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Abstract

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.

Main article text

Introduction

Nevada has been an important source of Triassic marine reptile fossils since the 19th Century producing abundant and well-preserved Middle Triassic (Leidy, 1868; Merriam, 1905, 1908, 1910; Sander et al., 1994, 1997; Fröbisch et al., 2006, 2013) and Late Triassic (Camp 1976, 1980) ichthyopterygian and sauropterygian fossils. Notably Early 20th Century field work led by John Merriam and Annie Alexander at the Fossil Hill locality in the Humboldt Range produced 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 *Omphalosaurus nevadanus* (Merriam, 1906) and *Phalarodon fraasi* (Merriam 1910). Later work by Camp (1976, 1980), Sander et al. (1994, 1997) and others illuminated rich Middle and Late Triassic marine reptile assemblages preserved in Nevada.

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

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 dispersed around or across wide expanses of ocean and ranged from sub-tropical to high temperate waters on the eastern margin of northern Panthalassa.

Institutional Abbreviations. USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.

Materials and Methods

Geological and Stratigraphic Setting

The new fossils reported here were collected from multiple horizons within the unnamed lower member of the Prida Formation of the Star Peak Group at Fossil Hill, on the eastern flank of the Humboldt Range in Pershing County, Nevada (Fig. 1). The Star Peak Group consists of a sequence of syndepositionally deformed carbonate-dominated units deposited on what was then the western shelf of North America (Nicholls & Silberling, 1977; Wyld, 2000). In the study area, the lower member of the Prida Formation forms the base of the Star Peak Group and sits unconformably atop the Permian/Lower Triassic aged Koipato Group volcanics (Wyld, 2000).

The lower member of the Prida formation transitions from siliciclastic sand and conglomerate layers near the contact with the underlying Koipato Group to dark-grey limestone above with intermittent microbialite, conglomerate and chert-dominated beds. The presence of conglomerates and microbialites indicate relatively shallow conditions with a general trend towards deeper water facies characteristic of the overlying Fossil Hill Member (Wyld, 2000). Gastropods and bivalves are abundant in lower layers whereas conodonts and ammonoids are found locally within middle and upper layers of the lower member. Scattered vertebrate fossils occur in multiple horizons within the lower member (Fig. 1), but are most abundant in the middle carbonate layers where they are associated with the conodont *Triassospathodus symmetricus* (Orchard, 1995) and the ammonoid *Prohungarites gutstadti* (Guex et al., 2010) indicating a late Spathian age (Subcolumbites ammonoid biozone).

Results

Systematic Paleontology

Ichthyopterygia Owen, 1840

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

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

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

Horizon and age. Found as surface float within an outcrop of Lower Triassic (upper Spathian) lower member of Prida Formation, Star Peak Group. Based on location and matrix lithology this jaw is inferred to derive from horizon FH1-7 (Fig. 1), which is Spathian based on the occurrence of the ammonoid *Prohungarites gutstadi* (i.e. Subcolumbites Zone of Guex et al., 2010) and conodonts *Triassospathodus symmetricus* (Orchard, 1995) and *Neostrachanognathus* sp. extracted from the matrix.

Description. USNM 559349 is a partial mandible measuring 82 mm long. The jaw fragment preserves portions of the dentary, surangular and splenial. The surfaces of the dentary and surangular are heavily striated and the orientation of these striations differs between the bones. Judging from the arrangement of the bones, the fragment likely represents a relatively posterior portion of the left mandibular ramus.

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

Teeth are isodont and conical with striated crowns. Tooth roots are extensively exposed above the alveolar margin such that they account for half or more of the exposed height of each tooth. Tooth crowns are distinguished from these exposed roots by a distinct margin and most crowns are slightly constricted at their base. Some crowns exhibit slightly higher convexity of their anterior surface relative to the posterior surface given them a slightly recurved appearance. The 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, 1996:Fig. 3). The tips of the teeth are relatively blunt. Tooth crowns are approximately 5mm tall and 1.5mm mesiodistal diameter, spacing between teeth ranges from 3mm to 6mm more widely spaced teeth may have replacement teeth between them. One 10mm gap along the tooth row likely to represents at least one missing tooth. Several teeth are broken, either at the root or the crown, revealing a pulp cavity without evidence of infolding of the dentine.

