Year: 2019

Chondrichthyan teeth from the Early Triassic Paris Biota (Bear Lake County, Idaho, USA)

Romano, Carlo ; Argyriou, Thodoris ; Krumenacker, L J

Accepted Manuscript

Title: Chondrichthyan teeth from the Early Triassic Paris Biota (Bear Lake County, Idaho, USA)

Authors: Carlo Romano Thodoris Argyriou L.J. Krumenacker, the Paris Biota Team

Please cite this article as: Romano, C., Argyriou, T., Krumenacker, L.J., the Paris Biota Team<ce:cross-ref id=črf0040ïefïd=ḟn0005>̈[1]</ce:cross-ref> Chondrichthyan teeth from the Early Triassic Paris Biota (Bear Lake County, Idaho, USA), *Geobios* (2019), https://doi.org/10.1016/j.geobios.2019.04.001

Chondrichthyan teeth from the Early Triassic Paris Biota (Bear Lake County, Idaho, USA) ✡

Carlo Romano [a,b,*], Thodoris Argyriou [a], L.J. Krumenacker [c], the Paris Biota Team ✝

[a] Palaeontological Institute and Museum, University of Zurich, Karl Schmid-Strasse 4, 8006 Zurich, Switzerland

[b] Museo Cantonale di Storia Naturale, Viale Carlo Cattaneo 4, 6900 Lugano, Switzerland

[c] Idaho Museum of Natural History, Idaho State University, 698 E. Dillon St., Pocatello, ID, 83201, USA

✝ The Paris Biota Team includes, in alphabetical order: Arnaud Brayard (team leader; Biogéosciences, Univ. Bourgogne Franche-Comté, Dijon, France), Kevin G. Bylund (Spanish Fork, UT, USA), Gilles Escarguel (LEHNA, Univ. Lyon 1, Lyon, France), Emmanuel Fara (Biogéosciences, Univ. Bourgogne Franche-Comté, Dijon, France), Nicolas Goudemand (IGFL, ENS-Lyon, Lyon, France), Pierre Gueriau (Synchrotron SOLEIL, Gif-sur-Yvette, France/Institute of Earth Sciences, University of Lausanne, Swiss), James F. Jenks (West Jordan, UT, USA), L.J. Krumenacker (Idaho Museum of Natural History, Idaho State Univ., Pocatello, ID, USA), Nicolas Olivier (Magmas et Volcans, Univ. Clermont Auvergne, Clermont-Ferrand, France), Daniel A. Stephen (Dpt. of Earth Sciences, Utah Valley Univ., Orem, UT, USA), Christophe Thomazo (Biogéosciences, Univ. Bourgogne Franche-Comté, Dijon, France), Mathieu Thoury (IPANEMA, Univ. Paris-Saclay/Synchrotron SOLEIL, Gif-sur-Yvette, France), and Emmanuelle Vennin (Biogéosciences, Univ. Bourgogne Franche-Comté, Dijon, France).

* Corresponding author. E-mail address: carlo.romano@pim.uzh.ch (C. Romano).

✡ Corresponding editor: Arnaud Brayard.

Abstract

A new, diverse and complex Early Triassic assemblage was recently discovered west of the town of Paris, Idaho (Bear Lake County), USA. This assemblage has been coined the Paris Biota. Dated earliest Spathian (Olenekian), the Paris Biota provides further evidence that the biotic recovery from the end-Permian mass extinction was well underway *ca.* 1.5 million years after the event. This assemblage includes mainly invertebrates, but also vertebrate remains such as ichthyoliths (isolated skeletal remains of fishes). Here we describe first fossils of Chondrichthyes (cartilaginous fishes) from the Paris Biota. The material is composed of isolated teeth (mostly grinding teeth) preserved on two slabs and representing two distinct taxa. Due to incomplete preservation and morphological differences to known taxa, the chondrichthyans from the Paris Biota are provisionally kept in open nomenclature, as Hybodontiformes gen. et sp. indet. A and Hybodontiformes gen. et sp. indet. B, respectively. The present study adds a new occurrence to the chondrichthyan fossil record of the marine Early Triassic western USA Basin, from where other isolated teeth (*Omanoselache*, other Hybodontiformes) as well as fin spines of *Nemacanthus* (Neoselachii) and *Pyknotylacanthus* (Ctenachanthoidea) and denticles have been described previously.

1. Introduction

Up to 90% (Raup, 1979) of marine species were wiped out during the largest Phanerozoic mass extinction event, which occurred at the Permian-Triassic boundary (251.959 ± 0.018 million years ago; Baresel et al., 2017). The biotic recovery that followed the end-Permian mass extinction event is frequently portrayed as delayed until the Middle Triassic, with depauperate Early Triassic faunas, though recent studies suggest a more complex recovery pattern (e.g., Brayard et al., 2011, 2015; Song et al., 2011; Scheyer et al., 2014; Hautmann et al., 2015; Hofmann et al., 2017; Foster and Sebe, 2017; Martindale et al., 2017). Fossil evidence for an early recovery are convincing for nekto-pelagic organisms like

conodonts and ammonoids (e.g., Orchard, 2007; Brayard et al., 2009) and is also observed in a number of well-diversified Early Triassic assemblages (e.g., Beatty et al., 2008; Hautmann et al., 2011; Foster et al., 2017).

One such exceptional assemblage has been recently discovered near the town of Paris, Bear Lake County (southeastern Idaho, USA), named the Paris Biota (Brayard et al., 2017). This assemblage of earliest Spathian (Olenekian, late Early Triassic) age comprises metazoan species of at least seven phyla (20 distinct orders) and includes remains of osteichthyan and chondrichthyan fishes. The Paris Biota was dated as earliest Spathian based on the occurrence of the ammonoid *Tirolites* (Brayard et al., 2017, 2019). Remarkably, the Paris Biota combines forms with Palaeozoic (Brayard et al., 2017; Botting et al., 2019) and middle Mesozoic (Doguzhaeva et al., 2018) imprints, highlighting the importance of the Early Triassic as a transitional epoch leading from the Palaeozoic to evolutionarily modern faunas (Sepkoski, 1984).

The aim of this paper is to describe remains of Chondrichthyes (cartilaginous fishes) from the Paris Biota, first depicted in Brayard et al. (2017). The presented material increases the diversity of dental morphologies from the marine western USA basin and adds a new occurrence to the Early Triassic chondrichthyan record of the eastern Panthalassa.

