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A new Lower Triassic ichthyopterygian assemblage from Fossil Hill, Nevada

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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
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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 posterior teeth resembling other Early Triassic ichthyopterygians particularly Grippia. This 31 32 Nevada assemblage marks a southward latitudinal extension for Early Triassic ichthyopterygians 33 along the eastern margin of Panthalassa and indicates repeated circum-oceanic dispersal events 34 in Early Triassic ichthyopterygians.

35

36 Main article text

37 Introduction

38 Nevada has been an important source of Triassic marine reptile fossils since the 19th Century 39 producing abundant and well-preserved Middle Triassic (Leidy, 1868; Merriam, 1905, 1908, 40 1910; Sander et al., 1994, 1997; Fröbisch et al., 2006, 2013) and Late Triassic (Camp 1976, 41 1980) ichthyopterygian and sauropterygian fossils. Notably Early 20th Century field work led by 42 John Merriam and Annie Alexander at the Fossil Hill locality in the Humboldt Range produced 43 several specimens of the ichthyosaur Cymbospondylus (Merriam 1908)-previously described by Leidy (1868) on the basis of fragmentary remains-as well as the type specimens of 44 45 Omphalosaurus nevadanus (Merriam, 1906) and Phalarodon fraasi (Merriam 1910). Later work

46 by Camp (1976, 1980), Sander et al. (1994, 1997) and others illuminated rich Middle and Late
47 Triassic marine reptile assemblages preserved in Nevada.

48

49 In contrast, knowledge of Early Triassic marine reptile fossils in this region is scant. The only 50 published Early Triassic marine reptile occurrence from Nevada is based on a partial jaw referred 51 to the enigmatic marine reptile genus *Omphalosaurus* and described as a second species, O. 52 nettarhynchus Mazin and Bucher, 1987. This specimen was collected from the Spathian-aged 53 informally designated "lower member" of the Prida Formation in the Humboldt Range, which 54 sits immediately below the well-known Fossil Hill Member of the Prida Formation famous for its 55 rich marine reptile assemblage including the aforementioned Cymbospondylus, Phalarodon and 56 Omphalosaurus nevadanus. Fragmentary, float-derived remains of Early Triassic ichthyosaurs 57 have been reported from Spathian horizons in southeastern Idaho (Massare and Callaway, 1994; 58 Scheyer et al., 2014) roughly 500 km to the northeast of the Fossil Hill locality. Even further to 59 the east, the early sauropterygian *Corosaurus alcovensis* Case, 1936 is known from the Alcova 60 limestone in Wyoming whose Early Triassic age was recently confirmed (Lovelace and 61 Doebbert, 2015).

62

Here, we report a new Early Triassic ichthyopterygian assemblage from the "lower member" of the Prida Formation at the Fossil Hill Locality. These fossils are Spathian (Lower Triassic) in age based on conodonts and ammonoids and sit stratigraphically below the diverse Middle Triassic marine reptile assemblage from the Fossil Hill Member of the Prida Formation. These occurrences extend the southward latitudinal range of early ichthyopterygians in North America and demonstrate that early in their evolutionary history, multiple ichthyopterygian taxa quickly

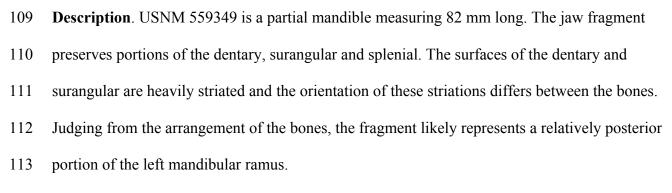
- 69 dispersed around or across wide expanses of ocean and ranged from sub-tropical to high
- 70 temperate waters on the eastern margin of northern Panthalassa.
- 71 Institutional Abbreviations. USNM, National Museum of Natural History, Smithsonian
- 72 Institution, Washington, D.C., U.S.A.
- 73
- 74 Materials and Methods
- 75 Geological and Stratigraphic Setting