Remarks. The tooth morphology observed in this specimen closely resembles that described for *Utatsusaurus hataii* from the Lower Triassic Osawa Formation of Kitakami, Japan (Shikama et al., 1978). Most notably, the teeth curve lingually and slightly posteriorly toward the tip, which is a feature that is uniquely known in *Utatsusaurus* among basal ichthyosaurs. Other shared 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 Triassic or later ichthyopterygian exhibits this suite of dental characters. The teeth of this specimen do diverge from *Utatsusaurus hataii* in their much larger size. The maximum tooth exposed height in this specimen is 10mm, whereas the maximum crown height and width are 5mm and 1.5mm respectively, compared with 3.3mm, 1.7mm and 0.9mm for the same measurements in the holotype of *Utatsusaurus hataii* (Motani, 1996). However, the holotype represents a juvenile (Motani, 1997c) so the size difference may partly be explained as age difference.

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 larger-toothed specimens from the eastern margin of Panthalassa (Nevada, British Columbia) represent a form allied with but distinct from *Utatsusaurus hataii*; however more complete material is needed before this can be confirmed. Recently, Cuthbertson et al. (2014) described another partial skull from the Vega Phroso Member, which they also referred to *Utatsusaurus* sp., although they concluded that the material originally referred to this genus by Nicholls and Brinkman (1993) was non-diagnostic at the genus level. Unfortunately this recently described material lacks a lower jaw or teeth and cannot be compared to USNM 559349.

Ichthyopterygia Owen, 1840

cf. Grippida Wiman, 1929

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

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

Horizon and Age. Collected from FH1-5 (Fig. 1) horizon which is Spathian based on the occurrence of the ammonoid *Prohungarites gutstadi* (Guex et al., 2010) and conodonts including *Triassospathodus* and *Neostrachanognathus*. This horizon is also characterized by distinctive 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.

Description. USNM 559350 (Fig. 3) is a partial maxilla measuring 20mm and bearing five teeth exposed in medial view. The teeth are robust cones exhibiting a trend of posteriorly increasing basal diameter whereas the crown height remains constant giving the posteriormost preserved tooth a distinctly rounded shape. There is a distinct constriction below the crown separating it 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.

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

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

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

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

Discussion

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

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

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

Intriguingly, the oldest marine reptile bearing horizons at Fossil Hill are associated with a prominent limestone marker bed bearing distinctive spherical structures ~1–2 cm in diameter (Fig. 4). We initially interpreted these structures as microbial 'oncoids.' Widespread microbialite-dominated facies are characteristic of Lower Triassic strata globally including in the Western United States (Pruss & Bottjer, 2004; Baud et al., 2007) and are interpreted as a byproduct of the end-Permian mass extinction and subsequent delayed biotic recovery of metazoan reefs (Pruss et al., 2004). A similar association between the basal sauropterygian *Corosaurus* and stromatolites in the Lower Triassic Alcova limestone has been reported previously (Storrs, 1991). More recently, similar spheroidal structures from the Humboldt Range and other localities in western North America have been interpreted as 'transient sponge reefs' (Brayard et al., 2011). Thus, the diversification and dispersal of Early Triassic marine reptiles was apparently well underway at the end of the Early Triassic (Scheyer et al., 2014) despite some lingering signs of continued environmental stress preserved in the same strata. Future work at this new locality, and elsewhere, may help to clarify the role that large-scale environmental changes played in shaping the early evolutionary history of Mesozoic marine reptiles.