2. Material and methods

The chondrichthyan material described below consists of seven isolated teeth preserved on two shale slabs (IMNH 1143/46168 and UBGD 30567). Six teeth (t1–t6) are preserved on slab IMNH 1143/46168 and one tooth (t7) on slab UBGD 30567. The material was found *in situ* in Paris Canyon, west of the town of Paris (Bear Lake County, Idaho, USA), and is part of the Paris Biota (Brayard et al., 2017). The sedimentary deposits of the Paris Biota correspond to alternating cm-thick mudstones with silty laminae and marls, and display some hummocky cross stratifications and erosion surfaces, indicating deposition in a distal upper offshore environment on a very flat platform, where distal storms acted intermittently (see Brayard et al., 2017 for further information on the locality, geology and palaeoenvironment).

Figure 1 summarizes the anatomical terminology used in the present paper, which mostly follows Fischer et al. (2010). The mesial and distal ends of the teeth are determined based on the orientation of the crown apex, which usually points in the direction of the pharynx (distal) in the living animal. The labial and lingual sides of the teeth have been determined based on the presence (or absence) of a labial depression on the labial root

surface, although there is less clarity regarding this feature in isolated teeth (Argyriou et al., 2017). We herein use open nomenclature in the sense of Bengtson (1988).

The following specimens were used as comparative material:

- PMU P.107 (*Palaeobates polaris* Stensiö, 1921; holotype), PIMUZ A/I 3888 (*P. polaris*; Romano and Brinkmann, 2010), SMNH P 1310 (*Acrodus oppenheimeri* Stensiö, 1921), and SMNH P 1311 (*A. spitzbergensis* Hulke, 1873) from the Early Triassic of Spitsbergen, Norway;
- PIMUZ T 3814 (*A. georgii* Mutter, 1998b; cf. Mutter, 1998a, 1998b; Rieppel, 1981) from the Middle Triassic of Switzerland;
- AMPG 550 (Hybodontiformes indet.; Argyriou et al., 2017) from the Lopingian of Greece.

In addition, close-up photographs of the teeth of the following specimens were obtained:

- BMNH P.54662 (*Acrodus flemingianus* De Koninck, 1863a; holotype) and BMNH P.12151 (*Acrodus* sp.; De Koninck, 1863a, 1863b) from the Early Triassic of Pakistan;
- UCMP 10251 (*Acrodus oreodontus* Wemple, 1906; holotype) from the Middle Triassic of Nevada, USA;
- TMP 97.74.10 (*Homalodontus aplopagus* (Mutter, De Blanger and Neuman, 2007), holotype; Mutter et al. 2008) and ULVP 46531 (*H. homalorhizo* (Mutter, De Blanger and Neuman, 2007); holotype; Mutter et al., 2008) from the Early Triassic of British Columbia, Canada.

Comparisons with other taxa, as mentioned in the text, are based on the information available in the literature.

Institutional abbreviations: AMPG: Museum of Palaeontology and Geology, National and Kapodistrian University of Athens, Greece; IMNH: Idaho Museum of Natural History, Pocatello, Idaho, USA; BMNH: Natural History Museum, London, UK; PIMUZ: Paläontologisches Institut und Museum, Universität Zürich, Switzerland; PMU: Palaeontological collections, Museum of Evolution, Uppsala University, Uppsala, Sweden; SMNH: Department of Palaeozoology, Swedish Museum of Natural History, Stockholm, Sweden; TMP: Royal Tyrrell Museum of Paleontology, Drumheller, Alberta, Canada; UALVP: University of Alberta, Laboratory for Vertebrate Paleontology, Edmonton, Alberta, Canada; UBGD: Université de Bourgogne, Géologie, Dijon, France; UCMP: University of California, Museum of Paleontology, Berkeley, California, USA.

3. Systematic palaeontology

Class Chondrichthyes Huxley, 1880

Cohort Euselachii Hay, 1902

Order Hybodontiformes Maisey, 1975

Family *incertae sedis*

Hybodontiformes gen. et sp. indet. A

Fig. 2

2017. *Acrodus* sp. - Brayard et al., figs 6i, S26a–d, tab. S1.

Material: A single slab, IMNH 1143/46168, containing six disarticulated teeth (t1–t6; Fig. 2). The preservation of the teeth ranges from largely complete to fragmentary. All teeth are seen in lingual or in labial aspects and share the same general architecture, crown ornamentation and anaulacorhize root vascularisation. Differences between teeth are noted in the degree of apical arching, the development of cusps and cusplets, and the level of crown asymmetry. The teeth are referred to the same taxon, which is characterized by a heterodont grinding-type dentition.

Occurrence: Paris Canyon, Lower Shale member, Thaynes Group; west of Paris, Bear Lake County, Idaho, USA.

Description: The order in which the teeth are described follows their state of preservation, starting with the most complete tooth t6, in which only the mesial and distal ends of the crown are slightly damaged (Fig. 2).

   Tooth t6 (Fig. 2(f)) is probably exposed in labial view due the presence of a depression in the root below the cusp (labial depression; Fig. 1). The tooth is mesiodistally elongate and measures *ca*. 12 mm in length and 4 mm in height. The crown is marked by a distinct main cusp, which is situated nearer to the distal end than to the mesial end, giving the tooth an asymmetrical shape in labial view. The crown tapers towards its mesial and distal ends. The crown line (occlusal crest) is convex mesial to the cusp and concave distal to the cusp. The longitudinal (occlusal) crest is strongly serrated in the mesial and distal parts, whereas in proximity to the main cusp it is straight to gently curved. The crown ornamentation consists otherwise of distinct, apicobasally running ridges. Frequently, the ridges ramify towards the crown base. The most prominent ridges lead from the crown-root junction to the tips of the aforementioned serrations. An additional set of apicobasal ridges, mostly located in the mesial part of the crown, are interspaced between the former ridges, but they seem to disappear before reaching the longitudinal crest. The apicobasal ridges interconnect basally, exhibiting a

reticulated pattern there. Additional, very short ridges beneath the occlusal crest occur at least near the main cusp. A small, mesiodistally constricted labial peg is visible at the level of the cusp. A transverse crest running from the crown apex to the crown-root junction is developed on the lingual side. Tooth t6 is constricted at the level of the crown-root junction. The root is about equally high throughout its length. The lingual root surface is marked by a series of large, apicobasally elongated foramina. In addition, much smaller and chaotically arranged foramina occur.

