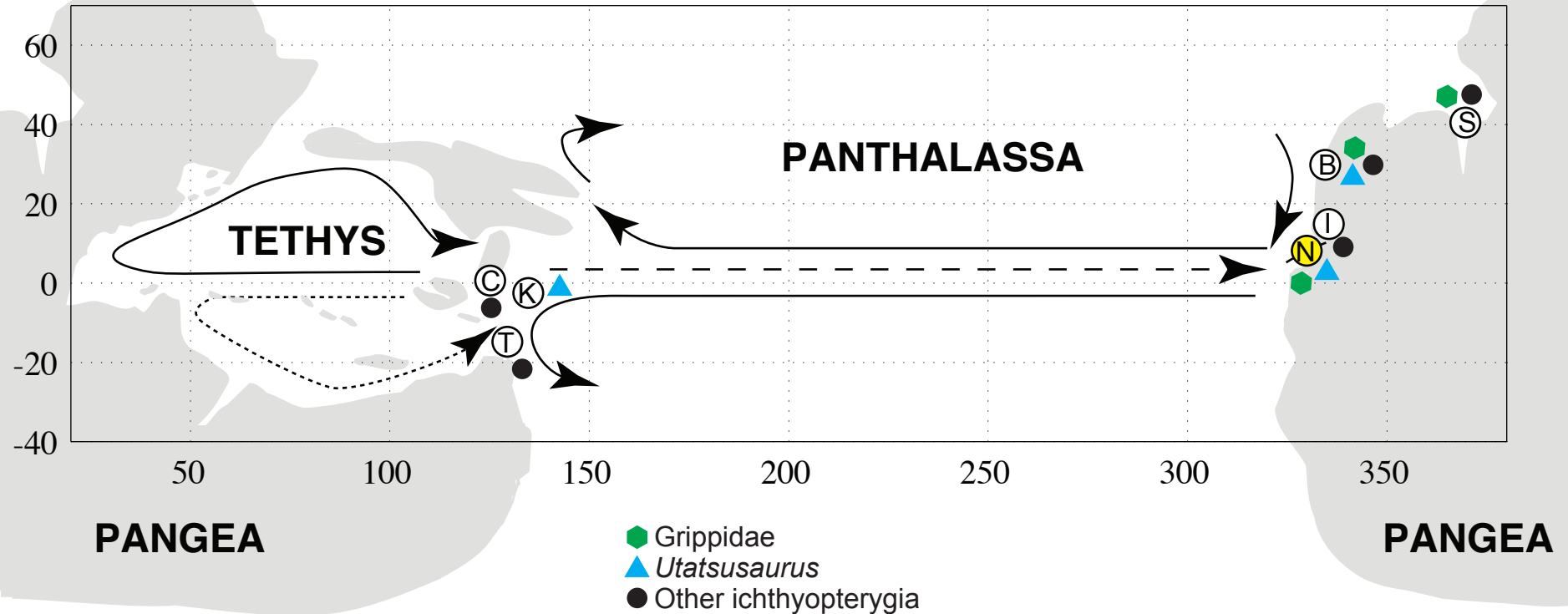
PeerJ

Figure 4(on next page)

Distribution of Early Triassic ichthyopterygians.

Paleogeographic distribution of Early Triassic ichthyopterygians, map modified from Brayard et al. (2009). Locality abbreviations as follows: (B) British Columbia; (C) South China; (I) Idaho; (K) South Kitakami; (N) Nevada (present study, highlighted in yellow); (S) Spitsbergen; (T) Timor. Arrows indicate inferred ammonoid dispersal routes (Brayard et al., 2009)

Grippidae

Utatsusaurus

Other ichthyopterygia

5

Distinctive sedimentary structures associated with horizon of USNM 559350

Spherical structures in FH1-5 that may represent microbial structures or sponges. This appears to be a widespread and distinctive regional Lower Triassic facies associated with recovery from the end-Permian mass-extinction. Vertebrate fossils also occur in this horizon including USNM 559350 described here. Hammer for scale is approximately 30 cm in length.

Table 1(on next page)

Summarized tooth measurements from USNM 559349 and USNM 559350.

All measurements in mm except for shape index and crown ratio, which are ratios.

Specimen		Proxmial width (mm)[a]	Exposed height (mm)[b]	Crown width (mm)[c]	Crown height (mm)[d]	Crown shape index[e]	Crown ratio[f]
USNM 559349	Max.	4.2	11.1	2.3	4.5	2.3	0.51
	Min.	2.5	6.4	1.9	2.7	1.3	0.39
	Mean	3.2	8.5	2.1	3.6	1.8	0.43
USNM 559350	Max.	1.6	2.5	2.1	1.7	2.1	0.88
	Min.	1.0	1.8	1.2	1.1	1.0	0.61
	Mean	1.4	2.2	1.6	1.5	1.4	0.69

1

[a] Measured as mesio-distal width of the root at the jawline, following Motani (1996).
[b] Measured as distance from tip of crown to jaw margin.
[c] Measured as mesio-distal width of the crown at its widest point.
[d] Base of crown is distinctive in USNM 559349 due to crown ornamentation; base of crown in USNM 559350 is less distinct but can be approximated by slight basal constriction.
[e] Calculated as crown height/crown width, following Massare (1987).
[f] Calculated as crown height/exposed tooth height, following Motani (1996).