

Survival of the thinnest: rediscovery of Bauer's (1898) ichthyosaur tooth sections from Upper Jurassic lithographic limestone quarries, south Germany

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Abstract The re-discovery of nine petrographic slides from the late 19th century at the palaeontological collections of the University of Zurich, showing thin-sectioned ichthyosaur teeth, revealed these slides be the only preserved remains of the historical collection of Upper Jurassic ichthyosaurs from the Bavarian State Collection for Palaeontology and Geology; fossil material which, up to now, was thought to have been completely destroyed during World War II. Here the history of these slides, from their origin in Munich as part of the doctoral thesis of Franz Bauer (1898) to their rediscovery in Zurich in 2010 is presented. Furthermore, a complete overview of all slides is given to elucidate their scientific value with the background of up-to-date knowledge of ichthyosaur dentition and tooth histology, including aspects of tissue and growth mark identification. As such, the sectioned teeth show an exposed layer of acellular cementum at the tooth neck, and sets of short and long period growth lines in the orthodentine. The slides of one tooth are part of the original syntype material of *Aegirosaurus leptospondylus* (WAGNER). They reveal an oval rather than a rectangular shape of the root, as well as the presence of peculiar vascular canals,

interpreted as secondary osteodentine deposition, in the peri-pulpal orthodentine.

Keywords History of science · Ichthyopterygia · *Ichthyosaurus trigonus* var. *posthumus* · *Aegirosaurus leptospondylus* · *Nannopterygius* · Orthodentine · Growth increments

Institutional abbreviations

BSPG Bavarian State Collection for Palaeontology and Geology, Munich = Bayerische Staatssammlung für Paläontologie und Geologie, München, Formerly Bayerische Paläontologische Staatssammlung
PIMUZ Paläontologisches Institut und Museum, University of Zurich, Switzerland

Introduction

General introduction

In 2010, a tray with nine petrographic thin-sections of two ichthyosaur teeth was discovered during renovation works in the Palaeontological Institute and Museum of the University of Zurich. From the labels still attached to the slides it was apparent that these slides were part of the doctoral thesis materials of Dr. phil. Franz Bauer in Munich, published in *Palaeontographica* in 1898. Besides the nine slides still preserved (Fig. 1), all other remains of the ichthyosaur specimens figured on plates 25–27 by Bauer (1898) were completely destroyed during World War II (WWII) on the 24–25. April 1944 during a bombing raid of the old Academy building in Munich, which housed the ‘Bayerische Paläontologische Staatssammlung’ (now

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Fig. 1 Photographs of all recovered slides of Bauer (1898). **a1–a8** BSPG AS XIX 504a–h (slides 1–7 and “8”), tooth from the “Oberndorfer specimen”, syntype material of *Aegirosaurus leptospondylus* (WAGNER, 1853) in Wagner (1853a), sectioned transversely and longitudinally. **b** BSPG AS I 1656, longitudinal section of a tooth from the “Solnhofen specimen”, referable to Ichthyosauria indet., aff. *Nannopterygius*

BSPG) at that time. The specimens were stored and displayed in public exhibition then (Dehm 1978). Similarly, all paper documents, including inventory, loan documents, field books, working notes, manuscripts, and theses, were lost to fire.

Bauer’s monograph (1898) work was often cited in the palaeontological literature (e.g. Bauer 1900b; Broili 1907; von Huene 1922; Kuhn 1934; Camp 1942). Especially references to the osteological description of the caudal region and tail fin referred to *Ichthyosaurus trigonus* var. *posthumus* by Bauer (1898) already appeared shortly after the original print in a review by Koken (1901, p. 476), the

monographic work on Triassic ichthyosaurs by Merriam (1908, p. 40), and in palaeobiological textbooks (e.g. Abel 1919, pp. 461, 463). The histological sections of the teeth shown in this work, however, went without further notice for some decades. Peyer (1945) was the first to mention and reproduce part of the histological details, i.e. figure 28 of plate 26, of Bauer (1898), when discussing the presence of minute bore canaliculi of *Mycelites ossifragus* Roux, 1887 (filamentous fungi = “kalkfressende Algen” of Bauer) in ichthyosaur teeth and other vertebrate hard tissues. In the same context, the figure was also reproduced in Peyer’s (1968) book on comparative odontology. Bauer (1898, p. 290) already interpreted the bore canaliculi as secondary disease symptoms instead of primary or post-mortem structures, a view which was validated by microstructural and ultrastructural studies of fungoid lesions in extant fish teeth (Schmidt 1954; Kerebel et al. 1979).