Tooth t3 is probably seen in lingual view due to the absence of a labial depression (Fig. 2(c)). It is mostly well-preserved, with only the middle part of its lingual crown surface damaged. It is nearly symmetrical in lingual aspect, though its mesial portion is slightly longer than the distal one. The tooth is highest centrally, where the crown forms a cusp, and tapers in mesial and distal directions. Tooth t3 is *ca*. 13 mm long, has a maximum height of 5.5 mm, and a minimum height of about 2 mm at the distal and mesial ends, respectively. The occlusal crest is straight to gently S-curved mesial and distal to the cusp. Further mesially and distally, the crown line is serrated, like in t6. The intercalated, very short ridges seem to occur in the central part of the crown (visible just apical to the damaged portion), but disappear halfway in mesial and distal direction. The root vascularization is similar to t6, meaning that it consists of a longitudinal series of apicobasally elongate foramina and numerous, randomly distributed small foramina.

Tooth t5 (Fig. 2(e)) is damaged, though its shape is still visible. It is not possible to decide whether its lingual or labial side is exposed. The crown is asymmetrical and shows a cusp. It is difficult to determine whether the cusp is displaced in mesial or in distal directions, but a distal shifting is favored here. The tooth has a length of *ca*. 14 mm and a maximum height of 4.5 mm. At the mesial and distal terminations, the tooth height measures about 1.5 mm. As far as preserved, the ornamentation of the crown seems similar to that of teeth t6 and t3. The crown line contains long, nearly straight segments mesial and distal to the main cusp, whereas farthest distally and mesially distinct serrations are evident. The root is damaged, but appears to be similar as in t6 and t3.

Tooth t4 (Fig. 2(d)) is poorly preserved, but has a very similar outline as t5. As for t5, it is uncertain which side of the tooth t4 is mesial and which one is distal. Tooth t4 is characterized by a slightly mesially or distally displaced crown apex, an almost straight crown line proximal to the main cusp, and a serrated crown line near the mesial and distal ends. The remaining crown ornamentation is not preserved. Tooth t4 is 13.5 mm long and 5 mm high at

the level of the cusp. Minimal height of the tooth is 1 mm and 1.5 mm, respectively. The root vascularization is not well visible, but appears similar to that of the other teeth.

Tooth t2 (Fig. 2(b)) is heavily weathered, but several features are discernible nonetheless. It is asymmetric, with its crown apex shifted distally. The crown line is convex and steep, both mesially and distally. Serrations on the occlusal crest are visible in the distal segment. The ornamentation of the crown, preserved as impressions, is similar to that of the other teeth (see t6 and t3). The intercalated short ridges are, however, developed almost throughout the portion mesial to the cusp (except farthest mesially). The short ridges are not visible in the distal portion, which is likely due to preservation. The root vascularization of t2 is the same as for the other teeth. Tooth t2 has a mesiodistal length of about 10 mm and a maximum height of 5 mm. It is about 2.5 mm high at its distal end and 1.5–2 mm high at its mesial termination.

Tooth t1 (Fig. 2(a)) is extremely poorly preserved, but its outline is still somewhat visible. This tooth differs from the other ones in possessing a high, well-defined main cusp and at least one, significantly smaller lateral cusplet distally. The main cusp, located somewhat centrally, is gently distally inclined. The crown ornamentation is not preserved. Compared to the height of the root, the crown is low mesial and distal to the main cusp. The root vascularization was probably the same as for the other teeth. Tooth t1 is approximately 9 mm long, with a maximum height of 4.5 mm at the level of the main cusp.

The morphologies of the six teeth of IMNH 1143/46168 and their proximity suggest that they belonged to different tooth files of the same species, possibly the same individual. The numbering of the teeth (t1–t6) reflects the putative order of their corresponding tooth file along the jaws, with the numbers increasing from symphyseal to lateral files. Teeth t1, t2, and t3 are mesiodistally shorter than, but apicobasally about as high as the other teeth, and they probably represent teeth of the anterior (mesial) tooth files. In lingual or labial view, teeth t1 and t3 are somewhat symmetrical, whereas all other teeth are distinctly asymmetrical, with the crown apex being shifted distally, where known. Teeth t4 and t5 could belong to the same tooth file or neighboring files based on their similar outline in lingual/labial view.

Hybodontiformes gen. et sp. indet. B

Fig. 3

2017. *Acrodus* sp. - Brayard et al., fig. S26e, tab. S1.

Material: A single tooth (t7; Fig. 3) preserved on slab UBGD 30567. The tooth is preserved as an impression. It is visible either in lingual or in labial aspect, which one it is cannot be determined.

Occurrence: Paris Canyon, Lower Shale Member, Thaynes Group; west of Paris, Bear Lake County, Idaho, USA.

Description: **Tooth t7** (Fig. 3) is elongate and straight, and the crown and root are about equally high throughout the length of the tooth. The tooth is about 10 mm long and about 3 mm high. It is lingually/labially constricted at the level of the crown-root junction. There is a weak main cusp situated slightly nearer to the supposed distal than to the mesial end of the tooth. The crown line (occlusal crest) is straight mesial to the main cusp and weakly serrated in the distal segment, although the latter could be enhanced by the mode of preservation as an impression. Mesial and distal to the main cusp, the ornamentation of the crown consists of mostly straight, densely arranged ridges that run perpendicular to the mesiodistal tooth axis, without forming any ramifications. The majority of these ridges extend from the occlusal crest to near the base of the crown, but without reaching the crown-root junction. The base of the crown is smooth. At the level of the main cusp, the ridges are sparse and arranged in a radial manner, centered at the cusp apex. Ramifications are observed on one of the radial ridges. The root vascularization is of the anaulacorhize type, with a longitudinal series of large foraminas.

4. Discussion

4.1. Early–Middle Triassic record of chondrichthyans from the USA and Canada

During the Early Triassic, most of the present-day western USA was covered by an epicontinental sea, which was situated in the equatorial domain and connected to the Panthalassa Ocean (Paull and Paull, 1993; Brayard et al., 2013; Caravaca et al., 2018). In the Middle Triassic, this epicontinental sea had vanished as the shoreline moved westwards due to local tectonics and eustatic sea level change.

Still very little is known about the fish fauna that lived in the marine western USA basin during the Early Triassic, despite the fact that occurrences of fossil Chondrichthyes and Osteichthyes in Lower Triassic rocks of the western United States have been known for over a century (Evans, 1904; Goddard, 1907). More recent fieldworks led to the discovery of Early Triassic fishes at new and classic localities in Idaho, Utah, Nevada and California (Mutter and Rieber, 2005; Romano et al., 2012, 2017; Koot, 2013; Brayard et al., 2017). These discoveries suggest that our knowledge of the western USA basin ichthyofauna could be much improved in the future through additional, systematic searching.

