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Actinopterygian and chondrichthyan ichthyoliths reveal enhanced cosmopolitanism in Late Triassic marine ecosystems

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ABSTRACT
The Late Triassic was a time of major evolutionary transition for marine vertebrates, with the emergence of important new clades and the expansion of durophagy. The diversity record of shallow marine vertebrates has been limited by poor preservation, and palaeogeographic ranges of common marine vertebrates is poorly constrained. Isolated ichthyoliths are an important resource for documenting taxonomic and ecological diversity in shallow marine environments and have a relatively high preservation potential. Here, we report the first Upper Triassic elasmobranchs, neopterygians and chondrosteans from Nevada, and contribute 14 new generic occurrences. The vertebrates represented in this survey include teeth of specialised durophages and piscivores, and a tentative reconstruction of the shallow marine ecosystem trophic niches based on dietary interpretations and known shelly macrofossils from this locality. The ichthyolith assemblage exhibited greater similarity to low-latitude Europe than high-latitude Canada localities, and the results of this study suggest that several taxa previously considered to be endemic to Europe may be cosmopolitan. The present study highlights the need for additional research in early Mesozoic ichthyoliths in order to establish diversity patterns, paleobiogeographic ranges, and timing of adaptive radiations among key groups of marine vertebrates in the Triassic Period in suboptimal preservation conditions.

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Introduction

The Triassic Period was a critical time for marine vertebrate evolution and ecology, with important groups appearing in the aftermath of the End-Permian mass extinction (Scheyer et al. 2014), and a series of adaptive radiations occurring in the Late Triassic among chondrichthyans (Cuny and Benton 1999), neopterygians (Tintori 1998; Lombardo and Tintori 2005; López-Arbarello et al. 2010), placodonts (Rieppel 2002; Crofts et al. 2017) and ichthyosaurs (Sander 2000; Kelley et al. 2014). Vertebrate adaptive radiations may be tied to global evolutionary events like the Mesozoic marine revolution (Vermeij 1993; Walker and Brett 2002; Benton and Wu 2022) and were likely to have influenced extinction first across the Norian–Rhaetian boundary (Renesto and Dalla Vecchia 2018) and then across the Triassic–Jurassic boundary (Fischer et al. 2014; Stumpf et al. 2017). Determining the vertebrate influence on marine ecosystems has been limited by the rarity of Konservat and Koncentrat Lagerstätten, which are not typically developed in shallow marine environments, the habitat of many marine vertebrates thought to be experiencing adaptive radiations in the Mesozoic.

Previous studies

Ichthyolith contributions of Upper Triassic marine sediments include the United Kingdom (Cross et al. 2018), China (Chen et al. 2007), Hungary (Ősi et al. 2013), France (Duffin 1993), and elsewhere. Very few studies have surveyed eastern Panthalassa deposits (Table 1), and no published surveys have explored ichthyoliths from Upper Triassic marine deposits in Nevada, where extensive shallow marine deposits are preserved, and the marine invertebrate record is well-documented (Laws 1982; Hogler 1992; Guex et al. 2004; Tackett and Bottjer 2016; Larina et al. 2021; Taylor et al. 2021). Ichthyolith assemblages from Canada (Johns et al. 1997) have mainly focused on elasmobranchs, but these assemblages bear little resemblance to ichthyoliths or specifically chondrichthyans from Europe, suggesting high levels of endemism between Tethys and eastern Panthalassa. Unfortunately, the paucity of research on ichthyoliths from the marine western USA hinders this interpretation.

Microvertebrates can be extracted from shallow marine carbonates where articulated preservation of vertebrates is unlikely, and therefore represent important and understudied resources for diversity and ecological interpretations. Microvertebrate assemblages may identify the paleoenvironmental parameters of taxonomic radiation events, informing about major macroevolutionary processes. Here, we present occurrence data and palaeoecological reconstruction of an ichthyolith assemblage from the lower Norian carbonate member of the Luning Formation in west-central Nevada, from the Berlin Ichthyosaur State Park (BISP), in order to better establish the presence and paleogeographic ranges of marine vertebrates during this important interval. Finally, we describe regional and latitudinal affinities exhibited by this microvertebrate assemblage.

Geological setting

The Luning Formation was deposited during the Carnian to the middle Norian (Muller and Ferguson 1939; Ferguson and Muller 1949; Silberling 1959), and consists of four distinct but informal members (Figure 1). The lowest three members, the clastic, shaly limestone and calcareous shale members, contain

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Table 1. Actinopterygii and chondrichthyes ichthyolith reports from Late Triassic marine deposits of Eastern Panthalassa.

Locality	Age	Reported Taxa	Reference	Figured ichthyoliths
British Columbia, Canada	Middle-Late Triassic	Elasmobranch denticles	Johns (1996)	yes
British Columbia, Canada	Middle-Late Triassic	Actinopterygii, *Acrodus, Polyacrodus* (*Omanoselache*), *Synechodus*, elasmobranch scales: *Parviscapha, Lobaticorona, Proprigalea, Undulaticorona, Parvidiabolus, Duplisuggestus, Coniunctio, Labascicorona, Rugosicorona, Gracilisuggestus, Fragilicorona, Labrilancea, Ornatilabrilancea, Minuticorona, Sacrisubcorona, Carinasubcorona, Glabrisubcorona, Complanicorona, Suaviloquentia*	Johns et al. (1997)	yes
British Columbia, Canada	Carnian	elasmobranch, actinopterygian	Zonneveld et al. (2007)	yes
California	Carnian	*Palaeobates*	Bryant (1914)	yes (drawn)
California	Carnian	*Hybodus, Acrodus*	Wemple (1914)	yes (drawn)
California	Carnian	*Acrodus, Hybodus*	Jordan (1907)	yes (drawn)
Oregon	Carnian	hybodontiform, colobodontiform	Metz (2019)	no
Nevada, USA	Carnian-Norian	'isolated ichthyoliths'	Lucas et al. (2007)	no
British Columbia, Canada	Norian	*Synechodus, Fragilicorona, Glabrisubcorona, Minuticorona, Labascicorona, Birgeria*	Orchard et al (2001a, b)	no
Bolivia	Norian	*?Birgiria*	Beltan et al. (1987)	yes
Chile	Rhaetian	*Glabisubcorona*	Sansom (2000)	yes

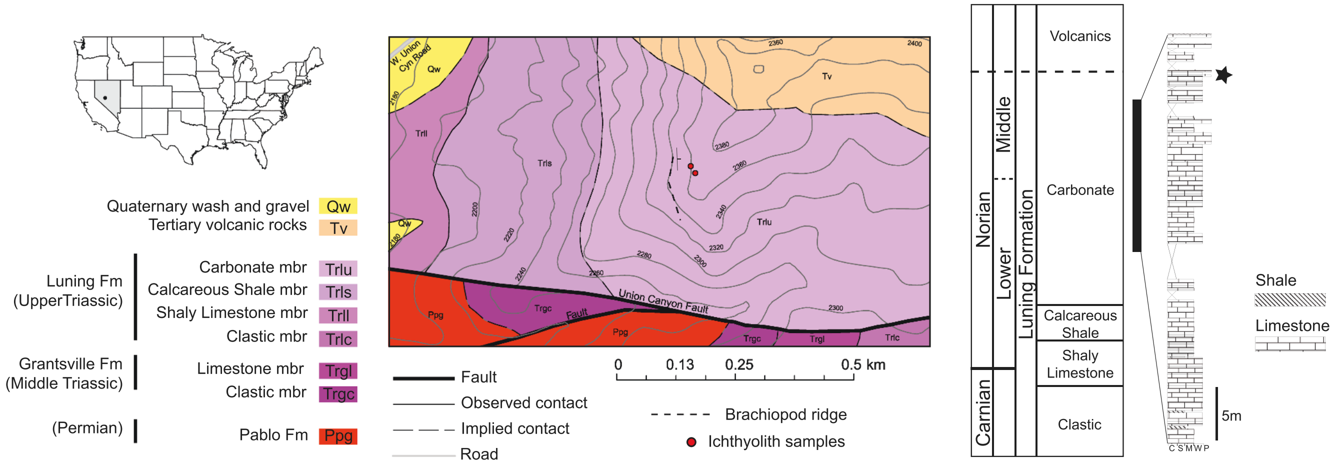

Figure 1. Locality map and stratigraphic column. Sample analysed in this study is indicated on column with black star (38°52′41.2″N, 117°34′35.6″W). Stratigraphic column terms are C = cover, M = mudstone, W = wackestone, P = packstone.

the Carnian–Norian boundary defined by ammonoids and conodonts (Balini et al. 2015) and an ichthyosaur Lagerstätte deposit (Hogler 1992; Montague-Judd 1999). The carbonate member is the thickest of the four members, and contains abundant benthic invertebrate fossils (Hogler 1992; Tackett and Bottjer 2016). The carbonate member of the Luning Formation was deposited on the continental side of a back-arc basin in eastern Panthalassa (Speed 1978; Reilly et al. 1980; Oldow 1984), and represents a well-ventilated shallow marine environment on a carbonate platform (Silberling 1959; Hogler 1992; Tackett and Bottjer 2016), with encrinites in the lowest part of the member, floatstones to packstones in the middle, and solitary corals present in the uppermost beds of the member, above which is disconformable Tertiary volcanics. Samples from this study were collected from the same sedimentary horizon as the bulk sample 'BISP 5' from Tackett and Bottjer (2016), *ca.* 20 metres above the prominent 'brachiopod ridge', a brachiopod-dominated packstone.