In 1947, Albert Besmer, published a doctoral thesis on the dentition of ichthyosaurs under the supervision of Prof. Bernhard Peyer. For this work, Besmer borrowed the original slides of Bauer (1898) for comparison to his material, which was composed of ichthyosaurs from the Middle Triassic of Monte San Giorgio, Ticino, Switzerland and from the Lower Jurassic (Lias ϵ) of Holzmaden in Baden-Württemberg, southwestern Germany. Although the slides had to be sent to Besmer prior to April 1944, it is unclear in which year exactly the slides were sent to Zurich, because there are no written loan forms or receipts from that time. Besmer, however, in his thesis acknowledged the late Prof. Broili, who apparently was responsible for the loan. Broili retired in 1939 but he was working as a volunteer for the State Collection until 1942, so probably the slides were sent to Zurich before that time. Besmer noted the prolonged time it took to complete his thesis due to obstacles caused by WWII (Besmer 1947, preface on p. 2, p. 7). After 1947, the slides remained first in the “Zoologisch-vergleichend anatomische Institut” and were stored and finally “forgotten” for seven decades in an unnamed drawer of the PIMUZ, which was formally established under that name in 1956.

Besides the two passages mentioned above, Besmer (1947) included two more references to the slides, namely on page 3 (Bauer 1898, plate 26, figs. 28–30) when discussing how Bauer (1898) already identified Kiprijanoff’s (1881) misidentification of bore canaliculi of *Mycelites ossifragus* as larger dentine tubules, as well as on page 11 (Bauer 1898, plate 26, figs. 28–30) when noting the overall similarity of his tooth sections to previously published accounts by Bauer (1898), Fraas (1891), Kiprijanoff (1881) and Owen (1840–1845). The osteological descriptions of Bauer (1898) are furthermore referenced in Bardet and Fernández (2000) and McGowan and Motani (2003), when discussing the assignment of the species studied by Bauer

(see “[Materials and methods](#)” below), but the thin-sections were not, for the reasons described above. Further mention of *Aegirosaurus leptospondylus* (WAGNER) material either in faunal or systematic overviews or in comparison to other material is found in Kuhn (1957, 1961, 1968, 1971), McGowan (1976), Buchy and López Oliva (2009), Maisch (2010), Angst et al. (2010), Fischer (2011) and Fischer et al. (2011). The ichthyosaur material described and figured by Bauer (1898) as “*Ichthyosaurus trigonus* Owen var. *posthumus* Wagner” belongs, according to Bardet and Fernández (2000), to three different specimens, which represent three separate taxa: (1) the ophthalmosaurid *Aegirosaurus leptospondylus* (the Oberndorfer specimen), (2) Ichthyosauria indet. close to *Caypullisaurus* or *Ophthalmosaurus* (the Häberlein specimen), (3) Ichthyosauria indet. aff. *Nannopterygius* (the Solnhofen specimen).

Concerning the Oberndorfer specimen, Bardet and Fernández (2000, p. 510) noted that the “specimen roughly shares the same character combination that the two new skeletons [the specimen in private col. Schwegler, designated as “neotype” and referred to as “SM unnumbered”; and BSPG 1954 I 608, designated as referred specimen by Bardet and Fernández] here described. The specific name *leptospondylus* is thus kept as valid and newly combined to *Aegirosaurus* [...]” Concerning the Solnhofen specimen, they further write that “because of the scarcity of the illustrations given by Bauer (1898) it is not possible to assign the Solnhofen specimen with certainty to this genus [to *Nannopterygius*] and it is thus only considered as an indeterminate ichthyosaur, possibly close to *Nannopterygius*.” (Bardet and Fernández 2000, p. 511).

According to McGowan and Motani (2003, p. 118), *Aegirosaurus leptospondylus* (WAGNER, 1853), originally described in Wagner (1853a) and as described and newly combined by Bardet and Fernández (2000, p. 504), is still valid, and both *Aegirosaurus* BARDET AND FERNÁNDEZ, 2000 from the Solnhofen Formation, Upper Jurassic (Early Tithonian), Bavaria, Germany, and *Nannopterygius* von Huene 1922 from the Kimmeridge Clay; Upper Jurassic (Kimmeridgian), Dorset, UK, belong to Ophthalmosauridae BAUR, 1887.

After 70 years of storage in Zurich (PIMUZ), all slides are again stored in the Bavarian State Collection for Palaeontology and Geology, Munich (BSPG).

Material of the Häberlein specimen, the oldest finding of an Upper Jurassic ichthyosaur, which was already described by Quenstedt (1851–1852), was not sectioned histologically by Bauer (1898), and is not further considered here.

The importance of the rediscovery and notification of some of the oldest, still preserved sections of ichthyosaur teeth from the 19th century, being part of the doctoral thesis documentation on one side and being the sole “survivors” of the original specimens of Upper Jurassic

ichthyosaurs from the Bavarian lithographic limestone quarries stored in Munich on the other, is obvious. Given the fact that eight of these slides belong to the purportedly lost original type material of *Ichthyosaurus leptospondylus* WAGNER, 1853 (Wagner 1853a, b), a note on the taxonomic status of the material is warranted and is in preparation elsewhere. Besides reconstructing the history of the slides, the purpose of this contribution is to give a complete overview of all slides preserved, and to elucidate the value of the slides with the background of up-to-date knowledge of ichthyosaur dentition and tooth histology, including aspects of tissue and growth mark identification.