In addition to the teeth of the Paris Biota described herein, other occurrences of Early Triassic chondrichthyans from Bear Lake County (Idaho) include two isolated fin spines, referred to *Nemacanthus* Agassiz, 1837 and *Pyknotylacanthus* Mutter et Rieber, 2005, respectively, as well as denticles probably belonging to the latter taxon (Evans, 1904; Maisey, 1977; Mutter and Rieber, 2005; Cappetta, 2012). Whereas the remains of *Pyknotylacanthus* are dated as early Spathian (*Columbites parisianus* Zone), the precise stratigraphic origin of the *Nemacanthus* fin spine is not well known (Evans, 1904; Schaeffer and Mangus, 1976; Mutter and Rieber, 2005). Youngquist (1952) casually mentions the presence of small chondrichthyan teeth referable to '*Polyacrodus*' (B. Schaeffer, pers. comm. in Youngquist, 1952) in rock samples collected near the town of Paris (note that '*Polyacrodus*' is a *nomen dubium*; Rees, 2008). In his thesis, Yamagishi (2006, as cited in Koot, 2013) also reports '*Polyacrodus*' teeth and denticles from Bear Lake County, as well as denticles from Hurricane, Washington County, Utah. An element interpreted as a piece of fossilized chondrichthyan cartilage collected near Georgetown, Bear Lake County (Romano et al., 2012), rather represents a poorly preserved carapace of a crustacean (Heinz Furrer, pers. comm. to C.R., 2013). In her thesis, Koot (2013) reports chondrichthyans from the Spathian of Bear Lake County and the Smithian of Utah. She furthermore mentions, for the very first time, the occurrences of chondrichthyan remains in Spathian strata of the Prida Fm. at Bloody Canyon, Nevada, and Spathian beds of the Union Wash Fm., Darwin Canyon, California. Koot (2013) highlights the widespread distribution of *Omanoselache* Koot, Cuny, Tintori et Twitchett, 2013, and the scarcity of neoselachians within the western USA basin.

There are several occurrences of Chondrichthyes in the Middle Triassic of Nevada. Wemple (1906) described teeth from Fisher and Cottonwood canyons, West Humboldt Range (Pershing County): a polycuspid tooth referred to as *Hybodus nevadensis* Wemple, 1906, and two low-crowned teeth that she ascribed to *Acrodus alexandrae* Wemple, 1906 and *A. oreodontus* Wemple, 1906, respectively. Davidson (1919) reported a partial fin spine from the Middle Triassic of Straight Canyon, West Humboldt Range. More recently, Rieppel et al. (1996) and Cuny et al. (2001) presented hybodontoid material from the Anisian Fossil Hill member of the Prida Fm., Favret Canyon (Augusta Mountains, Pershing County), among other teeth of *Acrodus spitzbergensis* Hulke, 1873, *A.* cf. *vermiformis* Stensiö, 1921 (= '*vermicularis*'; Rieppel et al., 1996), *A.* cf. *oreodontus*, *A. cuneocostatus* Cuny, Rieppel et Sander, 2001, and '*Polyacrodus*' *bucheri* Cuny, Rieppel et Sander, 2001 (= *Omanoselache bucheri*; see Koot et al., 2015). Besides, they also reported first neoselachian remains from the Middle Triassic, belonging to the synechodontiform *Mucrovenator* Cuny, Rieppel et Sander,

2001 (Koot, 2013). Koot (2013) reported chondrichthyan remains from Anisian strata of the Prida Fm. of Coyote Canyon (Pershing County).

Eastern Panthalassic occurrences of Early and Middle Triassic Chondrichthyes are also known from several sites in Canada. Regarding the Early Triassic, Wapiti Lake (British Columbia) and Banff National Park (Alberta) have yielded a plethora of articulated and disarticulated fishes (Schaeffer and Mangus, 1976; Mutter and Neuman, 2006, 2008; Mutter et al., 2007; Neuman, 2015), including chondrichthyans belonging to various taxa (e.g., *Listracanthus*, Eugeneodontida, Hybodontiformes). Recently, Koot (2013) reported *Homalodontus* Mutter, Neuman et De Blanger, 2008 (= *Wapitiodus* Mutter, De Blanger et Neuman, 2007), a ?hybodontoid of uncertain systematic affinities, and the eugeneodontid *Caseodus* from Griesbachian (earliest Triassic) deposits of Ellesmere Island, Canadian Arctic Archipelago. Both genera were previously known from younger deposits of western Canada (Mutter et al., 2007, 2008; Mutter and Neuman, 2008; Neuman, 2015), and their presence in the Sverdrup Basin marks their first occurrence in the Triassic of this region (Koot, 2013). Finally, from the Middle Triassic (Ladinian) Liard Fm. of British Columbia, Johns et al. (1997) describe teeth of '*Polyacrodus*' *contrarius* (Johns, Barnes et Orchard, 1997) (= *Omanoselache contrarius*; Koot et al., 2015), *Synechodus* sp. 1, and *Synechodus volaticus* Johns, Barnes et Orchard, 1997, as well as denticles of several taxa.

4.2. Comparative morphology

The chondrichthyan teeth from the Paris Biota described herein, IMNH 1143/46168 and UGBD 30567, belong to two morphologically distinct taxa, but they are too incompletely preserved for a sound identification at low taxonomic rank. A comparison of the Paris Biota teeth with previously described taxa, chiefly those from the Early and Middle Triassic of the USA and Canada (see Section 4.1), follows below.

The overall morphology of the teeth preserved on IMNH 1143/46168 resembles somewhat that of taxa referred to Acrodontinae Casier, 1959, a Late Pennsylvanian?–Late Cretaceous (mainly Mesozoic) hybodontoid subfamily with a widespread distribution (Rees, 2008; Ginter et al., 2010; Cappetta, 2012). The Acrodontinae encompasses three genera – namely *Acrodus* Agassiz, 1838, *Asteracanthus* Agassiz, 1837, and *Palaeobates* Meyer, 1849 (Maisey, 1989; Rees, 2008) – which are characterized by a low-crowned, heterodont grinding dentition. Specimen IMNH 1143/46168 shows more similarities with *Acrodus* (*sensu lato*) than with *Asteracanthus* or *Palaeobates*, especially with regard to the crown morphology and ornamentation. Although teeth of *Palaeobates* usually have a reticulated crown ornamentation

(Cappetta, 2012), some species like *Palaeobates polaris* Stensiö, 1921 also exhibit a transverse crest and apicobasal ridges (Stensiö, 1921; Romano and Brinkmann, 2010).