The new fossils reported here were collected from multiple horizons within the unnamed lower 76 77 member of the Prida Formation of the Star Peak Group at Fossil Hill, on the eastern flank of the 78 Humboldt Range in Pershing County, Nevada (Fig. 1). The Star Peak Group consists of a 79 sequence of syndepositionally deformed carbonate-dominated units deposited on what was then 80 the western shelf of North America (Nicholls & Silberling, 1977; Wyld, 2000). In the study area, 81 the lower member of the Prida Formation forms the base of the Star Peak Group and sits 82 unconformably atop the Permian/Lower Triassic aged Koipato Group volcanics (Wyld, 2000). 83 84 The lower member of the Prida formation transitions from siliciclastic sand and conglomerate 85 layers near the contact with the underlying Koipato Group to dark-grey limestone above with 86 intermittent microbialite, conglomerate and chert-dominated beds. The presence of 87 conglomerates and microbialites indicate relatively shallow conditions with a general trend 88 towards deeper water facies characteristic of the overlying Fossil Hill Member (Wyld, 2000). 89 Gastropods and bivalves are abundant in lower layers whereas conodonts and ammonoids are 90 found locally within middle and upper layers of the lower member. Scattered vertebrate fossils 91 occur in multiple horizons within the lower member (Fig. 1), but are most abundant in the middle

- 92 carbonate layers where they are associated with the conodont Triassospathodus symmetricus
- 93 (Orchard, 1995) and the ammonoid Prohungarites gutstadti (Guex et al., 2010) indicating a late
- 94 Spathian age (Subcolumbites ammonoid biozone).
- 95 Results
- 96 Systematic Paleontology
- 97 Ichthyopterygia Owen, 1840
- 98 cf. Utatsusaurus Shikama, Kamei and Murata, 1978
- 99
- 100 **Referred specimen**. USNM 559349 Partial mandible including teeth. (Fig. 2)
- 101 Locality. Fossil Hill, Humboldt Range, Pershing County, Nevada.
- 102 Horizon and age. Found as surface float within an outcrop of Lower Triassic (upper Spathian)
- 103 lower member of Prida Formation, Star Peak Group. Based on location and matrix lithology this
- 104 jaw is inferred to derive from horizon FH1-7 (Fig. 1), which is Spathian based on the occurrence
- 105 of the ammonoid Prohungarites gutstadi (i.e. Subcolumbites Zone of Guex et al., 2010) and
- 106 conodonts Triassospathodus symmetricus (Orchard, 1995) and Neostrachanognathus sp.

107 extracted from the matrix.

108



114

115 Thirteen lower teeth are present, along with an additional isolated tooth, which may be either a 116 disarticulated upper or lower tooth. The teeth are set within alveoli along a continuous groove. 117 No distinct bony septa between alveoli are visible but may be present at the bottom of the dental 118 groove, being concealed in matrix that is very difficult to remove through mechanical 119 preparation. The roots of some teeth are clearly expanded at the base and exhibit plications that 120 are coarser than crown striation. The most anterior tooth is completely exposed anteriorly, 121 revealing its root structure inside the dental groove. It is seen there that the root ceases its 122 expansion once inside the groove, and teeth are embedded to both the labial wall and the base of the groove. A narrow gap emerges between the lingual wall and the root toward the dentigerous 123 124 margin. Tooth implantation is likely subthecodont (sensu Motani, 1997a), although histological 125 study is necessary to firmly establish this. The root cross-section is much wider than long, as 126 reported for Utatsusaurus hataii (Motani, 1996).

127

Teeth are isodont and conical with striated crowns. Tooth roots are extensively exposed above 128 129 the alveolar margin such that they account for half or more of the exposed height of each tooth. 130 Tooth crowns are distinguished from these exposed roots by a distinct margin and most crowns 131 are slightly constricted at their base. Some crowns exhibit slightly higher convexity of their 132 anterior surface relative to the posterior surface given them a slightly recurved appearance. The 133 teeth are also recurved lingually toward the tip, as clearly seen in the most anterior tooth (Fig 2B). This curvature closely resembles what was described for Utatsusaurus hataii (Motani, 134 135 1996: Fig. 3). The tips of the teeth are relatively blunt. Tooth crowns are approximately 5mm tall 136 and 1.5mm mesiodistal diameter, spacing between teeth ranges from 3mm to 6mm more widely 137 spaced teeth may have replacement teeth between them. One 10mm gap along the tooth row

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likely to represents at least one missing tooth. Several teeth are broken, either at the root or thecrown, revealing a pulp cavity without evidence of infolding of the dentine.