Biographical data on Bauer and Besmer

Franz Bauer

Franz Bauer (see Electronic Supplementary Material for a more exhaustive biography and bibliography of Franz Bauer) was born in Dollnstein near Solnhofen, studied theology in Eichstätt and worked there as a priest in pastoral care before studying natural sciences in Munich in 1895. He completed a doctoral thesis under Prof. Karl Alfred von Zittel in 1897. From 1901, Bauer had an appointment as associate professor of Geology and Palaeontology at the Chemistry Department, Technical University of Munich. He published several scientific articles and abstracts, including anthropological themes (Bauer 1900a) and three on palaeontological issues (Bauer 1898, 1900b, 1901 [the latter being his postdoctoral/habilitation thesis]), before having a tragic accident in 1903 on the Risserkogel Mountain near Tegernsee, south of Munich.

Albert Besmer

Albert Besmer (1900–1981) was born in Zurich, Switzerland, studied at the Universities of Zurich and Fribourg, and since 1928 worked as a dentist in Zurich. He finished his doctoral thesis under the supervision of Prof. Dr. Bernhard Peyer (Zoological Institute) at the Medical Faculty of the University of Zurich in 1947. To our knowledge, Besmer published only his thesis, for which the original slides from Bauer (1898) were sent to him by Prof. Dr. Ferdinand Broili (1874–1946).

Materials and methods

Slides with petrographic thin-sections

Nine slides with petrographic thin-sections of ichthyosaur teeth were identified as being part of the doctoral thesis materials of Bauer (1898). Previous to this date, the

collection of Upper Jurassic ichthyosaurs from Bavarian lithographic limestone quarries in the ‘Bayerische Paläontologische Staatssammlung’ (now BSPG) was thought to have been completely destroyed during WWII (Dehm 1978).

Eight of the nine slides (Figs. 1a1–a8, 2a) belong to a single ichthyosaur tooth (BSPG AS XIX 504a–h), which was sectioned both transversally through the crown (serial sections: slides 1–7, Fig. 1a1–a7) and longitudinally through the root base (slide originally without number, here referred to as slide “8”, Figs. 1b, 2b, 4). In the original caption to plate 26, Bauer (1898) noted that the transverse sections seen in figures 28–30 belong to a tooth from the Oberndorfer specimen, which is part of the syntype material of *Ichthyosaurus leptospondylus* WAGNER, 1853. Following the discussion of Bardet and Fernández 2000, the longitudinal sections would now be referable to *Aegirosaurus leptospondylus*.

The remaining slide (Figs. 1b, 2b) shows an ichthyosaur tooth (BSPG AS I 1656) longitudinally sectioned from crown to root. The plane of section lays slightly parasagittally, thus the cusp of the crown is missing. Bauer (1898, p. 285) mentioned that figure 27 of plate 26 shows a longitudinal section of a tooth belonging to the Solnhofen specimen, which was excavated at the Maxbruch, Solnhofen, in 1894. According to Bardet and Fernández (2000), this tooth

would be referable to an indeterminate ichthyosaur close to the ophthalmosaurid *Nannopterygius*.

To sum up, BSPG AS XIX 504a–h belongs to the Oberndorfer specimen = *Aegirosaurus leptospondylus*; whereas BSPG AS I 1656 belongs to the Solnhofen specimen = *Nannopterygius*.

Analysis of the slides

The slides were first photographed with a Nikon D2x with Nikkor 105 mm micro lens (Fig. 1). The tooth microstructure was then analysed in normal transmitted and polarized light using a Leica DM2500 M composite microscope mounted with a Leica DFC 420 C digital camera.

Results and discussion

Matching slides and original drawings

Due to the level of detail (especially of the pattern of micro-cracks in the histological tissues) in the drawings of Bauer (1898), it was possible to relocate and match the exact areas (Fig. 3) in the original images of figure 28–30 of plate 26: figure 28 shows part of slide 6; figure 29 part of slide 5 and figure 30 part of slide 4. The planes of

Fig. 2 Overview of microscopic images of all sections. **a1–a8** BSPG AS XIX 504a–h (slides 1–7 and “8”), tooth from the Oberndorfer specimen, referable to *Aegirosaurus leptospondylus*, sectioned transversely and longitudinally. Note resorption pit and remnant of enamel probably belonging to a replacement tooth at lower right margin of root in **a8**. **b** BSPG AS I 1656, longitudinal section of a tooth from the Solnhofen specimen, referable to Ichthyosauria indet. aff. *Nannopterygius*