In *Acrodus* species, the crown is usually ornamented with a longitudinal crest and ridges that radiate from this crest towards the edges and which ramify towards the crown base (Cappetta, 2012). Whereas most species possess only a single longitudinal crest (Cappetta, 2012), others exhibit two crests that are separated by a sulcus (see below). The anterior teeth of *Acrodus* are typically short and the lateral teeth mesiodistally elongated. In some species, the teeth may show a low central cusp (e.g., *A.?* *olsoni* Johnson, 1981; *A. flemingianus* De Koninck, 1863a), as well as several lateral cusplets, such as in *A. anningiae* Agassiz, 1843, *A. spitzbergensis* Hulke, 1873, or *A. oppenheimeri* Stensiö, 1921 (Agassiz, 1833–43; Waagen, 1895; Johnson, 1981; Ginter et al., 2010; Cappetta, 2012), whereas in other species neither cusps nor cusplets are developed (e.g., *A. georgii* Mutter, 1998b; cf. Mutter, 1998a, 1998b; Rieppel, 1981). The cusps and cusplets are, however, usually not as high and acute as in IMNH 1143/46168. In some species, the crown of the lateral teeth is nearly flat (e.g., *A. vermiformis*), although in other species (e.g., *A. spitzbergensis*, *A. georgii*) the crown shows some apical arching (Stensiö, 1921; Rieppel, 1981; Mutter, 1998a, 1998b). In several species of *Acrodus*, the posterior teeth are twisted (Cappetta, 2012) – a feature not observed in the material from the Paris Biota, potentially due to the fact that posterior teeth are absent.

Several *Acrodus* (*s.l.*) teeth were described from the Middle Triassic of Nevada (see above, Section 4.1). Whereas the tooth morphologies of IMNH 1143/46168 are distinct from those of *A. alexandrae* Wemple, 1906, *A. spitzbergensis*, *A.* cf. *vermiformis* Stensiö, 1921, and *A. cuneocostatus* Cuny, Rieppel et Sander, 2001, there are some resemblances between IMNH 1143/46168 and *A. oreodontus* Wemple, 1906. These similarities include the asymmetry and rounded lateral contour of the crown, the ornamentation consisting of ridges radiating from the occlusal crest, and the relative height of the crown and the root. However, the holotype of *A. oreodontus* (UCMP 10215), and also most lateral teeth referred to *A. spitzbergensis* (Stensiö, 1921; Rieppel et al., 1996; Cuny et al., 2001; Koot, 2013), differ from the Paris Biota teeth in having two parallel longitudinal crests issuing from the apex of the central cusp and separated by a shallow trough along most of their length. However, the absence of these parallel crests could be preservational. The tooth described as *A.* cf. *oreodontus* by Rieppel et al. (1996) from the Middle Triassic of Nevada has a pronounced central cusp, located midway along the mesiodistal axis of the crown, and lacks any lateral cusplets. This morphology is not present on IMNH 1143/46168 and it is, thus, questionable whether the teeth are conspecific or not. Maisey (1977) compared the morphology of the

holotype of *A. oreodontus* (UCMP 10215) to that of lateral teeth of '*Palaeospinax*' (*nomen dubium*; Klug and Kriwet, 2008), but more material is required to better assess the taxonomic status of this species (Rieppel et al., 1996). None of the early Mesozoic *Acrodus* species (e.g., Wemple, 1906; Rieppel et al., 1996; Cuny et al., 2001) exhibit serrated cutting edges as strongly as the Paris Canyon teeth t3 and t6. A further difference between Mesozoic *Acrodus* (e.g., Stensiö, 1921; Cappetta, 2012) and the teeth described herein lies in the ornamentation pattern, for example the presence of more intricate and frequently anastomosing ridges in the former. In conclusion, the referral of IMNH 1143/46168 from the Paris Biota to *Acrodus* is not permitted due to a number of morphological deviations.

Some teeth of IMNH 1143/46168 superficially resemble dental material traditionally referred to '*Polyacrodus*'. Rees (2008) considers '*Polyacrodus*' a *nomen dubium* and he provisionally reallocated all teeth to *Hybodus*. Other authors referred some '*Polyacrodus*' species to *Lissodus* (Błażejowski, 2004; Fischer 2008). Lately, Koot et al. (2015) reascribed several Triassic '*Polyacrodus*' species to *Omanoselache* Koot, Cuny, Tintori et Twitchett, 2013 (= *Prolatodon* Pla, Márquez-Aliaga et Botella, 2013), a genus previously described from the Permian of Oman (Koot et al., 2013). IMNH 1143/46168 shares with *Omanoselache* a heterodont dentition characterized by mesiodistally elongate teeth, which are symmetrical and arched in the anterior files and asymmetrical in the posterior files. However, the main cusp is moderate in *Omanoselache* (Koot et al., 2013, 2015; Pla et al., 2013), whereas in IMNH 1143/46168 it is prominent on one tooth (t1). Lateral cusplets are absent on all except one tooth of IMNH 1143/46168 (t1), while in *Omanoselache* cusplets are also present on the lateral teeth. Given the current state of knowledge, referral of the teeth from the Paris Biota to *Omanoselache* is thus not supported.

There are also a few similarities between IMNH 1143/46168 and *Homalodontus* Mutter, Neuman et De Blanger, 2008 (= *Wapitiodus* Mutter, De Blanger et Neuman, 2007) from the Early Triassic of Canada (see above, Section 4.1). However, in contrast to IMNH 1143/46168 several anterior tooth files of *Homalodontus* are marked by a prominent central cusp and an absence of lateral cusplets, although according to Mutter et al. (2007) tiny lateral cusplets are present on some teeth of *Homalodontus homalorhizo* (Mutter, De Blanger et Neuman, 2007) and two teeth of *H. aplopagus* (Mutter, De Blanger et Neuman, 2007). Other differences include the absence of a serrated crown line and the symmetrical, apically flat lateral teeth of *Homalodontus*. A close affinity between IMNH 1143/46168 and this taxon is hence excluded.

On the basis of these comparisons, affinities of IMNH 1143/46168 with *Acrodus* (*s.l.*) or *Omanoselache* appear possible, but due to several morphological differences and

preservation, IMNH 1143/46168 cannot be confidently referred to either of these genera. Because of those differences and due to the incomplete preservation of most teeth, we prefer to preliminarily leave IMNH 1143/46168 in open nomenclature, as gen. et sp. indet. A within Hybodontiformes, until more material becomes available.

Unlike IMNH 1143/46168, the tooth imprint t7 (UGBD 30567) from the Paris Biota does not form strong serrations along the whole occlusal crest. Moreover, the crown ornamentation of UGBD 30567 is composed of ridges that do not ramify, and the ridges are arranged in a radial pattern at the level of the main cusp. These features suggest that t7 likely belongs to a different taxon than t1–t6 (IMNH 1143/46168), although intraspecific variation cannot be fully excluded in such a restricted sample size.