Material and methods

Dissolution and imaging

The carbonate matrix from shelly invertebrate bulk sampling was retained and subjected to acid dissolution using a buffered acetic acid solution (Jeppsson et al. 1999). Hand samples of rock were placed into a bag made from fibreglass mosquito screening material (Saint Gobain brand), allowing liberated grains smaller than *c.* 2 mm to settle out of the netting. Lithologic materials large enough to be retained within the net were then placed into fresh buffered acid baths and acid residues smaller than *c.* 2 mm were sieved into three size fractions: >250 μm, 250–125 μm and 125–75 μm. These residues were transferred to quantitative filter paper and allowed to dry for 24–48 h before being moved to storage containers. The greatest number of dermal denticles and teeth were recovered from the two largest size fractions and were analysed in the present study. The residues of different size fractions were immersed in a KOH solution (Sibert et al. 2017) in order to stain the apatitic minerals a distinctive pink colour, but multiple efforts did not yield microvertebrate components that had taken up the KOH. This may be due to diagenesis that destroyed the organic matter, though these carbonate rocks generally have low diagenetic values, including high strontium to manganese ratios (Tackett et al. 2014).

Using a Zeiss V.12 Focus Precision microscope, microvertebrates and other microfossils were recovered, and attached to gridded microfossil trays using gum Arabic. Microvertebrate ichthyoliths were imaged using a mounted Zeiss ICc 5 digital camera and ZEN imaging software, twenty Z-stacked images were compiled of the microvertebrate fragments. Adobe Photoshop was used to sharpen and lighten images and remove backgrounds. Ichthyoliths were identified based on descriptions and images in previously published work on both isolated and articulated palaeontological examples (Table 2). Most chondrichthyan denticles cannot readily be assigned to a specific taxonomic group (though see Johns 1996 for examples of denticle taxa), due to the high degree of variability of denticle morphology within an individual and many denticle morphotypes are shared across taxa (Dillon et al. 2017), though some denticle types can be categorised ecologically, but we did not undertake this interpretation here.

The ichthyolith assemblage presented here is not interpreted as representing discrete individuals. The various vertebrates observed in acid residues from BISP employed different tooth/scale replacement strategies, and caution is recommended to avoid over-interpretation of population dynamics without considering these differences. For example, several taxa interpreted to be durophages used a dental palette that did not continuously replace teeth (e.g. Stumpf et al. 2017), and chondrichthyans may have continuously replaced both teeth and denticles, including the durophagous taxa (Cuny and Risnes 2005).

Food Web

Dietary modes of vertebrates and estimated body size were assigned based on previous interpretations, sourced from articulated specimens or modern analogues or reasoned interpretations in the published literature (Table 2), and any specimens without clear taxonomic affinities tied to previously published dietary interpretations were not assigned a dietary mode. Vertebrates were generally categorised as durophages and piscivores with degrees of specialisation for the former and size categories for the latter. Durophages were differentiated as specialised durophages, whose diets were predominantly hard-shelled prey and whose dentition reflected a broad contact surface, and semi- or hemi-specialised durophages, which had some capacity for consuming hard-shelled prey, but whose dentition could have accommodated other foods as well. Piscivores were separated by size to broadly reflect their prey size. A basic food web was generated based on the roles of the vertebrates and with shelly invertebrate data from Tackett and Bottjer (2016; 'BISP 5'). Other BISP fauna reported previously are not included in the present web because they are from the underlying calcareous shale member or from lower in the carbonate member which exhibits a substantially different invertebrate fauna despite representing a similar depositional environment, a taxonomic change noted in Tackett and Bottjer (2016).

Cluster analysis

To assess similarity among assemblages of ichthyoliths, a cluster analysis was performed. Occurrence data was downloaded from the Palaeobiology Database on 10 April 2021, for all marine chondrichthyan and actinopterygian fishes from the Late Triassic, identified at least to a genus level. Few collections contain occurrences of more than a single taxon, therefore occurrence data for regions of interest were combined prior to comparison. Regions include Europe, Asia, South America, Oceania (New Zealand and Australia), Svalbard (remaining a separate group with no nearby occurrences) and North America. North America was divided into three subgroups: Canada, the United States (excluding data from this study) and Nevada (including all tooth and non-denticle occurrences from this study) to identify differences among existing collections and the Berlin Ichthyosaur State Park collection. A presence-absence matrix was constructed for these regions of all chondrichthyan and actinopterygian genera identified by teeth. Teeth were only included in this cluster analysis as other ichthyoliths, such as denticles, could not be assigned to a specific taxon and were removed from the dataset. Cluster analysis was carried out in R (R Core Team 2020) using Bray-Curtis to calculate distance and agglomerative nesting using the Ward method to produce nested clusters.

Cluster analysis was run both with and without singleton taxa. Oceania and South American collections were entirely removed when singletons were not included in the analysis, as they only contain single occurrence taxa. Three tiers of analysis were performed. First, singletons were included, and secondly, singletons were excluded, eliminating singletons also eliminated two regions Oceania and South America. Thirdly, a combination of previously known USA data was combined with BISP data.

Osteichthyan scales

Osteichthyan scales (Fig. 2AD–AE) were recovered and identified based on the quadrate shape, resembling morphotype 3 scale illustrated by Landon *et al.* (2017) and Cross *et al.* (2018).

Results

Taxonomic diversity

The dissolved limestones yielded different types of ichthyoliths, including teeth, dermal denticles, and scales (Figure 2). No conodonts were observed in the residues. Ichthyoliths from the present survey were of generally good quality, but with signs of abrasion (missing apical caps or roots were a common feature). No morphotypes are allocated in this study, due to the relatively low quality of the materials, except for specimens from two unknown taxa which require additional study but are figured here. All ichthyoliths were isolated, so a distinct possibility for synonymy exists; however, this is a typical feature of working with ichthyliths, especially those derived from chondrichthyans.

Seven genera were confidently identified, including *Gyrolepis, Severnichthys acuminatus (Birgeria acuminata* and *Saurichthys longidens* types), *Dapedium, Lepidotes* (and junior synonym *Sphaerodus), Lissodus*, and *Rhomphaiodon* (Table 2). Several specimens were recovered which closely resembled the aforementioned taxa, but could not be confidently attributed, and others were observed that bore a close resemblance to taxa which were not confidently observed in these samples, including cf. *Colobodus*, cf. *Brembodus* and cf. *Duffinselache*. Two morphotypes recovered did not bear any clear resemblance to known taxa, including conical teeth with a ridged surface, apical cap, and a slight curve, somewhat resembling *Gyrolepis*, but specimens of this genus are not known to exhibit robust ridges; here we describe these specimens as possible paleonisciformes. Another group of teeth is fairly squat and acorn-shaped, with a possible apical cap, also surrounded by ridges, is not placed in any taxonomic group, as no clear relationships can be determined based on this morphology. A conservative estimate of generic diversity observed in this sample is 10 genera, comprising at least seven actinopterygians, at least three chondrichthyans, one reptile, and one microvertebrate specimen of unknown affinity.