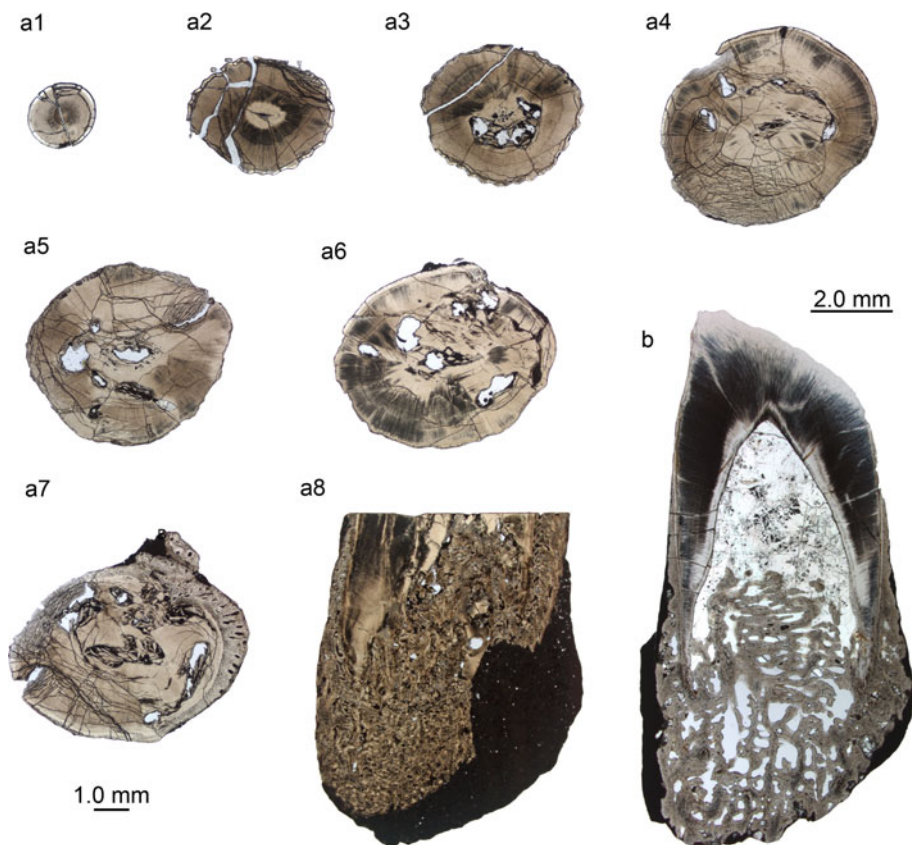
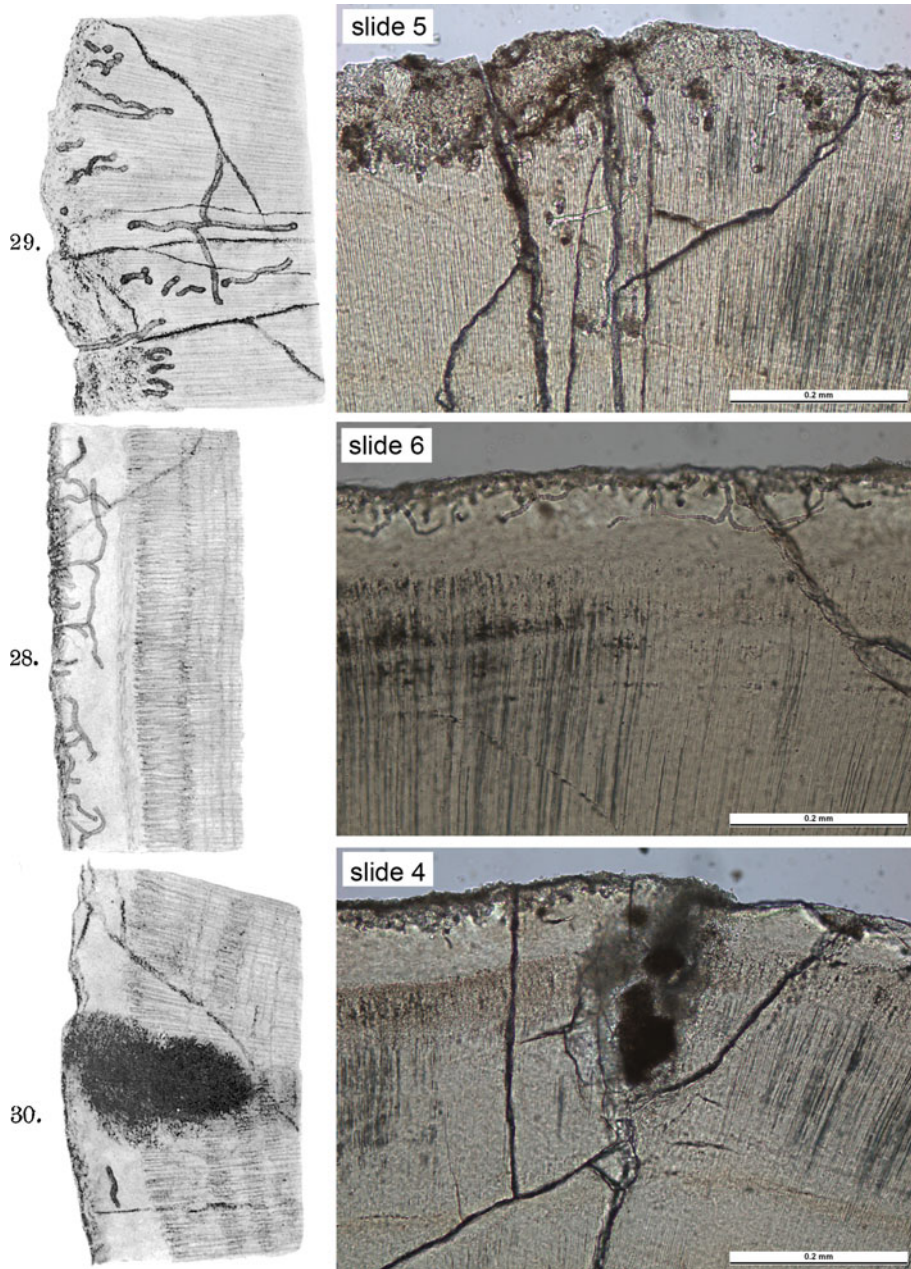