140

141 Remarks. The tooth morphology observed in this specimen closely resembles that described for 142 Utatsusaurus hataii from the Lower Triassic Osawa Formation of Kitakami, Japan (Shikama et 143 al., 1978). Most notably, the teeth curve lingually and slightly posteriorly toward the tip, which is 144 a feature that is uniquely known in Utatsusaurus among basal ichthyosaurs. Other shared 145 features include: isodont dentition, tall exposed roots, blunt conical striated crown, slightly constricted base of some crowns, and absence of infolding in the pulp cavity. No other Early 146 147 Triassic or later ichthyopterygian exhibits this suite of dental characters. The teeth of this 148 specimen do diverge from Utatsusaurus hataii in their much larger size. The maximum tooth 149 exposed height in this specimen is 10mm, whereas the maximum crown height and width are 150 5mm and 1.5mm respectively, compared with 3.3mm, 1.7mm and 0.9mm for the same 151 measurements in the holotype of *Utatsusaurus hataii* (Motani, 1996). However, the holotype 152 represents a juvenile (Motani, 1997c) so the size difference may partly be explained as age 153 difference.

154

A partial skull from the Lower Triassic Vega Phroso Member of the Sulphur Mountain Formation from British Columbia, Canada was referred to *Utatsusaurus* sp. by Nicholls and Brinkman (1993), based largely on the presence of the same dental features detailed above. The teeth of the British Columbia specimen are similar in size to those of the Nevada specimen described here (Nicholls & Brinkman, 1993) and distinctly larger than those found in the holotype of *Utatsusaurus hataii* from Japan (Motani, 1996). It is therefore possible that these

161 larger-toothed specimens from the eastern margin of Panthalassa (Nevada, British Columbia) 162 represent a form allied with but distinct from Utatsusaurus hataii; however more complete 163 material is needed before this can be confirmed. Recently, Cuthbertson et al. (2014) described 164 another partial skull from the Vega Phroso Member, which they also referred to Utatsusaurus 165 sp., although they concluded that the material originally referred to this genus by Nicholls and 166 Brinkman (1993) was non-diagnostic at the genus level. Unfortunately this recently described 167 material lacks a lower jaw or teeth and cannot be compared to USNM 559349. 168 169 Ichthyopterygia Owen, 1840 170 cf. Grippida Wiman, 1929 171 172 **Referred specimen**. USNM 559350 Partial maxilla including teeth. (Fig. 3) 173 Locality. Fossil Hill, Humboldt Range, Pershing County, Nevada. 174 Horizon and Age. Collected from FH1-5 (Fig. 1) horizon which is Spathian based on the 175 occurrence of the ammonoid Prohungarites gutstadi (Guex et al., 2010) and conodonts including 176 *Triassospathodus* and *Neostrachanognathus*. This horizon is also characterized by distinctive 177 spherical structures originally interpreted as microbial (i.e. 'oncoids') but more recently suggested to represent sponge "reefs" (Brayard et al., 2011) see further discussion below. 178 179 **Description**. USNM 559350 (Fig. 3) is a partial maxilla measuring 20mm and bearing five teeth 180 exposed in medial view. The teeth are robust cones exhibiting a trend of posteriorly increasing

181 basal diameter whereas the crown height remains constant giving the posteriormost preserved

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

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

anteriormost crown height and width are 1.0mm and 0.7mm respectively; in the second
posteriormost tooth, which is better preserved than the posteriormost tooth, crown width and
height are 2.1mm and 0.9mm. The tooth enamel appears smooth and polished with little
indication of striation, however, this could be attributed to tooth wear. Faint plication is visible
on some roots. Although some teeth are abraded none expose the pulp cavity clearly enough to
determine presence or absence of infolded dentine.

190

191 In medial view the teeth are attached to the lingual wall of the maxilla (pleurodont). An 192 expanded bone of attachment conceals the bases of the two posteriormost teeth, suggesting the 193 modified form of pleurodonty termed subpleurodonty (Motani, 1997a) at least in the posterior 194 region of the maxillary tooth row. While only a single row of teeth is observed, a shallow 195 depression on the lingual margin of the tooth row immediately anterior to the second 196 posteriormost tooth could represent the attachment facet of a missing tooth. If this were the case 197 it would most likely represent a second row immediately lingual to the preserved teeth. Wide 198 spacing between the four anteriormost teeth would easily accommodate an additional offset tooth 199 row as observed in the maxillary dentition of Grippia (Motani, 1997b) and Gulosaurus 200 (Cuthbertson et al., 2013).