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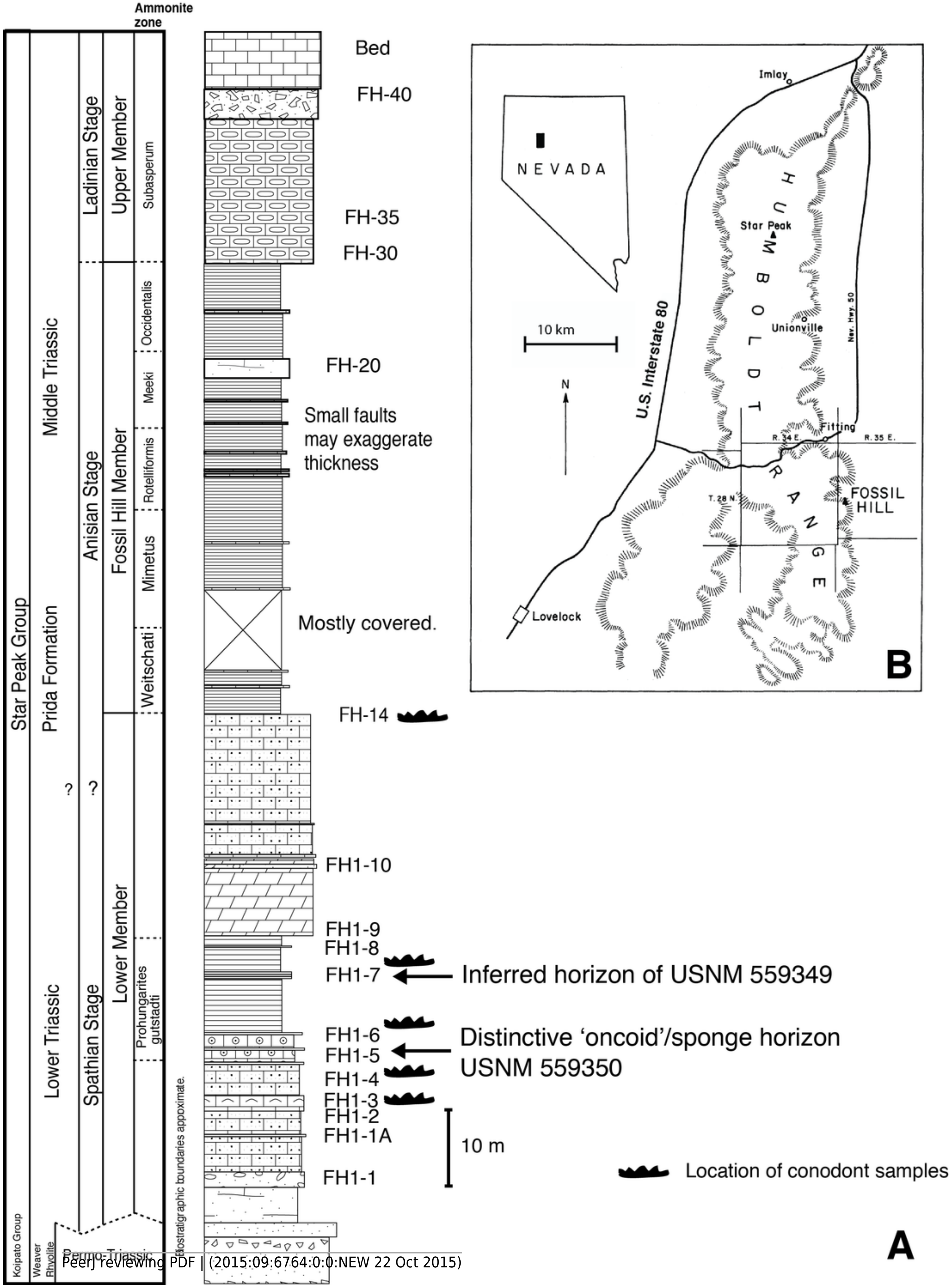
1

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).