Fig. 3 Matching slides 4–6 (BSPG AS XIX 504d–f) with figs. 28–30 of plate 26 of Bauer (1898); (fig. 28 = slide 6, no. 504f—fig. 29 = slide 5, no. 504e—fig. 30 = slide 4, no. 504d). Note that the new microscopic images (slides 4–6) have been rotated 90° clockwise for technical reasons



sectioning of the figured slides are thus situated at mid-crown height (figures 29, 30) and at the neck of the tooth (figure 28). As such, we can be positively sure that these slides were indeed used to create the original figures. In all three slides, the shown orthodontine and outer enamel layer is in various stages of deterioration due to borings of *Mycelites ossifragus*. Furthermore, it is plausible to assume that the slides 2 and 3 are those Bauer (1898, p. 287) referred to when mentioning the presence of “Furchen” (=grooves) in two cross sections, which were apparently cut 2.0 and 3.0 mm below the tip of the crown of a small ichthyosaur tooth.

The slide with the longitudinal section (Fig. 4) is more difficult to match with the original figure 27 of plate 26 of Bauer (1898), for the following reasons:

1. The image of the sectioned tooth in the figure does not express the same level of detail as seen in figures 28–30 due to the lower level of magnification.
2. The image presents a tooth sectioned exactly through the tip of the crown complete with undamaged borders of the tissues.
3. The image lacks any indication of micro-cracks, changes in coloration of the orthodontine, the enamel

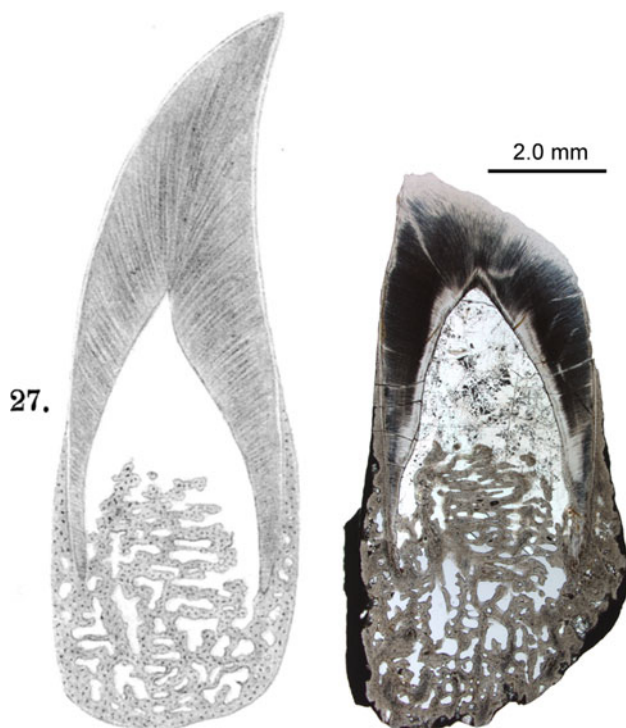


Fig. 4 Matching the longitudinal section (BSPG AS I 1656) (on the left) with fig. 27 of plate 26 of Bauer (1898) (on the right)

or the cementum layers, as well as differences in radicular and pulpal mineral infillings.