Table 2. Occurrences and reported dietary modes of identified taxa. 'Cf' taxa are assumed to share the same diet as the taxon to which they are compared.

	n	*Material*				*Diet*	*Diet Reference*	Original reference	Identification Reference
Fin spine	1	scale				n/a			
Acorn	3	tooth				n/a			
Osteichthyan scale	4	Scale				n/a		Huxley 1880	Cavicchini et al. 2018
cf. Colobodus	3	Tooth	Actinopterygia	Chondrostei	Perleidiformes	Durophage – specialised	Boss 1982 (but Zuoyu et al. 2008 consider them hemidurophagous)	Agassiz 1843	Norden et al 2015; Allard et al. 2015
Gyrolepis sp.	6	Tooth	Actinopterygia	Chondrostei	Paleonisciformes	Piscivore – small	Tintori 1998; Storrs 1994; Cross et al. 2018	Agassiz 1843	Korneisel et al 2015; Cross et al. 2018
cf. Gyrolepis	2	Tooth	Actinopterygia	Chondrostei	Paleonisciformes	Piscivore – small	Tintori 1998; Storrs 1994; Cross et al. 2018	-	-
Gyrolepis scale	1	Scale	Actinopterygia	Chondrostei	Paleonisciformes	Piscivore – small	Tintori 1998; Storrs 1994; Cross et al. 2018	-	Lakin et al. 2016
Severnichthys acuminatus Birgeria type	19	Tooth	Actinopterygia	Chondrostei	Paleonisciformes	Piscivore – medium	Mears et al. 2016; Cross et al. 2018	Storrs 1994	Duffin 1993
cf. Severnichthys acuminatus Birgeria type	5	Tooth	Actinopterygia	Chondrostei	Paleonisciformes	Piscivore – medium	Mears et al. 2016; Cross et al. 2018	-	-
Severnichthys acuminatus Saurichthys type	5	Tooth	Actinopterygia	Chondrostei	Paleonisciformes	Piscivore – medium	Mears et al. 2016; Cross et al. 2018	Storrs 1994	Cross et al. 2018
cf. Severnichthys Saurichthys type	2	Tooth	Actinopterygia	Chondrostei	Paleonisciformes	Piscivore – medium	Mears et al. 2016; Cross et al. 2018	-	-
cf. Brembodus	1	Tooth	Actinopterygia	Neopterygia	Pycnodontiformes	Durophage – specialised	Lombardo and Tintori 2005	Tintori 1981	Lombardo and Tintori 2005
Dapedium sp.	7	Tooth	Actinopterygia	Neopterygia	Semionotiformes	Durophage – specialised	Thies and Hauff 2011; Lombardo and Tintori 2005; Smithwick and Johanson 2015	Leach 1892	Smithwick and Johanson 2015
cf. Dapedium	4	Tooth	Actinopterygia	Neopterygia	Semionotiformes	Durophage – specialised	Thies and Hauff 2011; Lombardo and Tintori 2005; Smithwick and Johanson 2015	-	-
Lepidotes sp.	2	Tooth	Actinopterygia	Neopterygia	Semionotiformes	Durophage – specialised	Stumpf, 2017; Thies et al. 2021	Agassiz 1843, Agassiz, 1832	Muller 2011
Ridged tooth (palaeonisciform)	2	Tooth	Actinopterygia					-	-
Pycnodontiform molariform tooth	1	Tooth	Actinopterygia	Neopterygia	Semionotiformes	Durophage – unknown	Lombardo and Tintori 2005	Agassiz 1835	Stumpf et al. 2017
Morphotype 1	2	Denticle	Chondrichthyan			n/a	-	-	-
Morphotype 2	7	Denticle	Chondrichthyan			n/a	-	-	-
Morphotype 3	1	Denticle	Chondrichthyan			n/a	-	-	-
Morphotype 4	1	Denticle	Chondrichthyan			n/a	-	-	-
Morphotype 5	1	Denticle	Chondrichthyan			n/a	-	-	-
Morphotype 6	13	Denticle	Chondrichthyan			n/a	-	-	-
Morphotype 7	1	Denticle	Chondrichthyan			n/a	-	-	-
Hybodontiform fragment	3	Tooth	Chondrichthyan	Euselachii	Hybodontiformes	Durophage – specialised	-	Patterson 1966	-
cf. Duffinselache	4	Tooth	Chondrichthyan	Neoselachia		Durophage – specialised	Cuny et al. 2001	Andreev and Cuny 2012	Cavicchini et al. 2018; Landon et al. 2017
Lissodus sp.	1	Tooth	Chondrichthyan			Durophage – specialised	Manzanares et al. 2018; Cuny and Benton 1999	Brough 1935	Moreau et al. 2021; Cross et al. 2018
Rhomphaiodon sp.	6	Tooth	Chondrichthyan		Synechodontiformes	Durophage – semi-specialised	Lakin et al. 2016	Duffin 1993	Allard et al. 2015; Lakin et al. 2016
Archosauriformes fragment	1	Tooth	Reptilia			Piscivore – large	-	Cope 1869	Ősi et al. 2013
cf. Nothosauridae fragment	3	Tooth	Reptilia			unknown		Rieppel and Wild 1996	Ősi et al. 2013
TOTAL	112								

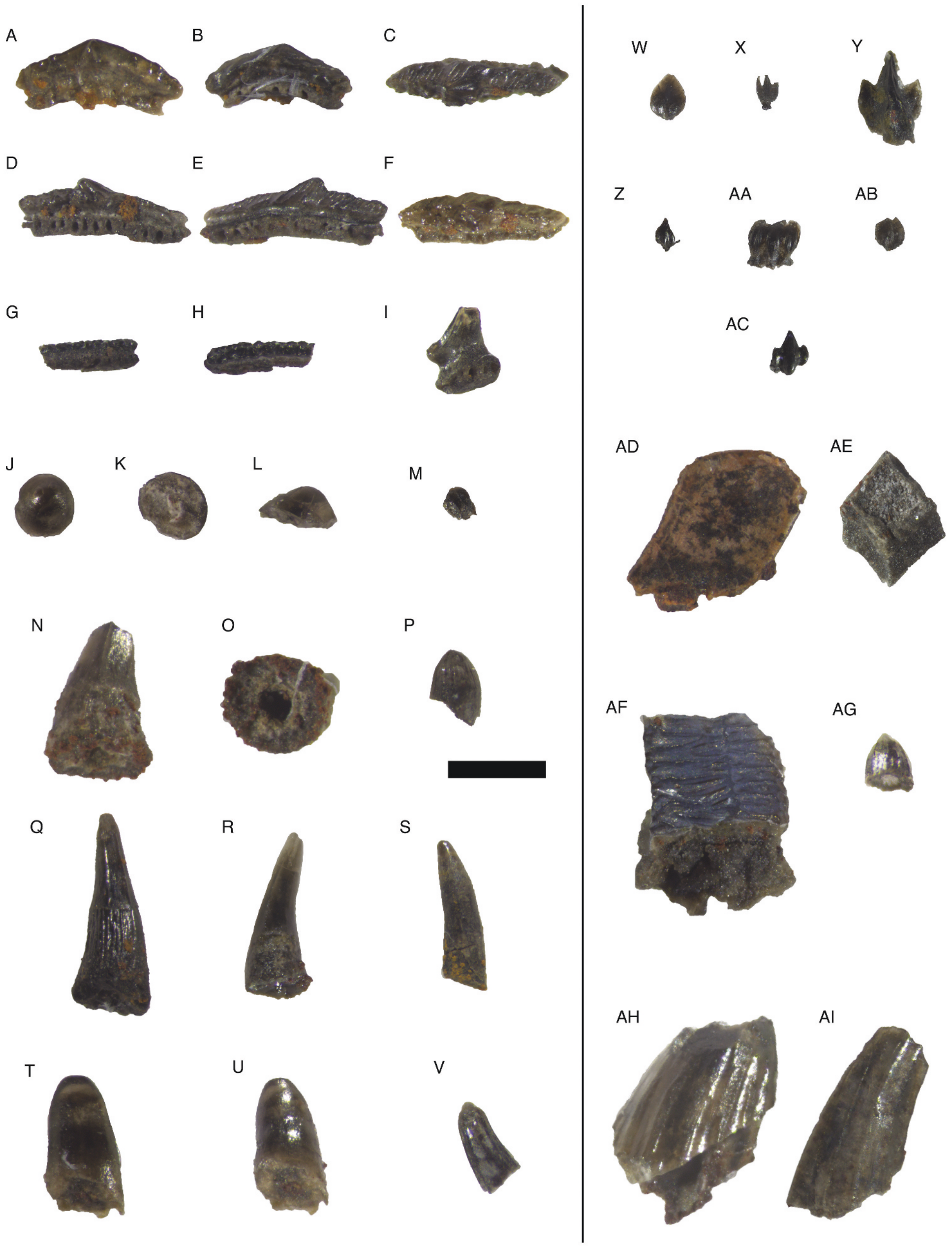

Figure 2. Ichthyoliths from the upper carbonate member of the Luning Formation in Berlin Ichthyosaur State Park. A–J: Chondrichthyes teeth. A–C: *Lissodus* anterior tooth, (A) labial, (B) lingual, (C) occlusal. D–H: cf. *Duffinselache* posterolateral, (D) labial, (E) lingual, (F) occlusal. I: *Rhomphaiodon* tricuspid. J–X: osteichthyes teeth. J–L: *Lepidotes*, M: *Sphaerodus* (junior synonym of *Lepidotes*), N–O: *Severnichthys acuminatus Birgeria acuminata* type, P: cf. *Colobodus*, Q–R: *Severnichthys acuminatus Saurichthys longidens* type, S: *Gyrolepis*. T–U: *Dapedium*, V: palaeonisciform ridged tooth. W–AC: Chondrichthyes dermal denticles. W: Morphotype 1, X: Morphotype 2, Y: Morphotype 3, Z: Morphotype 4, AA: Morphotype 5, AB: Morphotype 6, AC: Morphotype 7. AD–AF: osteichthyes scales. AD–AE: osteichthyan scale indet, AF: *Gyrolepis* scale. AG: Unknown affinities. AG: 'Acorn', unknown affinity. AH–AI: Reptilian teeth. AH: cf. Nothosauriform fragment, AI: archosauridae fragment. Scale bar represents 500 microns.