201

Remarks. Among Early Triassic ichthyopterygians small, robust teeth similar to those reported
here are typical of the posterior dentition of *Grippia* (Motani, 1997b). Rounded teeth are also
observed in the Early Triassic genus *Chaohusaurus* (Motani & You, 1998) and, to a lesser
extent, *Gulosaurus* (Cuthbertson et al. 2013). *Grippia* was previously reported from the Lower
Triassic Vega Phroso Member of the Sulphur Mountain Formation in British Columbia

207 (Brinkman et al., 1992). This specimen was later redescribed as a distinct taxon, *Gulosaurus* 208 helmi (Cuthbertson et al., 2013) and found to be sister taxon to Grippia longirostris. Similarly, 209 recent work by Ji et al. (in press a), established a new clade Grippioidea including *Grippia*, 210 Gulosaurus, Utatsusaurus Parvinatator although the precise relationships among these taxa 211 varied somewhat depending on taxon and character inclusion. The enigmatic marine reptile 212 Omphalosaurus nettarhynchus (Mazin & Bucher, 1987) previously reported from Spathian 213 Lower Member of the Prida Formation also possesses rounded dentition, but is distinct from this 214 specimen by its much larger size and in exhibiting a broad pavement of rounded teeth on the 215 mandible.

216

217 Alternatively this specimen may have some affinity with *Chaohusaurus*, an Early Triassic 218 ichthyopterygian from China in which some specimens also show distinctly rounded posterior 219 dentition (Motani & You, 1998), although these teeth are generally smaller and more tightly 220 packed than in USNM 559350, averaging approximately ten teeth over 20mm rather than the 221 five teeth observed over the same distance in this specimen. Chaohusaurus was previously 222 regarded as a grippidian partly on the basis of possessing multiple maxillary tooth rows and 223 rounded posterior dentition (Motani, 1999) however more recent analyses (Cuthbertson et al. 224 2013, Ji et al., in press a) do not support this placement. Thus the dentition observed in USNM 225 559350 is strongly suggestive of affinity with other Early Triassic ichthyopterygians but more 226 precise placement will require more complete skeletal material.

227

228 Discussion

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229 Despite the fragmentary nature of the remains described here their resemblance with the 230 distinctive dentitions of other Early Triassic ichthyopterygians allows tentative comparisons to 231 be drawn. The presence of Utatsusaurus-like and Grippia or Chaohusaurus -like forms suggests 232 similarity with the Lower Triassic Vega Phroso assemblage from the Wapiti Lake region of 233 British Columbia, from which Utatsusaurus (Nicholls & Brinkman, 1993; Cuthbertson et al., 234 2014) and Grippidians (Brinkman et al., 1992; Cuthbertson et al., 2013) have also been reported. 235 However, the type locality of Utatsusaurus is in the Osawa Formation of Japan (Shikama et al., 236 1978), whereas the type localities of Grippia and Chaohusaurus are in the Vikinghøgda 237 Formation (= "Sticky Keep Formation" of older references) of Spitsbergen (Wiman, 1929, 1933; 238 Hounslow et al., 2008) and the Nanlinghu Formation of Anhui Province, China (Young & Dong, 239 1972) respectively. Thus Early Triassic ichthyopterygian taxa were widely distributed around the 240 margins of northern Panthalassa (Cuthbertson et al., 2013). 241

242 This broad distribution early in their evolutionary history, from numerous Late Spathian 243 (Subcolumbites Zone) localities of broadly coeval age (Scheyer et al., 2014), has made it 244 difficult to pinpoint the biogeographic origins of the group. However, recent work in China has 245 extended the occurrence of ichthyopterygians down into the underlying Procolumbites Zone 246 (Motani et al., 2014; Ji et al., in press b). Furthermore, the occurrence of diverse and endemic 247 hupehsuchians, widely regarded as the ichthyopterygian sister-group and the plesiomorphic 248 ichthyosauromorph Cartorhynchus (Motani et al., 2015) are consistent with an origin of 249 ichthyopterygians near the south China block in equatorial western Panthalassa.