The slide on the other hand, shows a similar but not congruent shape and distribution of tissues seen in the image. Otherwise, the crown, as well as complete tissue borders is not visible. The slide furthermore shows histological details such as a pattern of micro-cracks or changes in coloration, which apparently have not been used in the production of the original figure. There are two possibilities: first, the slide is indeed the original on which figure 27 is based, in which case Bauer would have presented a highly stylized, reconstructed depiction of this ichthyosaur tooth, not uncommon at the time of lithographic printing; second, the slide does indeed belong to the sectioned tooth shown by Bauer, but is not the section on which figure 27 is based. In this case, we would have to assume the presence of another section on which the crown might have been completely present, but which, unfortunately, was not preserved. Because the present slide represents the lower section of the tooth only, the second possibility, also less appealing, cannot be ruled out completely.

The slides 1–7 and “8” (BSPG AS XIX 504a–h)

The tip of the crown (slide 1; Fig. 2a1) shows a concentric circular core of orthodontine ringed with a thin layer of

enamel. Enamel striation is absent. The dentine tubules are arranged perpendicular to the outer surface of the tooth; the central tubules extend towards the tip of the crown, whereas the tubules surrounding the central area show the radial arrangement, as seen in the other transverse sections. The junction between enamel and orthodontine is smooth without any dentine infolding.

Slides 2–6 (Fig. 2a2–a6) show an oval shape of the enamel and orthodontine. Coarse striation of the enamel is present in slides 2 and 3. At the enamel-dentine junction a hypomineralised interglobular zone of the orthodontine is visible (Fig. 5a, b). Slides 3 and 5 also reveal the presence of peculiar scattered vascular canals (vaguely reminiscent of primary osteons in bone) in the peri-pulpal orthodontine (Fig. 5c–f). The vascular canals, which appear to be directly connected with the pulp cavity, are here interpreted to have resulted from secondary deposition of pulpal osteodontine, leading to a decrease in size of the pulp cavity in these slides. Based on the scarcity of material, the origin of this osteodontine tissue remains unknown. The other transverse slides did not show similar vascular canals.

Where preserved, slides 4–6 again show a smooth outer enamel layer, as well as a smooth enamel-dentine junction. In slide 7 (Fig. 2a7), a small central core of pulpal cellular osteocementum is surrounded by the orthodontine, which itself is surrounded by cellular osteocementum vascularised by mostly radially oriented canals. At the dentine-cementum junction (Fig. 5g, h) the hypomineralised layer, i.e. the granular layer of Tomes (e.g. Tomes 1876; see also Peyer 1968; Dean 2000), is present. Furthermore, a thin layer of acellular cementum, recently identified for the first time in ichthyosaur teeth, i.e., in *Platypterygius australis* from the Cretaceous of Australia (Maxwell et al. 2011), is also identifiable between the orthodontine and the outer cellular osteocementum. Slide “8” (Fig. 2a8) shows the remainder of the root of the tooth, i.e. dentine surrounded by pulpal and external osteocementum and the thin layer of acellular cementum, in longitudinal section. A resorption pit and a small part of dentine, possibly of a replacement tooth are visible at the lower right margin of the section.

The longitudinal section (BSPG AS I 1656)

On this slide (Figs. 1b, 2b) the root and the neck of the tooth in longitudinal section is preserved. The orthodontine is bordered by pulpal osteocementum and external osteocementum (Fig. 6a, b). As in the transverse sections, a thin layer of acellular cementum lies between the orthodontine and the external cellular cementum (Fig. 6b). The layer extends from the proximal tips of orthodontine up to the neck of the tooth, at which it is exposed as in *P. australis* (Maxwell et al. 2011). The enamel and associated part of the orthodontine of the crown are not preserved on the slide.