Most of the observed taxa are newly described for Eastern Panthalassa during the Triassic Period. The temporal and geographic ranges are discussed below, with morphological descriptions of the taxa reported herein.

Lissodus

While common at other Upper Triassic localities containing ichthyoliths, only one specimen of *Lissodus* was observed at BISP (Figure 2A–C). The specimen is broadly triangular, exhibiting a pronounced central cusp with a rounded tip. Multiple striations descend down both lingual and labial surfaces, as well as the labial side of the crown. The *Lissodus* specimen observed in our sample does exhibit characteristic features including a fairly low-angled main cusp with a labial peg (though it is fairly eroded). The specimen exhibits some slight bifurcating ridges on the lingual surface of the crown (notably different from the nonbifurcating ridges of the cf. *Duffinselache*, Figure 2D-F). Ridges are not always present on *Lissodus* ichthyoliths, but ridges are also not uncommon, as can be observed in *Lissodus* reported by Norden et al. (2015) and Cavicchini et al. (2018). Specimens of *Lissodus* are common in Europe during the Triassic, but this is the first report of *Lissodus* in a Mesozoic marine setting for the western United States. A euryhaline preference has been suggested for *Lissodus* (Maisey 1989), supported by their widespread occurrence in diverse environments from the Permian to Cretaceous, including freshwater settings.

cf. *Duffinselache*

The chondrichthyan *Duffinselache* is reported from the Rhaetian sediments in the UK, Belgium and France, and we report four specimens that very likely to belong to this genus (Figure 2D–H), although lacking some key features. This new occurrence represents a significant temporal and geographic expansion of this genus, should more specimens be recovered that can confidently be assigned to this genus. The cf. *Duffinselache* specimens do exhibit main cusps that are inclined in one direction, consistent with posterior teeth of this genus (Mears et al. 2016; Cavicchini et al. 2018), although our specimens exhibit more ridges than specimens illustrated elsewhere, and are about one-third the size. They also exhibit ridges which climb the crown, which is inconsistent with *Duffinselache* reported in the United Kingdom (Cavicchini et al. 2018).

Rhomphaiodon

Six *Rhomphaiodon* teeth were observed, all tricuspid types (Figure 2I), which exhibit ridged crowns, pitted with vascular foramina and with very short, lateral cusps (similar to types figured in Lakin et al. 2016), and about one-half the size of *Rhomphaiodon* specimens figured elsewhere. Specimens of *Rhomphaiodon* are only known from Triassic and rare Lower Jurassic deposits of Europe.

Hybodontiform fragments

Three fragments with low-lying cusps, similar to those in cf. *Duffinselache*, were observed that lacked roots and were incomplete along the longitudinal transect. Therefore, we could not relate these fragments to a genus, but their overall morphology suggests a durophagous specialisation.

Sargodon

Specimens of Sargodon are primarily known only from Late Triassic marine deposits of Europe, and here we report two specimens which appear to belong to that genus. The Sargodon specimens reported here (Fig. 2J–K) closely resemble the molariform teeth reported in Rhaetian deposits of the UK (Moreau et al. 2021), with concave portions and a robust rim, although our specimens are about one-third the size of the referenced specimens.

Lepidotes

One specimen was observed that most resembled *Lepidotes* (Figure 2J–L), which is likely to be a wastebasket term, representing multiple genera (Cross et al. 2018). Specimens identified as *Lepidotes* are reported from throughout the Mesozoic, mostly in Europe, but with one occurrence in fluvial sediments of the Upper Triassic Chinle Formation in Arizona (Schaeffer and Dunkle 1950). The *Lepidotes* specimen observed is rounded and robust, without a central tubercle, although this ornament is rarely preserved (Müller 2011). Another specimen identified as belonging to the genus *Sphaerodus* was recovered (Figure 2M). *Sphaerodus* is only known previously from European deposits of Triassic and Jurassic age. The genus *Sphaerodus* is considered to represent a junior synonym of *Lepidotes*, but our specimen is notably smaller than the *Lepidotes* specimen with a more protruding rounded crown. Based on the current understanding of the relationship between *Lepidotes* and *Sphaerodus*, we consider these specimens to belong to the same genus for our diversity and cluster analyses.

cf. *Colobodus*

The fish genus *Colobodus* may not range into the Late Triassic (Mutter 2004), though specimens have been recovered in Rhaetian deposits of the United Kingdom (Nordén et al. 2015) and Luxembourg (Duffin and Delsate 1993), and from Carnian deposits (Tintori et al. 2014). Specimens of *Colobodus* are also reported from the Anisian marine deposits in Nevada (Rieppel et al. 1996). The three specimens observed in the BISP sample (Figure 2P) are in poorer condition than those from the UK, and reliable characteristics are lacking; therefore, they are considered cf. *Colobodus*.

Severnichthys acuminatus (Birgeria acuminata and *Saurichthys longidens* type)

Specimens of *Severnichthys acuminatus* were the most abundant taxon in the sampled materials, and both heterodont morphs were observed at Berlin Ichthyosaur State Park, including *Birgeria acuminata* (Figure 2N–O) and *Saurichthys longidens* types (Figure 2Q–R). While these morphs have been previously considered to be distinct taxa, Storrs (1994) synonymised the taxa based on a jaw containing both types. Specimens of *Severnichthys acuminatus Birgeria acuminata* types are the most abundant, a proportion similar to observations in Lakin et al. (2016). Specimens of *S. acuminatus Birgeria acuminata* type exhibit deep ridges and roots are usually present. Teeth of *S. acuminatus Saurichthys longidens* type are usually curved similarly to *Gyrolepis* but are wider towards the roots. Unlike most teeth from Berlin Ichthyosaur State Park, the *S. acuminatus* teeth are similar in size to specimens from the same taxon illustrated elsewhere, whereas most of the other identified taxa are consistently smaller than published images. The genus *Severnichthys* has not been previously reported from North America during the Triassic, or any other period, although *Saurichthys* has been reported from Lower and Middle Triassic marine deposits in Nevada (Sander et al. 1994; Romano et al. 2017) and *Birgeria* has been observed in Norian marine deposits of British Columbia (Orchard et al. 2001a, 2001b) and possibly Bolivia (Beltan et al. 1987).

If *Saurichthys* and *Birgeria* are separate genera, they potentially cannot be distinguished based on isolated ichthyoliths (Gozzi 2004, referenced by Lombardo and Tintori 2005), while other workers consider these to be two tooth morphotypes from one genus, *Severnichthys* (Storrs 1994). Isolated teeth from both genera co-occur in the Triassic (Lombardo and Tintori 2005). Here, we consider them to represent one genus in order to present a conservative diversity estimate, although the taxonomic standing for *Severnichthys, Birgeria* and *Saurichthys* is not resolved and may need to be reconsidered.

Gyrolepis

Teeth of *Gyrolepis* and at least one scale were observed in the sampled residues (Figure 2S, 2AF). The scale surface exhibited distinct rivulets, similar to those figured in Lakin et al. (2016). The teeth are gently curved, tapered and usually smooth, which may be a taphonomic feature, and with tips that are clear to honey-coloured. Specimens belonging to *Gyrolepis* have been reported from the Lower Triassic in marine deposits from Nevada (Muller and Ferguson 1939) and fluvial deposits of Norian age (Camp and Welles 1956). The *Gyrolepis* teeth observed in these samples are one-half the typical, illustrated size of *Gyrolepis* elsewhere.

Dapedium

Dapedium is the third-most abundant tooth recovered from BISP samples (Figure 2T–U), but this genus has only been previously reported from Europe, in Triassic and Jurassic-age marine sediments, appearing first in the Norian Stage. The *Dapedium* specimens exhibit vertical zonation in colour, varying from honey-brown to nearly black, and are conical in shape with a rounded tip, most closely resembling *Dapedium* specimens with peg-like, and somewhat styliform morphology.