UGBD 30567 vaguely resembles teeth of *Homalodontus* (Homalodontidae Mutter, Neuman et De Blanger, 2008, = Wapitiodidae Mutter, De Blanger et Neuman, 2007) from the Early Triassic of Canada (see above, Section 4.1). Tooth t7 is similar to the posterior mesial teeth of TMP 97.74.10 (holotype of *H. aplopagus*) in exhibiting a crown that is not arched and about as high as the root throughout its length, the presence of a faint central cusp, and an ornamentation consisting (mainly) of densely arranged ridges that run perpendicular to the mesiodistal axis of the tooth. However, UGBD 30567 differs from TMP 97.74.10 in the absence of basal ramifications on those ridges, and the radial arrangement of the ridges at the level of the central cusp. UGBD 30567 differs from UALVP 46531 (holotype of *H. homalorhizo*) in the absence of arching of the crown and root, although this character could be related with the relative position of the tooth on the jaw. In addition, the ridges reach the crown-root junction in *H. homalorhizo*, which is not the case in the tooth imprint from the Paris Biota.

Due to incomplete preservation, a secure generic or specific attribution of UGBD 30567 cannot be achieved, though some resemblances with *Homalodontus* are noted here. UGBD 30567 is therefore left in open nomenclature as gen. et sp. indet. B. within Hybodontiformes.

5. Concluding remarks

The chondrichthyan teeth from the Paris Biota (Bear Lake County, Idaho, USA; Brayard et al., 2017), deposited ~1.5 million years after the end-Permian mass extinction event (Ovtcharova et al., 2006; Baresel et al., 2017) during the earliest Spathian (Olenekian, Early Triassic), belong to two distinct species, probably representing new taxa. Nevertheless, the incomplete state of preservation of IMNH 1143/46168 and UGBD 30567 and the limited

knowledge of Triassic Hybodontiformes with similar dental morphologies currently preclude the referral of the Paris Biota chondrichthyans at a low taxonomic level. Until more material is found, the specimens are left in open nomenclature as Hybodontiformes gen. et sp. indet. A and Hybodontiformes gen. et sp. indet. B, respectively.

The Permian-Triassic boundary mass extinction event severely decimated marine invertebrates, though Chondrichthyes appear to have not undergone elevated extinctions (Vázquez and Clapham, 2017). The present study confirms the widespread distribution of Hybodontiformes in the Early Triassic western USA basin (Koot, 2013), which contrasts with the western Tethys, where a relatively higher neoselachian component is apparent (Koot et al., 2015). Both taxa from the Paris Biota are characterized by grinding lateral teeth suitable for processing hard-shelled prey that occur abundantly in this assemblage (Brayard et al., 2017). The presented material as well as other recently discovered fish fossils (Mutter and Rieber, 2005; Romano et al., 2012, 2017; Koot, 2013), show that our knowledge of the ichthyofauna from the marine western USA basin can be much improved through more sampling.

Acknowledgements

References

Agassiz, L., 1833–1843. Recherches sur les poissons fossiles III. Petitpierre, Neuchâtel.

Argyriou, T., Romano, C., Carrillo-Briceño, J.D., Brosse, M., Hofmann, R., 2017. The oldest record of gnathostome fossils from Greece: Chondrichthyes from the Lopingian of Hydra Island. Palaeontologia Electronica 20.1.8A, 1–9.

Baresel, B., Bucher, H., Bagherpour, B., Brosse, M., Guodun, K., Schaltegger, U., 2017. Timing of global regression and microbial bloom linked with the Permian-Triassic boundary mass extinction: implications for driving mechanisms. Scientific Reports 7, 43630.

Beatty, T.W., Zonneveld, J-P., Henderson, C.M., 2008. Anomalously diverse Early Triassic ichnofossil assemblages in northwest Pangea: a case for a shallow-marine habitable zone. Geology 36, 771–774.

Bengtson, P., 1988. Open nomenclature. Palaeontology 31, 223–227.

Błażejowski, B., 2004. Shark teeth from the Lower Triassic of Spitsbergen and their histology. Polish Polar Research 25, 153–167.

Botting, J.P., Brayard, A., the Paris Biota Team, 2019. A late-surviving Triassic protomonaxonid sponge from the Paris Biota (Bear Lake County, Idaho, USA). Geobios 52, xxx-xxx.

Brayard, A., Escarguel, G., Bucher, H., Monnet, C., Brühwiler, T., Goudemand, N., Galfetti, T., Guex, J., 2009. Good genes and good luck: ammonoid diversity and the end-Permian mass extinction. Science 325, 1118–1121.

Brayard, A., Vennin, E., Olivier, N., Bylund, K.G., Jenks, J., Stephen, D.A., Bucher, H., Hofmann, R., Goudemand, N., Escarguel, G., 2011. Transient metazoan reefs in the aftermath of the end-Permian mass extinction. Nature Geoscience 4, 693–697.

Brayard, A., Bylund, K.G., Jenks, J.F., Stephen, D.A., Olivier, N., Escarguel, G., Fara, E., Vennin, E., 2013. Smithian ammonoid faunas from Utah: implications for Early Triassic biostratigraphy, correlation and basinal paleogeography. Swiss Journal of Palaeontology 132, 141–219.

Brayard, A., Jenks, J.F., Bylund, K.G., the Paris Biota Team, 2019. Ammonoids and nautiloids from the earliest Spathian Paris Biota and other early Spathian localities in southeastern Idaho, USA. Geobios 52, xxx-xxx.

Brayard, A., Meier, M., Escarguel, G., Fara, E., Nützel, A., Olivier, N., Bylund, K.G., Jenks, J.F., Stephen, D.A., Hautmann, M., Vennin, E., Bucher, H., 2015. Early Triassic Gulliver gastropods: Spatio-temporal distribution and significance for biotic recovery after the end-Permian mass extinction. Earth-Science Reviews 146, 31–64.

Brayard, A., Krumenacker, L.J., Botting, J.P., Jenks, J.F., Bylund, K.G., Fara, E., Vennin, E., Olivier, N., Goudemand, N., Saucède, T., Charbonnier, S., Romano, C., Doguzhaeva, L., Thuy, B., Hautmann, M., Stephen, D.A., Thomazo, C., Escarguel, G., 2017.

Unexpected Early Triassic marine ecosystem and the rise of the Modern evolutionary fauna. Science Advances 3, e1602159.

Cappetta, H., 2012. Handbook of Paleoichthyology 3E. Chondrichthyes, Mesozoic and Cenozoic Elasmobranchii: Teeth. Dr. Friedrich Pfeil, München.