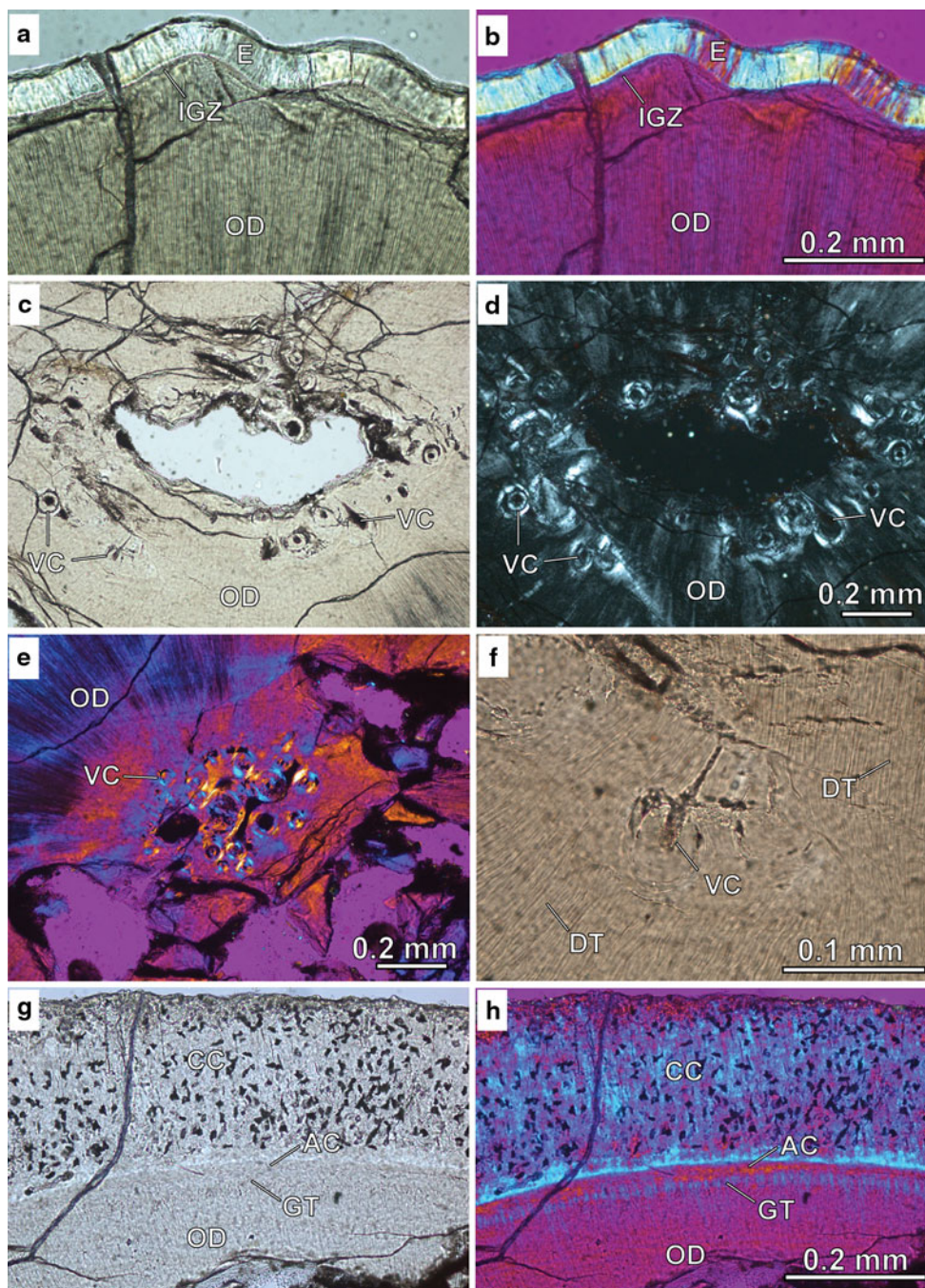


Fig. 5 Histological details of the transverse sections on slides 2, 3, 5, 7 (BSPG AS XIX 504b, c, e, g). **a, c, f** and **g** seen in normal transmitted light, **d**, in polarised light and **b, e** and **h** in polarized light with lambda compensator. **a, b** Close-up of striated enamel and orthodentine (slide 2). Note interglobular zone of dentine at enamel–dentine junction. **c, d** Central pulp area of tooth showing vascular canals in the orthodentine (slide 5). **e** Central area of tooth with vascular canals surrounded by orthodentine (slide 3). **f** Close-up of

vascular canal seen in **c** (slide 5). Note how dentine tubules deviate around the canal. **g, h** Close-up of the cementum–dentine junction at the level of the neck of the tooth (slide 7). Note zones of acellular cementum and the granular layer of Tomes. **AC** acellular cementum, **CC** cellular cementum, **DT** dentine tubules, **E** enamel, **GT** granular layer of Tomes, **IGZ** interglobular zone of orthodentine, **OD** orthodentine, **VC** vascular canals

The pulpal osteocementum reaches up to ca. 1/3 of the pulp cavity. The vascularisation is higher than in the external osteocementum layer. The fibrous arrangement of

the pulpal osteocementum (Fig. 6a) is more ordered (yellow and blue colours in polarised light with Lambda compensator) towards the pulp cavity and grades into an