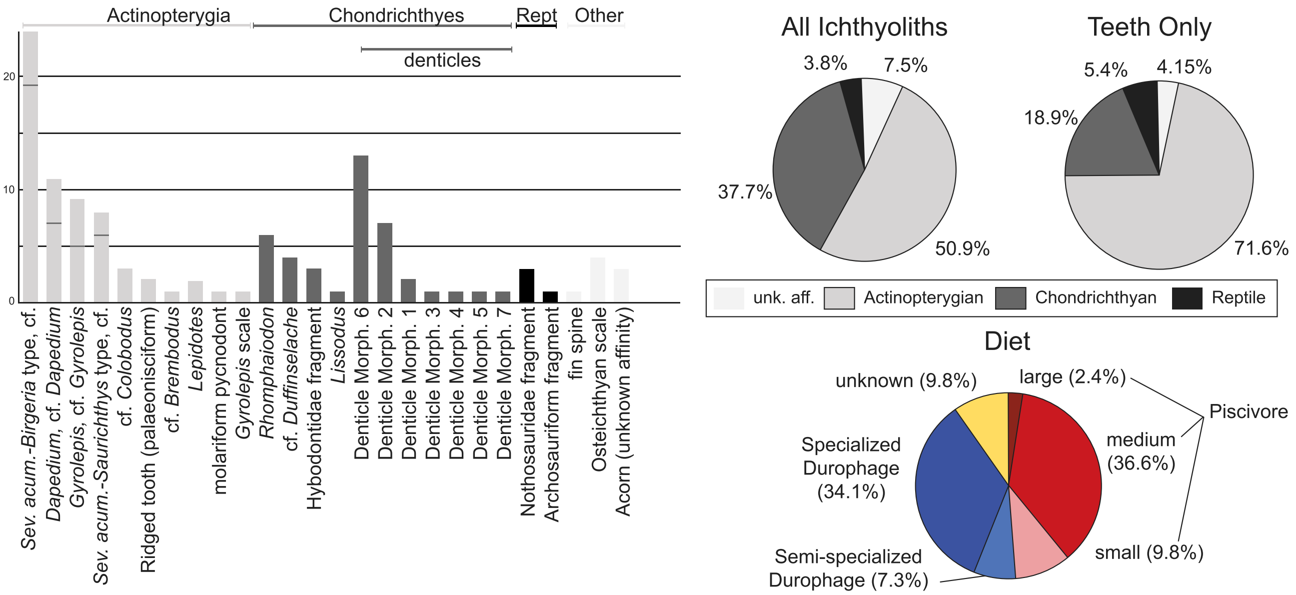

Figure 3. Summary of ichthyoliths recovered from Berlin Ichthyosaur State Park. ‘cf’ taxa are grouped with their comparable taxon, and indicated with a separating line on the bar.

Tubercles around the crown or base were not observed, as they appear in Rhaetian specimens from the UK (Lakin et al. 2016; Cavicchini et al. 2018), and are about one-half the diameter of those figured specimens.

cf. *Brembodus*

One specimen resembling the genus *Brembodus* was recovered. This genus is only known from Norian deposits in Italy (Tintori 1981). This specimen is difficult to specify beyond the pycnodontiformes, as its robust, low-lying crown is somewhat oval and lacks other diagnostic features.

Paleonisciform ridged tooth

Two teeth recovered closely resembled *Gyrolepis*, with somewhat curved, conical shapes and apical caps, but with robust longitudinal ribs covering the surfaces (Figure 2V). No known Late Triassic forms of *Gyrolepis* have this type of ornamentation. If these specimens do belong to *Gyrolepis*, they will likely represent a new species.

Pycnodontiform molariform tooth

One molariform tooth was recovered that could not be identified to a genus, but exhibited the same robust, rounded surface observed in other pycnodonts from this sample.

Chondrichthyan dermal denticles

Chondrichthyan ichthyoliths were typically of poor quality but were relatively abundant in the smaller size fraction (Figure 4). These dermal microfossils tended to be broken along the crown-root junction. Denticles found were assigned to seven different morphotypes based on similarities between crown and pedicle features using a system established by Johns (1996).

The denticle *morphotype 1* (*n* = 1, Figure 2W) displayed a minor anterior crown overhang, and a smooth, unornamented subcrown surface. Crown morphology was of uniform depth, sheet-like and with no surface features, though the specimens do have a posterior point. The specimen was eroded below the crown-pedicle junction, so little can be determined about the pedicle morphology in these denticles, though it appeared to be very narrow.

The denticle *morphotype 2* (*n* = 9, Figure 2X) displayed no anterior crown overhang, subpedicle surfaces were rhomboid and pedicle shape was plain and truncated. The subcrown surfaces of morphotype 2 specimens were mostly eroded but could be considered having many long ridges and a medial keel. The crowns consisted of three cusps with fine sharp edges, interkeel notches and tapering depth.

The denticle *morphotype 3* (*n* = 1, Figure 2Y) displayed no anterior crown overhang, and one mesial central ridge on the subcrown surface. The specimen of this morphotype was eroded above the junction, with a weathered interior space. The crown displayed three cusps with bicresting central ridges and interkeel notches, and tapering depth.

The denticle *morphotype 4* (*n* = 1, Figure 2Z) displayed a tetrapetaloid subpedicle surface, prominent anterior crown overhang, a central keel on the subcrown surface and a simple tetrahedroid pedicle type. The crown morphology displayed a cordiform shape with a bump in the anterior direction and was of uniform depth.

The denticle *morphotype 5* (*n* = 1, Fig. 2AA) displayed no or minimal anterior crown overhang, and a long central keel on the subcrown surface. The crown morphology consisted of three distinct ridges, all of which were bisecting. The pedicle on this morphotype is eroded away at the crown-pedicle junction. This specimen may represent a compound hybodont scale (Reif 1978), a relatively rare condition among Triassic elasmobranchs (Maisey and Denton 2016).

The denticle *morphotype 6* (*n* = 17, Fig. 2AB) displayed minor anterior crown overhang and a smooth, unornamented subcrown surface. The crown was unornamented except for anterior mesial platforms and protrusions. The pedicle-crown junctions are very thin, and mostly broken.

The denticle *morphotype 7* (*n* = 1, Fig. 2AC) displayed a tetrapetaloid subpedicle surface, a minor anterior crown overhang, a smooth and unornamented subcrown surface and a simple tetrahedroid pedicle type. The crown morphology includes interkeel notches of cascading length, with rounded tips and uniform depth.

Osteichthyan scales

Osteichthyan scales (Fig. 2AD–AE) were recovered and identified based on the quadrate shape, resembling morphotype 3 scale

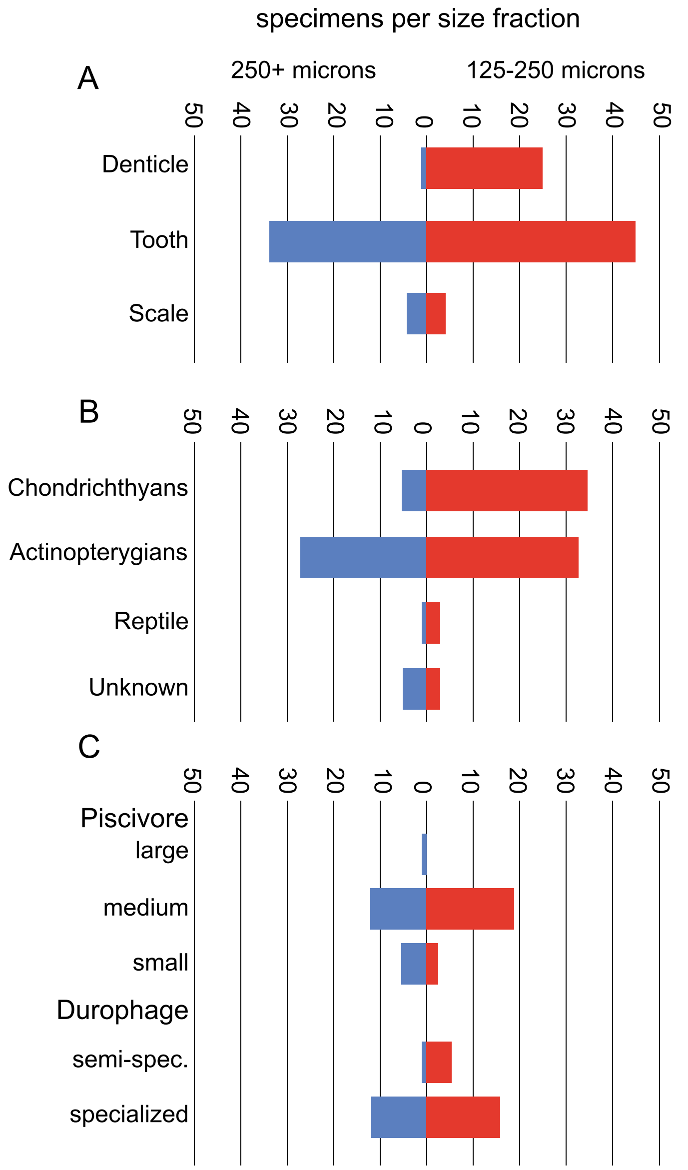

Figure 4. Ichthyolith yields from two sieve size fractions. A. Ichthyolith type. B. Taxonomy. C. Palaeoecology/Diet.

illustrated by Landon et al. (2017) and Cross et al. (2018).

Fin spine

One example of an elongate ichthyolith with ridges on one side and a slight curve was observed in the acid residues, most closely resembling the hybodontiform fin spine figured by Lakin *et al.* (2016), but without additional features we do not assign it to a specific group.