250

251 The inferred nearshore lifestyle of most Early Triassic ichthyosaurs has led others to propose that 252 these marine reptiles dispersed along coastlines or across transient epicontinental corridors 253 (Cutherbertson et al., 2013). However, the biogeographic history of other aquatic and even 254 terrestrial reptile groups is marked by occasional transoceanic disperals (e.g. Rocha et al., 2006; 255 Velez-Juarbe et al., 2007). Brayard et al. (2009) identified trans-Panthalassan distribution 256 patterns in Spathian ammonoid, with similar ammonoid faunas in Nevada, Kitakami and British 257 Columbia, which they attributed to oceanographic currents. The occurrence of some Early 258 Triassic marine reptile taxa (e.g. *Utatsusaurus*) on opposite shores of Panthalassa might reflect 259 sporadic crossing of deep ocean basins by these lineages, potentially facilitated by the same 260 ocean currents that mediated transoceanic dispersals of contemporaneous marine invertebrates. 261 The wide distribution of early Triassic sauropterygians, including the South China Block (Jiang 262 et al., 2014) and western margin of North America (Storrs, 1991; Lovelace & Doebbert, 2015) 263 on opposite shores of Panthalassa indicates to a similar dispersal history in the early members of 264 that marine reptile clade. Isolated terranes such as South Kitakami, South Primoyre and Chulitna 265 could have served as stepping-stones for shallow marine taxa. Dispersal along coastlines around 266 the northern margins of Panthalassa remains an alternative scenario that could explain the broad 267 distribution of Early Triassic ichthyopterygians, however, the apparent absence ichthyopterygian 268 fossils from high latitudes on the west coast of northern Panthalassa remains a puzzle under this 269 scenario.

270

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

272 prominent limestone marker bed bearing distinctive spherical structures ~1-2 cm in diameter

273 (Fig. 4). We initially interpreted these structures as microbial 'oncoids.' Widespread

274	microbialite-dominated facies are characteristic of Lower Triassic strata globally including in the
275	Western United States (Pruss & Bottjer, 2004; Baud et al., 2007) and are interpreted as a
276	byproduct of the end-Permian mass extinction and subsequent delayed biotic recovery of
277	metazoan reefs (Pruss et al., 2004). A similar association between the basal sauropterygian
278	Corosaurus and stromatolites in the Lower Triassic Alcova limestone has been reported
279	previously (Storrs, 1991). More recently, similar spheroidal structures from the Humboldt Range
280	and other localities in western North America have been interpreted as 'transient sponge reefs'
281	(Brayard et al., 2011). Thus, the diversification and dispersal of Early Triassic marine reptiles
282	was apparently well underway at the end of the Early Triassic (Scheyer et al., 2014) despite some
283	lingering signs of continued environmental stress preserved in the same strata. Future work at
284	this new locality, and elsewhere, may help to clarify the role that large-scale environmental
285	changes played in shaping the early evolutionary history of Mesozoic marine reptiles.
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289	
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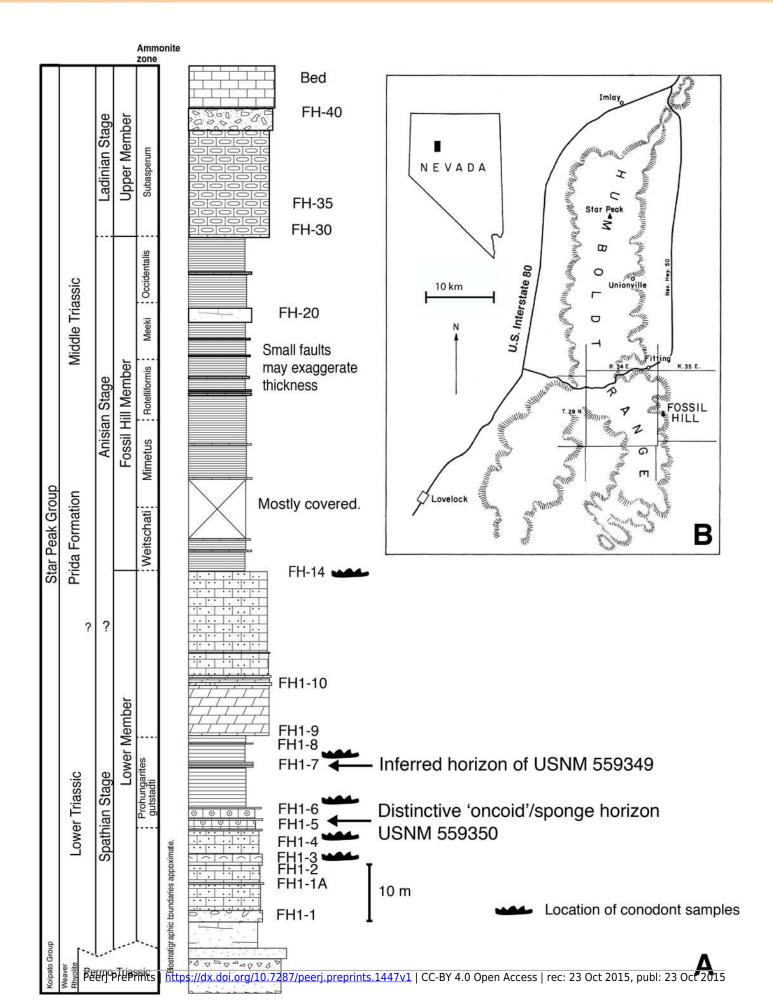
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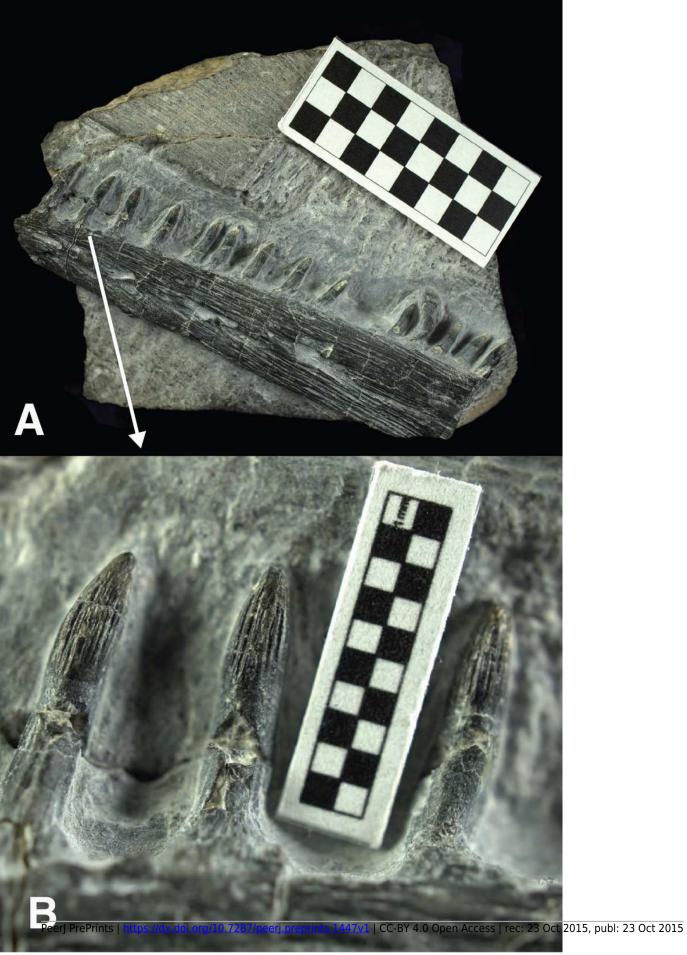
Summarized stratigraphy and regional map