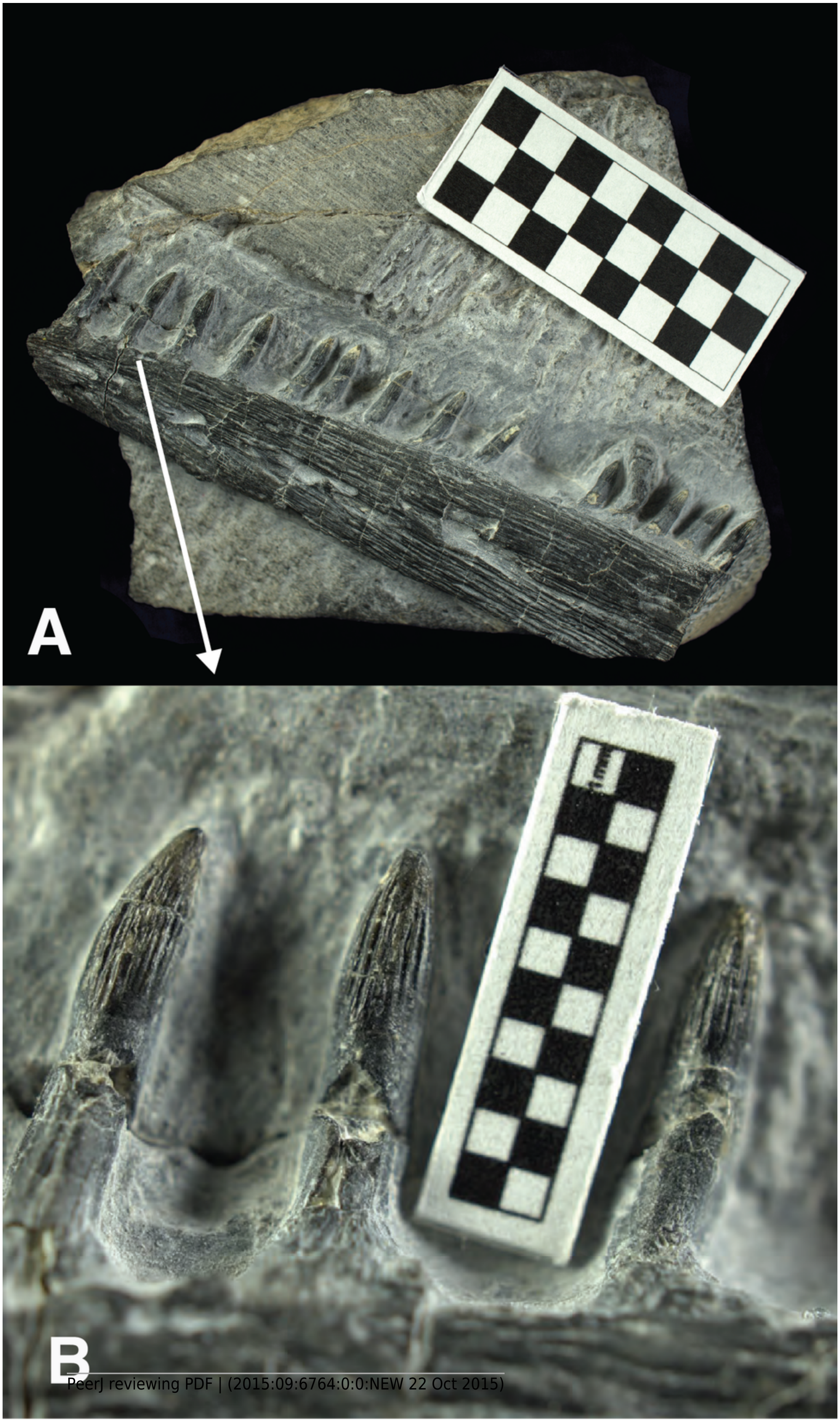

Ammonite zone
Star Peak Group
Koipato Group
Weaver Rhyolite
Prida Formation
Middle Triassic
Lower Triassic
Permo-Triassic
Ladinian Stage
Anisian Stage
Spathian Stage
Upper Member
Fossil Hill Member
Lower Member
Subasperum
Occidentalis
Meeki
Rotelliformis
Mimetus
Weitschati
Prohungarites gutstadti
?
?
Biostratigraphic boundaries approximate.
Bed
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
Location of conodont samples
A
NEVADA
10 km
N
U.S. Interstate 80
Nev. Hwy. 50
Imlay
Star Peak
Unionville
Fitting
Lovelock
HUMBOLDT RANGE
R. 34 E.
R. 35 E.
T. 28 N.
FOSSIL HILL
B

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.