'Acorn' (unknown affinity)

Three ridged teeth with a rounded tip were recovered, one specimen with a possible apical cap (Fig. 2AG). No roots were observed, suggesting that these may represent a broken form of a longer tooth, similar perhaps to the palaeonisciform specimens described above. Without additional specimens, these cannot be reliably placed in any group.

Reptiles: Nothosauridae and Archosauriform fragments

Three fragments resembling those of nothosaurids were observed (Figure. 2AH–AI), similar to those in Ősi et al. (2013), with strong ridges and large size. Ichthyosaurs are reported from the shaly limestone unit below the carbonate member of the Luning Formation (Hogler 1992; Montague-Judd 1999), but no ichthyoliths were recovered in these previous studies, and among ichthyosaurs of similar size, for example, those in Slater et al. (2016), the ridges are more thread-like and closely spaced than the fragments observed here. The archosaur fragment also exhibits very fine ridges that are well spaced.

Diversity summary

Chondrichthyans were less abundant and had lower overall diversity than was observed among the actinopterygians, especially when only teeth were considered (Figure 3). The chondrichthyans were represented by greater numbers of neoselachians than euselachians (hybodontiformes)(Table 2), but denticles were not identified to taxonomic groups, and thus may not be accurate representations of ichthyolith distribution. Semionotiformes were the most abundant neopterygians (*Dapedium* and *Lepidotes*), and *Severnichthys acuminatus Birgeria acuminata* type was the most abundant chondrostean.

Sieve Size

Some differences in taxonomic composition were observed between the two primary size fractions examined (Figure 4). Most chondrichthyan denticles were found in the 125–250 μm fraction (comprising 33.7% of the 125–250 μm fraction, and 2.5% of the >250 μm fraction) (Figure 4A). Chondrichthyan and reptilian teeth comprised a larger proportion of the total dental ichthyolith assemblage in the 125–250 μm range than the >250 μm fraction (Figure 4B).

Some genera were only observed in one size fraction; all denticle types appeared exclusively in the 125–250 μm size fraction, except Morphotype 3, which was the largest denticle type observed. Several teeth were also only observed in the smaller size fraction, including *Lissodus* and the smaller *Lepidotes* specimen identified to the junior synonym *Sphaerodus*, and fragments of pycnodont molariform teeth, hybodontiform teeth, and cf. Nothosauridae teeth. The ridged palaeonisciform tooth, 'acorn' teeth of unknown affinity, cf. *Brembodus*, and *Lepidotes* were only observed in the larger size fraction, with denticle Morphotype 3, specimens of cf. *Duffinselache, Rhomphaiodon, Dapedium, Severnichthys acuminatus*, cf. *Colobodus*, and *Gyrolepis* are observed in both size fractions.

Denticles were mostly found in the smaller size fraction, but even excluding these from ichthyolith counts, chondrichthyans were more abundant in the smaller size fractions (13.5% in 125–250 μm, 10% in >250 μm).

Dental ichthyoliths representing different feeding modes were not evenly distributed between the size ranges examined (Figure 4C). The >250 μm size fraction teeth consisted of 54.3% piscivores, with medium-sized piscivores being the most common, making up 34.3% of the total individuals present. In the 125–250 μm range, durophages make up 46.7% of the total teeth specimens, with this being dominated by the specialised durophages who make up 35.6% of the total. Medium-sized carnivores make up a larger proportion of the total carnivores in both the 125–250 μm and >250 μm sizes.

Most of the genera identified in this survey are smaller than specimens of the same genera observed elsewhere, and this may be due to the upper limit (*c.* 2 mm) of the netting apertures used to separate rock from liberated residues, but netted bag contents were periodically examined for larger vertebrate components and none were observed.

Diet

Dietary modes among the extracted ichthyoliths were nearly equal parts durophages and non-durophage carnivores (Figure 3), with all

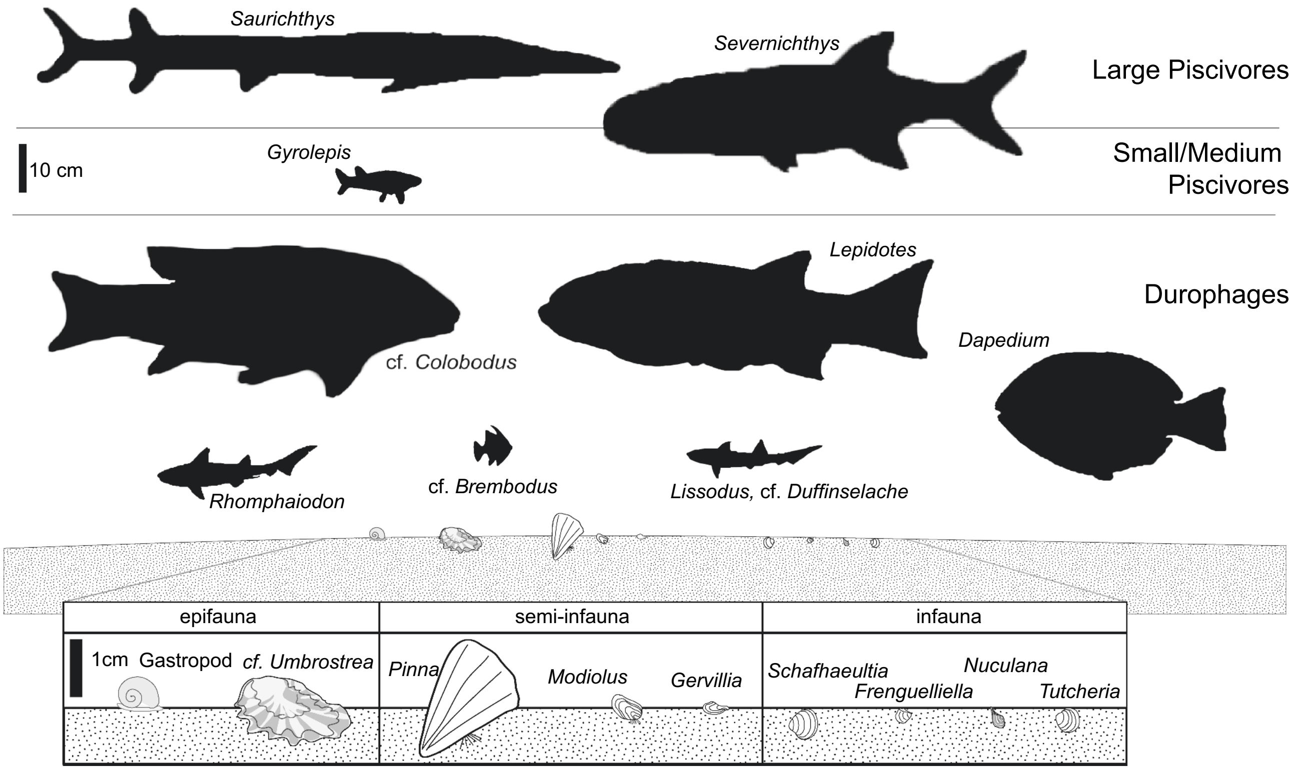

Figure 5. Reconstructed food web for marine vertebrates recovered from the upper Carbonate Member of the Luning Formation, and shelly invertebrates from Tackett and Bottjer (2016). Size and diet reconstructions are derived from references in Table 1

chondrichthyans assigned to taxa reported to have utilised a durophagous lifehabit. Among non-chondrichthyans (mostly actinopterygians), ichthyoliths commonly exhibited morphologies or were assigned to taxa described as likely being semi-specialised for durophagy, but only *Dapedium* is considered to be semi-specialised for durophagy (Smithwick 2015). Among non-durophages, medium-sized piscivores were most common. Genera that specialised in durophagous feeding were more diverse than the carnivores. Large, medium, and small carnivores are only represented by one taxon, respectively (Archosauriform, *Severnichthys acuminatus,* and *Gyrolepis*).

Palaeogeography

These are the first-reported chondrichthyans from Upper Triassic marine sediments in Nevada. Among the chondrichthyans, all three taxa were identified that had not been previously reported from marine sediments in Nevada or eastern Panthalassa for the entire Triassic: cf. *Duffinselache, Lissodus,* and *Rhomphaiodon*. Chondrichthyans have been reported, but not figured, from California in the shallow marine Hosselkus Formation (Wemple 1906; Jordan 1907; Bryant 1914), and some chondrichthyans are known from the fluvial deposits of the Chinle Formation, including *Lissodus* and other hybodontiforms.

Actinopterygians were observed whose ranges were significantly increased by their presence in marine sediments from Nevada. We were not able to definitively identify *Colobodus* in our samples, but *Colobodus* is known from the middle Triassic in eastern Panthalassa. While *Gyrolepis* is known from the Norian in the western United States, this is the first report of the taxon in marine sediments of this interval in eastern Panthalassa. The abundant Late Triassic European taxon *Severnichthys acuminatus Birgeria acuminata* type and *Saurichthys longidens* type are reported for the first time in eastern Panthalassa, though *Saurichthys* and *Birgeria* were previously reported as independent genera. The taxon *Dapedium* is observed for the first time outside of Europe during the Late Triassic. Specimens belonging to the genus *Lepidotes* from the western USA are only known from lacustrine deposits during the Triassic, so this occurrence is the first marine observation from this interval.