(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).



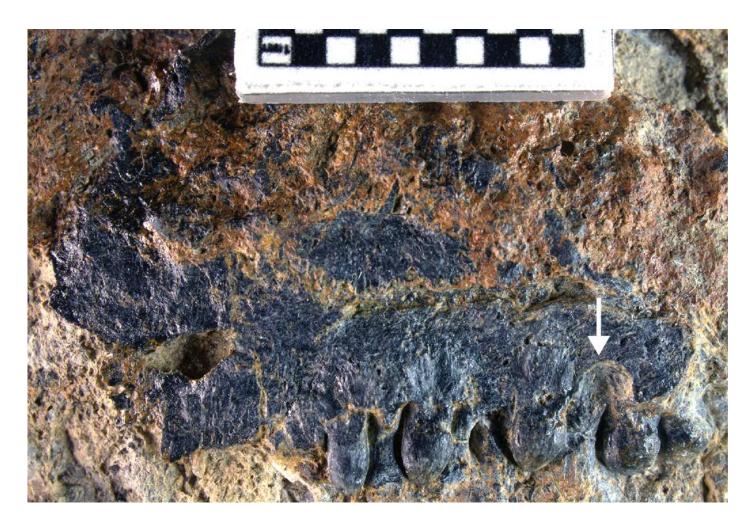
Specimen USNM 559349, partial ichthyopterygian jaw cf. Utatsusaurus.

- (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.



USNM 559350 Partial ichthyopterygian maxilla cf. Grippidia.

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.



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.