Caravaca, G., Brayard, A., Vennin, E., Guiraud, M., Le Pourhiet, L., Grosjean, A.-S., Thomazo, C., Olivier, N., Fara, E., Escarguel, G., Bylund, K.G., Jenks, J.F., Stephen, D.A., 2018. Controlling factors for differential subsidence in the Sonoma Foreland Basin (Early Triassic, western USA). Geological Magazine 155, 1305-1329.

Cuny, G., Rieppel, O., Sander, P.M., 2001. The shark fauna from the Middle Triassic (Anisian) of North-Western Nevada. Zoological Journal of the Linnean Society 133, 285–301.

Davidson, P., 1919. A cestraciont spine from the Middle Triassic of Nevada. University of California Publications, Bulletin of the Department of Geology 11, 433–435.

De Koninck, L., 1863a. Descriptions of some fossils from India, discovered by Dr. A. Fleming, of Edinburgh. The Quarterly Journal of the Geological Society of London 19, 1–19.

De Koninck, L., 1863b. Notice sur les fossiles de l'Inde découverts par M. le Dr Fleming, d'Edimbourg. Mémoires de la Société Royale des Sciences de Liège 18, 553–579.

Doguzhaeva, L., Brayard, A., Goudemand, N., Krumenacker, L.J., Jenks, J., Bylund, K.G., Fara, E., Olivier, N., Vennin, E., Escarguel, G., 2018. An Olenekian (Early Triassic) gladius associated with soft tissue remains from Idaho, USA, indicative of a squid-like coleoid cephalopod at the onset of Mesozoic Era. Acta Palaeontologica Polonica 63, 341–355.

Evans, H.M., 1904. A new cestraciont spine from the Lower Triassic of Idaho. University of California Publications, Bulletin of the Department of Geology 3, 397–402.

Fischer, J., 2008. Brief synopsis of the hybodont form taxon *Lissodus* Brough, 1935, with remarks on the environment and associated fauna. Paläontologie, Stratigraphie, Fazies 16 (Freiberger Forschungshefte C 528), 1–23.

Fischer, J., Schneider, J.W., Ronchi, A., 2010. New hybondontoid shark from the Permocarboniferous (Gzhelian–Asselian) of Guardia Pisano (Sardinia, Italy). Acta Palaeontologica Polonica 55, 241–264.

Foster, W.J., Danise, S., Twitchett, R.J., 2017. A silicified Early Triassic marine assemblage from Svalbard. Journal of Systematic Palaeontology 15, 851–877.

Foster, W.J., Sebe, K., 2017. Recovery and diversification of marine communities following the late Permian mass extinction event in the western Palaeotethys. Global and Planetary Change 155, 165–177.

Ginter, M., Hampe, O., Duffin, C., 2010. Handbook of Paleoichthyology 3D. Chondrichthyes. Paleozoic Elasmobranchii: Teeth. Dr. Friedrich Pfeil, München.

Goddard, M., 1907. Fish remains from the marine Lower Triassic of Aspen Ridge, Idaho. University of California Publications, Bulletin of the Department of Geology 5, 145–148.

Hautmann, M., Bucher, H., Brühwiler, T., Goudemand, N., Kaim, A., Nützel, A., 2011. An unusually diverse mollusc fauna from the earliest Triassic of South China and its implications for benthic recovery after the end-Permian biotic crisis. Geobios 44, 71–85.

Hautmann, M., Bagherpour, B., Brosse, M., Frisk, Å., Hofmann, R., Baud, A., Nützel, A., Goudemand, N., Bucher, H., 2015. Competition in slow motion: the unusual case of benthic marine communities in the wake of the end-Permian mass extinction. Palaeontology 58, 871–901.

Hofmann, R., Hautmann, M., Bucher, H., 2017. Diversity partitioning in Permian and Early Triassic benthic ecosystems of the Western USA: a comparison. Historical Biology 29, 918–930.

Johns, M.J., Barnes, C.R., Orchard, M.J., 1997. Taxonomy and biostratigraphy of the Middle and Late Triassic elasmobranch ichthyoliths from Northeastern British Columbia. Canadian Government Publishing, Ottawa.

Johnson, G.D., 1981. Hybodontoidei (Chondrichthyes) from the Wichita-Albany group (early Permian) of Texas. Journal of Vertebrate Paleontology 1, 1–41.

Klug, S., Kriwet, J., 2008. A new basal galeomorph shark (Synechodontiformes, Neoselachii) from the Early Jurassic of Europe. Naturwissenschaften 95, 443–448.

Koot, M.B., 2013. Effects of the late Permian mass extinction on chondrichthyan palaeobiodiversity and distribution patterns. Ph.D. thesis, Plymouth University (unpubl.).

Koot, M.B., Cuny, G., Tintori, A., Twitchett, R.J., 2013. A new diverse shark fauna from the Wordian (Middle Permian) Khuff Formation in the interior Haushi-Huqf area, Sultanate of Oman. Palaeontology 56, 303–343.

Koot, M.B., Cuny, G., Orchard, M.J., Richoz, S., Hart, M.B., Twitchett, R.J., 2015. New hybodontiform and neoselachian sharks from the Lower Triassic of Oman. Journal of Systematic Palaeontology 13, 891–917.

Maisey, J.G., 1977. The fossil selachian fishes *Palaeospinax* Egerton, 1872 and *Nemacanthus* Agassiz, 1837. Zoological Journal of the Linnean Society 60, 259–273.

Maisey, J.G., 1989. *Hamiltonichthys mapesi* gen. et sp. nov. (Chondrichthyes; Elasmobranchii), from the Upper Pennsylvanian of Kansas. American Museum Novitates 2931, 1–42.

Martindale, R.C., Foster, W.J., Velledits, F., 2017. The survival, recovery, and diversification of metazoan reef ecosystems following the end-Permian mass extinction event. Palaeogeography, Palaeoclimatology, Palaeoecology 513, 100-115.

Mutter, R.J., 1998a. Tooth variability and reconstruction of dentition in *Acrodus* sp. (Chondrichthyes, Selachii, Hybodontoidea) from the Grenzbitumenzone (Middle Triassic) of Monte San Giorgio (Ticino, Switzerland). Geologia Insubrica 3, 23–31.

Mutter, R.J., 1998b. Zur systematischen Stellung einiger Bezahnungsreste von *Acrodus georgii* sp. nov. (Selachii, Hybodontoidea) aus der Grenzbitumenzone (Mittlere Trias) des Monte San Giorgio (Kanton Tessin, Schweiz). Eclogae Geologicae Helvetiae 91, 513–519.

Mutter, R.J., Rieber, H., 2005. *Pyknotylacanthus spathianus* gen. et sp. nov., a new ctenacanthoid from the Early Triassic of Bear Lake (Idaho, USA). Revista Brasileira de Paleontologia 8, 139–148.