Reptiles are among the best-known marine vertebrates from Triassic deposits in Nevada, but reptile taxa could not be positively identified to the genus level in this analysis. Reptile taxon *Nothosaurus* is questionably known from the middle Triassic of eastern Panthalassa.

Other potential predators were not observed in the studied sedimentary deposit, such as ammonoids (though macrofossils are found in surrounding strata), echinoderms (no macrofossils or stereom) or arthropod fragments.

Food web

A more complete food web (Figure 5) is reconstructed using ichthyoliths and invertebrate macrofossils from the same sedimentary horizon (Tackett and Bottjer 2016). The most common taxa are demersal consumers of seafloor invertebrates (durophages) and medium-sized piscivores, and a small number of smaller, tertiary consumers (e.g. *Gyrolepis*).

Nearly half of ichthyolith dental fossils represented specialised or semi-specialised durophages. Based on bulk sample invertebrate fossils, the potential prey of the observed durophagous vertebrates was limited to larger semi-infauna (*Pinna*), cementing bivalves (cf.

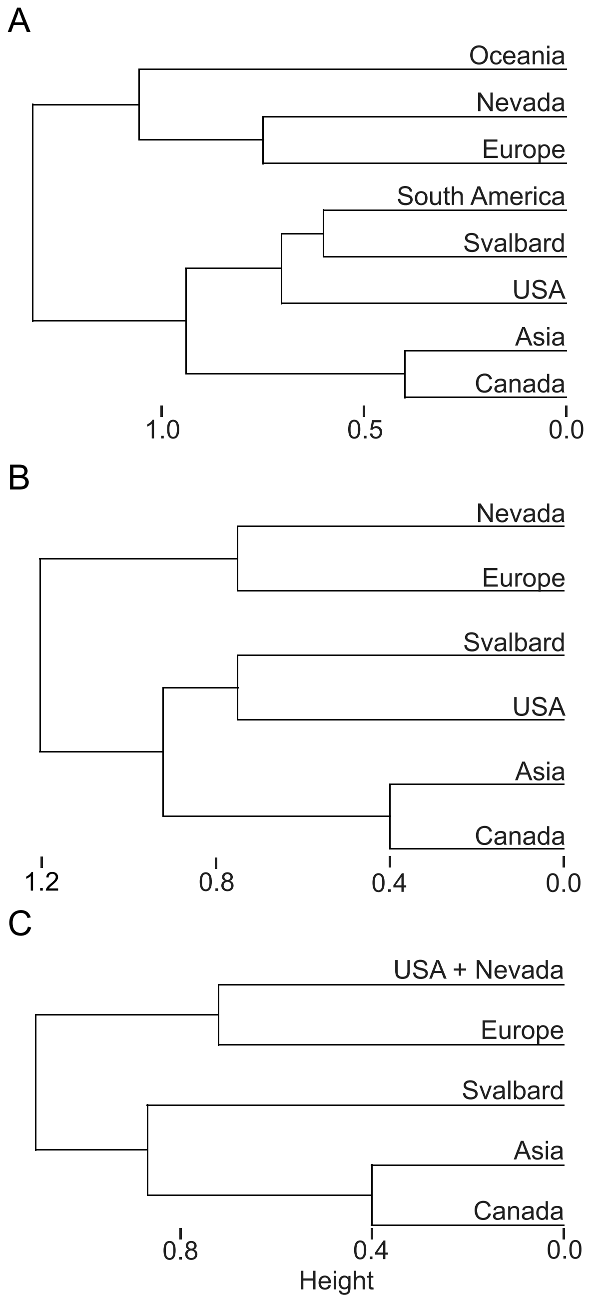

Figure 6. Cluster analysis of Berlin Ichthyosaur State Park ichthyoliths compared to marine ichthyolith assemblages from other regions, data from the Palaeobiology Database. (A) All Late Triassic chondrichthyes and actinpterygians grouped by region including Oceania. (B) All Late Triassic chondrichthyes and actinpterygians grouped by region, excluding singletons. (C) All Late Triassic chondrichthyes and actinpterygians grouped by region with new Nevada data included in USA group.

Umbrostrea) and gastropods; burrowing bivalves were present but rare, and would not likely be susceptible to seafloor browsing by demersal durophages.

Cluster analysis

Cluster analyses of the ichthyoliths from BISP and other regions were used to compare taxonomic similarity (Figure 6). Two regions (South America and Oceania, which includes New Zealand and Australia) are composed of very limited marine vertebrate records, and grouped separately (Oceania with Nevada [BISP] and Europe, and South America with Svalbard) (Figure 6A). These correlations are likely to be spurious, representing a limited sampling effort, and additional discoveries have the potential to induce large shifts. In all analyses, the BISP assemblage nested closely with Europe (Figure 6A-C), but when western USA occurrences are considered separately, they are grouped with Svalbard, and show very little similarity to Europe or BISP samples from Nevada (Figure 6B). When the results of the present study were combined with other marine records from the western USA, the ichthyoliths were most closely related to those from Europe, while Svalbard, Asia, and western Canada formed a second group, with the latter two being the most closely related (Figure 6C).

Discussion

Diversity observations

Ichthyoliths from carbonate residues of the upper Luning Formation yielded at least 13 marine vertebrate genera, of which at least nine genera are newly reported from Upper Triassic marine deposits of eastern Panthalassa. Several of the most common taxa (e.g. *Dapedium, Rhomphaiodon*) are not known from beyond Tethyan Europe during the Triassic, and their occurrences in the western USA represent substantial expansions of their geographic range. Two common taxa observed are known from marine deposits in the western USA: *Gyrolepis* and *Severnichthys acuminatus* (with specimens of both *Saurichthys longidens* and *Birgeria acuminata* types, represented by one *Saurichthys* occurrence). These genera were not previously known from the Upper Triassic in the western USA, which extends their temporal ranges in marine systems and suggests that the geographic ranges for common taxa are not yet well constrained.

The observations reported herein are the first actinopterygians reported from Upper Triassic marine sediments in Nevada. While the Late Triassic is considered to be an interval of adaptive radiation among neopterygians, especially pycnodontiformes (Tintori 1998; Lombardo and Tintori 2005), no obvious pycnodonts were identified in the sample, although *Sphaerodus* had been previously suggested to belong to this order. Semionotiformes were more diverse and abundant among the neopterygians, including *Lepidotes* and *Dapedium* – although the latter may be a unique order, Dapediiformes (Cawley et al. 2021). The general absence of pycnodonts in the isolated ichthyolith assemblages examined here may be the result of their palate dentitions, though the taphonomy of palate components is not well understood. The pycnodontiform radiation reported from Europe may be further constrained, temporally and geographically, by new ichthyolith surveys.

Chondrichthyan ichthyoliths described in this study are the first to be reported from the Upper Triassic marine sediments in Nevada. Chondrichthyans reported in this survey are similar to those from Upper Triassic sections in Europe, including the UK, and provide key data on the degree of endemism for these genera. In contrast to the actinopterygian taxonomic patterns, isolated ichthyoliths are the primary fossil resource for chondrichthyans, and in regions where they have been surveyed from Panthalassan deposits, chondrichthyan ichthyoliths diversity is high (e.g. Rieppel et al. 1996; Johns et al. 1997). The chondrichthyans described here from the upper Luning Formation are primarily neoselachian, and while dental ichthyoliths were not as diverse as the actinopterygians, a variety of dermal denticles were recovered that support their important role in the ecosystem and highlight the need for further work on this group.

Palaeoecology

Durophages and piscivores were equally abundant in this survey (Figure 3), and this result was influenced by the sieve size fractions (Figure 4C). The ecological importance of durophages in BISP is consistent with the observation that durophages are becoming more taxonomically diverse and abundant elsewhere in the world, and Europe in particular (Tintori 1998). Reconstructed sizes of durophagous taxa observed in BISP suggest a variety of fish sizes, with representatives filling ecological niches that were similar but with shelly invertebrate prey of different sizes. Piscivore size was more restricted, primarily dominated by medium-sized predators, though larger predators might appear to be absent due to a tendency for larger fragments to exhibit greater degrees of taphonomic breakage or abrasion, to which smaller ichthyoliths are not subject, and therefore the latter may be artificially inflated. Tooth replacement may also be inconsistent among palate durophages if teeth are rarely replaced.

Durophages were more diverse than piscivores in the BISP assemblage, accounting for nine of the reported genera, which includes both chondrichthyans and actinopterygians. The shelly invertebrates from this horizon at BISP show a distinct difference from lower samples from the same geologic member reported in Tackett and Bottjer (2016), exhibiting a decline in non-cementing epifauna (mostly brachiopods). Additional work is needed to determine if the decline in reclining epifauna is related to the proliferation of durophages in shallow marine environments.