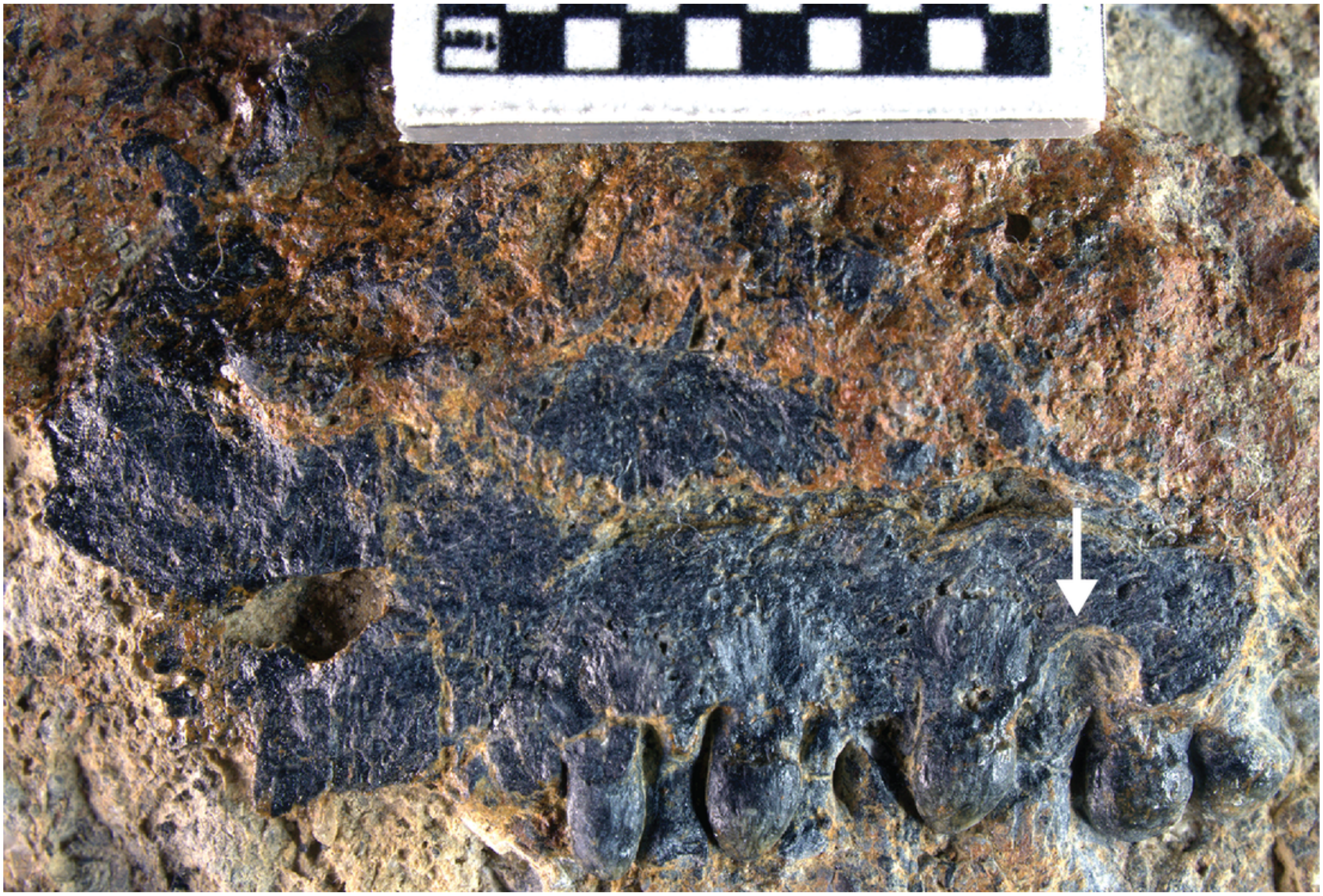
(B) Magnified view of anterior dentition, squares on scale bar equal 1 mm.


A
B

3

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.



4

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.