Mutter, R.J., Neuman, A.G., 2006. An enigmatic chondrichthyan with Paleozoic affinities from the Lower Triassic of western Canada. Acta Palaeontologica Polonica 51, 271–282.

Mutter, R.J., Neuman, A.G., 2008. New eugeneodontid sharks from the Lower Triassic Sulphur Mountain Formation of western Canada. In: Cavin, L., Longbottom A., Richter, M. (Eds.), Fishes and the break-up of Pangaea. Geological Society Special Publications (London) 295, 9–41.

Mutter, R.J., De Blanger, K., Neuman, A.G., 2007. Elasmobranchs from the Lower Triassic Sulphur Mountain Formation near Wapiti Lake (BC, Canada). Zoological Journal of the Linnean Society 149, 309–337.

Mutter, R.J., Neuman, A.G., De Blanger, K., 2008. *Homalodontus* nom. nov., a replacement name for *Wapitiodus* Mutter, de Blanger and Neuman, 2007 (Homalodontidae nom.

nov., ?Hybodontoidea), preoccupied by *Wapitiodus* Orchard, 2005. Zoological Journal of the Linnean Society 154, 419–420.

Neuman, A.G., 2015. Fishes from the Lower Triassic portion of the Sulphur Mountain Formation in Alberta, Canada: geological context and taxonomic composition. Canadian Journal of Earth Sciences 52, 557–568.

Orchard, M.J., 2007. Conodont diversity and evolution through the latest Permian and Early Triassic upheavals. Palaeogeography, Palaeoclimatology, Palaeoecology 252, 93–117.

Ovtcharova, M., Goudemand, N., Hammer, Ø., Guodun, K., Cordey, F., Galfetti, T., Schaltegger, U., Bucher, H., 2015. Developing a strategy for accurate definition of a geological boundary through radio-isotopic and biochronological dating: the Early-Middle Triassic boundary (South China). Earth Science Reviews 146, 65–76.

Paull, R.A., Paull, R.K., 1993. Interpretation of Early Triassic nonmarine-marine relations, Utah, U.S.A.. In: Lucas, S.G., Morales, M. (Eds.), The nonmarine Triassic. New Mexico Museum of Natural History and Science Bulletin 3, 403–409.

Pla, C., Márquez-Aliaga, A., Botella, H., 2013. The chondrichthyan fauna from the Middle Triassic (Ladinian) of the Iberian Range (Spain). Journal of Vertebrate Paleontology 33, 770–785.

Raup, D.M., 1979. Size of the Permo-Triassic bottleneck and its evolutionary implications. Science 206, 217–218.

Rees, J., 2008. Interrelationships of Mesozoic hybodont sharks as indicated by dental morphology – preliminary results. Acta Geologica Polonica 58, 217–221.

Rieppel, O., 1981. The hybodontiform sharks from the Middle Triassic of Mte. San Giorgio, Switzerland. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 161, 324–353.

Rieppel, O., Kindlimann, R., Bucher, H., 1996. A new fossil fish fauna from the Middle Triassic (Anisian) of north-western Nevada. In: Arratia, G., Viohl, G. (Eds.), Mesozoic fishes. Systematics and Paleoecology. Dr. Friedrich Pfeil, München, 501–512.

Romano, C., Brinkmann, W., 2010. A new specimen of the hybodont shark *Palaeobates polaris* with three-dimensionally preserved Meckel's cartilage from the Smithian (Early Triassic) of Spitsbergen. Journal of Vertebrate Paleontology 30, 1673–1683.

Romano, C., Kogan, I., Jenks, J., Jerjen, I., Brinkmann, W., 2012. *Saurichthys* and other fossil fishes from the late Smithian (Early Triassic) of Bear Lake County (Idaho, USA), with a discussion of saurichthyid palaeogeography and evolution. Bulletin of Geosciences 87, 543–570.

Romano, C., Jenks. J.F., Jattiot, R., Scheyer, T.M., Bylund, K.G, Bucher, H., 2017. Marine Early Triassic Actinopterygii from Elko County (Nevada, USA): implications for the Smithian equatorial vertebrate eclipse. Journal of Paleontology 97, 1025–1046.

Schaeffer, B., Mangus, M., 1976. An Early Triassic fish assemblage from British Columbia. Bulletin of the American Museum of Natural History 156, 127–216.

Scheyer, T.M., Romano, C., Jenks, J., Bucher, H., 2014. Early Triassic marine biotic recovery: the predators' perspective. PLoS ONE 9, e88987.

Sepkoski, J.J., Jr., 1984. A kinetic-model of Phanerozoic taxonomic diversity 3. Post-Paleozoic families and mass extinctions. Paleobiology 10, 246–267.

Song, H., Wignall, P.B., Chen, Z.-Q., Tong, J., Bond, D.P.G., Lai, X., Zhao, X., Jiang, H., Yan, C., Niu, Z., Chen, J., Yang, H., Wang, Y., 2011. Recovery tempo and pattern of marine ecosystems after the end-Permian mass extinction. Geology 39, 739–742.

Stensiö, E., 1921. Triassic fishes from Spitzbergen 1. Adolf Holzhausen, Wien.

Vázquez, P., Clapham, M.E., 2017. Extinction selectivity among marine fishes during multistressor global change in the end-Permian and end-Triassic crises. Geology 45, 395–398.

Waagen, W., 1895. Salt-Range fossils 2: fossils from the Ceratite Formation 1. Pisces–Ammonoidea. Palaeontologia Indica 13(2), 1–323.

Wemple, E.M., 1906. New cestraciont teeth from the West-American Triassic. University of California Publications, Bulletin of the Department of Geology 5, 71–73.

Yamagishi, H., 2006. Permo-Triassic elasmobranch fauna: diversity, paleobiogeography and recovery after the mass extinction. Ph.D. thesis, University of Tokyo (unpubl.).

Youngquist, W., 1952. Triassic conodonts from southeastern Idaho. Journal of Paleontology 26, 650–655.

Figure captions

Fig. 1. Morphological nomenclature used in the present paper (mostly following Fischer et al. 2010). Mesial is left.

Fig. 2. Teeth t1 to t6 (**a-f**) of IMNH 1143/46168 from the early Spathian (Olenekian, Early Triassic) Paris Biota, Idaho (Bear Lake County), USA. The white arrow in picture 'a' points at the lateral cusplet of the tooth.

Fig. 3. Tooth imprint t7 of UBGD 30567 from the early Spathian (Olenekian, Early Triassic) Paris Biota, Idaho (Bear Lake County), USA.