Food webs

While about half of the ichthyolith specimens represented a diet specialised for shell-crushing, the targeted prey for this life-mode is not clearly identifiable. Cementing bivalves are generally larger and may have fallen outside the gape size of these fish, and their robust attachment to a subsurface renders them more difficult to consume by full ingestion crushers (Yonge 1979). Infaunal bivalves were not likely to be available for consumption by demersal predators, unless the sediment was actively churned. Gastropods were relatively abundant in this bulk sample, in a variety of sizes, and while mobile, were not likely to have been faster than the demersal fish. Semi-infaunal bivalves like *Pinna* were likely to have been too large, though smaller taxa like *Modiolus* and *Gervillia* may have been small enough to be readily consumed. Other potentially vulnerable epifauna such as sponges or crinoids were unlikely to be dietary staples, as their disarticulated microfossils represented very rare biosedimentary components of the carbonate residues.

The paucity of stationary epifaunal invertebrates in this sample is notably different from only slightly older bulk samples from lower in the Luning Formation Carbonate Member, which were dominated by rhynchonellid brachiopods (Tackett and Bottjer 2016). Future work should examine the changing populations of biosedimentary microvertebrate fossils.

Vertebrate Palaeogeography

The present survey is the first study of non-conodont microvertebrates remains from Upper Triassic marine sediments in Nevada. Many of the actinopterygian and chondrichthyan taxa observed in the present study have only been previously documented in Tethyan marine deposits. Several western USA taxa are known from this time interval in fluvial or lacustrine deposits of the Chinle Formation: *Gyrolepis, Lissodus, and Lepidotes*. The presence of similar genera between marine deposits of Tethys and in nonmarine settings from the western USA suggests that similar genera should be observed in marine deposits of the western USA. As these faunas were apparently freshwater adapted, the presence of similar genera of marine vertebrates in regional proximity is predicted and confirmed with the present study. The range expansion patterns for these genera are not yet known.

The taxa observed in BISP confront the endemism of many Late Triassic vertebrate taxa, and suggest that many apparently endemic taxa may have been cosmopolitan, e.g. cf. *Duffinselache* and *Rhomphaiodon*. More work is needed in order to establish the expansion patterns of the marine vertebrate taxa, but their presence in Nevada is clear evidence for broad ranges of many taxa and that durophagy was expanding in many regions during the Late Triassic.

The Late Triassic is considered to be a time of adaptive radiation among neopterygians (Tintori 1981, 1998), and while this report does not contain time-series information, the presence of several neopterygian taxa (e.g. *Dapedium, Lepidotes*) in eastern Panthalassa supports the wide range and ecological success of these groups. The fact that no teeth were observed that could be clearly attributed to the Pycnodontiformes suggests that this group may not have been ecologically important during the early Norian in this region, though they may have been important components of Tethys as early as the early Norian (Tintori et al. 2014).

Some chondrichthyan genera reported from the present survey are known from nonmarine deposits from the Chinle Formation, also Norian-aged, though the lack of other studies on chondrichthyan ichthyoliths precludes a robust interpretation of migration patterns for these genera.

Cluster analyses of marine vertebrate assemblages suggested that ichthyolith assemblages are controlled more by latitudinal affinity than geographic proximity, overriding the palaeogeographic barriers between the Tethys and Panthalassan ocean realms, but these results can only be tentatively interpreted, due to the paucity of ichthyolith surveys for the Late Triassic. Early Norian chondrichthyans of Nevada more closely resemble the chondrichthyan assemblages from European primarily Rhaetian-age deposits than Canadian shallow marine deposits (Figure 6), although this may be due to a difference in scope of other surveys. Comparison with actinopterygian assemblages is difficult due to the lack of studies of Late Triassic marine actinopterygians in the western USA. Canadian ichthyolith assemblages bear a stronger similarity to those of Asia, which may be an open-ocean signal or a higher latitude Panthalassa signal. Cluster analysis of known ichthyoliths highlighted shared genera, as well as the need for additional research on Triassic ichthyoliths, in particular the Southern Hemisphere. The assemblage from BISP aligned most readily with other shallow marine, mid-latitude deposits from Europe, but future Panthalassan surveys may result in greater similarity with other regions. The different clustering of the western USA prior to the present survey is notable, however, and highlights the effect of sampling effort with regard to ichthyoliths.

If additional research supports a latitudinal affinity for marine vertebrates, in particular those in shallow marine ecosystems, migration patterns may reveal evolutionary hotspots for adaptive radiations. Indeed, latitudinal similarity has been previously reported for other taxa in eastern Panthalassa, including calcareous algae (Bucur et al. 2020) and spongiomorphs (Stanley et al. 1994), while reef types exhibit greater regional patterns irrespective of latitude (Martindale et al. 2015). Taxonomic similarity may also be decoupled from ecologic similarity: common shelly benthic invertebrates are substantially different between similar types of deposits in Tethys and Panthalassa while exhibiting similar ecological changes during the Norian Stage (Tackett and Bottjer 2012, 2016). Identifying the controlling factors of ranges for different taxa with unique biological constraints is a powerful tool for macroevolutionary analysis and palaeoecological niche analysis.

Norian marine ecosystems and the Mesozoic marine revolution

Shelly invertebrates from shallow marine ecosystems in low latitudes appear to have experienced significant changes during the Norian Stage of the Late Triassic (Tackett and Bottjer 2012; Tackett and Bottjer 2016), exhibiting an increase in cementing taxa and burrowing taxa, new adaptations for swimming in bivalves (Hautmann 2004), and non-seafloor attachment strategies in crinoids (Baumiller et al. 2010). The present survey of ichthyoliths represents a sampling of potential predators from a critical interval of palaeoecological change in shelly invertebrates, and is substantial evidence for the importance of durophages in shallow marine ecosystems in eastern Panthalassa. Additional work is needed to establish patterns of change in these vertebrate populations and to determine whether specialised durophages co-vary with a decline in vulnerable invertebrate groups.

Ichthyolith best practices

In extracting ichthyoliths from carbonate matrix, acid residues were examined from sieve size fractions >125 µm, and several taxonomic groups were only observed in the 125–250 µm size fraction, suggesting that smaller size fractions must be examined in ichthyolith surveys. The 125–250 µm range accounted for the majority of the ichthyoliths collected (73 ichthyoliths versus 39), including nearly all chondrichthyan denticles. No obvious ichthyoliths were observed in size fractions smaller than 125 µm. Furthermore, many of the teeth recovered from both the >250 µm and 125–250 µm size fraction were smaller than those observed in other reports, suggesting an ichthyolith assemblage that may be overlooked without examination of these smaller size fractions. Smaller size fraction sediments may be critical materials for accurately characterising the ecological structure of marine vertebrates in shallow marine deposits.

The methods used in the present study showed a size preference between certain materials recovered. Carnivore teeth were more likely to be found within the >250 µm range, while teeth consistent with those of durophagous predators were more commonly found in the 125–250 µm residues. The abundance of durophagous teeth in smaller size fractions strongly suggests that the role of durophages in shallow marine ecosystems can be artificially minimised, especially notable since many durophages are reported to have reached sizes similar to those of non-durophagous carnivores (Figure 5).

Conclusion

Ichthyoliths are described from the Luning Formation for the first time, representing marine vertebrates from a carbonate system in the early Norian Stage of the Late Triassic, resulting in the observations of at least 14 genera not previously known from this region. Dietary modes for the observed genera include several groups specialised in durophagy, with neopterygian, chondrostean, and chondrichthyan representatives. Ichthyoliths, including teeth, dermal denticles, and scales, have enormous capacity for expanding our current understanding of marine palaeoecology, as this single study increased the known diversity of marine vertebrates in the western United States in the Late Triassic from four to at least 14 genera. Many of the taxa observed at the Berlin Ichthyosaur State Park were previously known only from Europe during the Late Triassic, challenging the current view of marine vertebrate endemism during this interval, although additional research is needed to establish whether this represents a latitudinal feature, or that many of these marine fishes were truly global in range. The observations in this study suggest that the neopterygian radiation influenced shallow marine ecosystems beyond Tethys, and ongoing work will further constrain the temporo-spatial features of vertebrate adaptive radiations in the Triassic Period.

Finally, the fact that ichthyoliths can be readily extracted from shallow marine carbonates suggests that more vertebrate diversity surveys can be conducted without the presence of a classic 'bone bed'. More research is needed to better understand the distribution of ichthyoliths in shallow marine carbonates to better predict microvertebrate yields. Acid residue examination is a powerful tool for reconstructing the ecosystems from sedimentary deposits which lack well-preserved macrofossils. The known diversity of marine ecosystems in Nevada during the Norian Stage was significantly increased as a result of these methods.

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