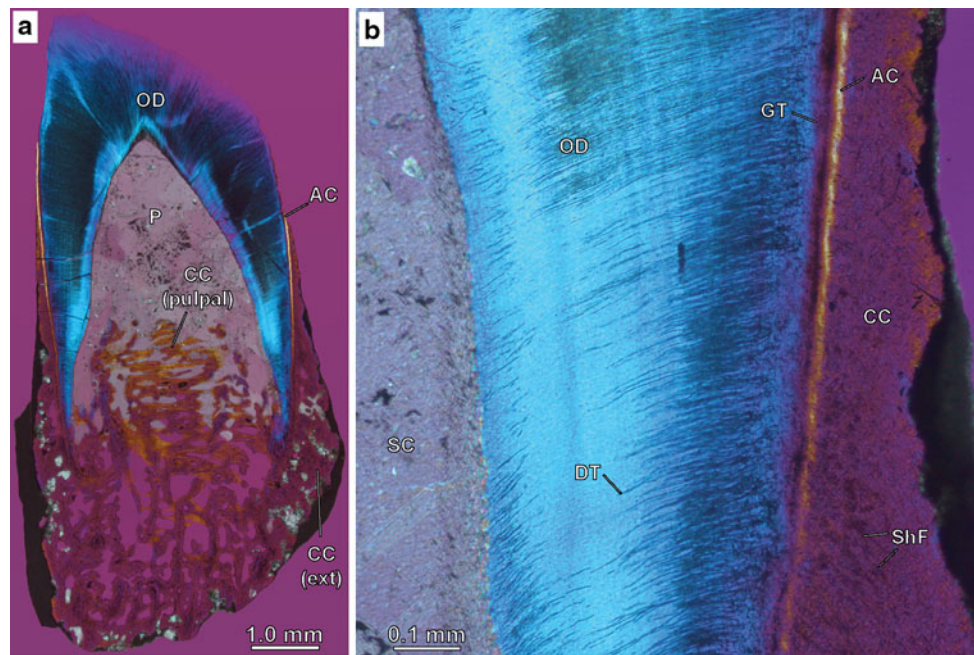


Fig. 6 Histological details of the longitudinal section BSPG AS I 1656. Images in **a** and **b** are both seen in polarized light with lambda compensator. **a** Complete view of the sectioned tooth. At the root the orthodontine (blue colours) is embedded in vascularised pulpal and external cellular cementum of the osteocementum type. Note the differences in structural orientation between the ordered upper pulpal cementum (yellow and blue colours) and the irregular external and basal root cementum (pink colours). At the cementum–dentine

junction, a thin layer of acellular cementum is visible (yellow colour). **b** Close-up of the orthodontine pillar. Coarse parallel Sharpey's fibres are visible in the external cellular osteocementum. The orthodontine shows a weak banding often obscured by dark dentine tubules. The pulp cavity is filled with sparitic calcite minerals. AC acellular cementum, CC cellular cementum, DT dentine tubules, GT granular layer of Tomes, OD orthodontine, P pulp cavity, SC sparitic calcite, ShF Sharpey's fibres

unordered diffuse tissue towards the root base (pink colour). Similarly the external osteocementum has an unordered structure (pink colour). The external border of both the pulpal and external osteocementum is irregular due to cavities and canals. Furthermore, coarse parallel Sharpey's fibres are present in the external osteocementum at the tooth neck (Fig. 6b), whereas they appear less ordered and conspicuous in the root base. The Sharpey's fibres are the remnants of the non-mineralised periodontal ligament anchoring the cementum to the periradicular bone in the living animal.

Incremental growth in dentine

In both the transverse and longitudinal sections of both teeth sectioned by Bauer (1898), incremental growth marks of the orthodontine can be identified in polarized light (Fig. 7), although they are often obscured by the dentine tubules, micro-cracks or diagenetic colouration. In the transverse sections, the markings appear as sub-circular light and dark banded rings in polarised light, whereas they appear as light and dark band lines in longitudinal sections, paralleling the outer dentine border. The lines can be separated into two sets (Fig. 7), a very fine short period line set where the spaces between lines varies around 2–3 μm

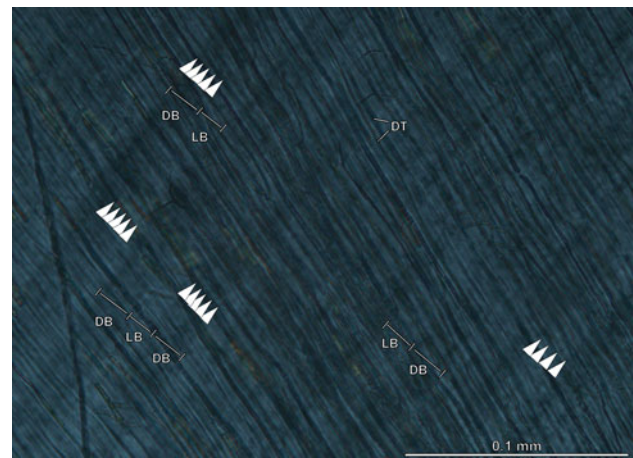


Fig. 7 Detail of the orthodontine showing incremental lines of growth in polarised light in the longitudinal section (BSPG AS I 1656, Ichthyosauria indet. aff. *Nannopterygius*). Two sets of incremental lines are visible: the first set is composed of very fine dark and light lines (indicated by arrow heads), interpreted as daily lines of von Ebner. The second set consists of broader dark and light bands, indicating longer time periods, i.e. Andresen lines. DB dark band, DT dentine tubules, LB light band

(=0.002–0.003 mm) and a coarser, long period line set where spaces vary around 15–20 μm (=0.015–0.02 mm). This is in contrast to the findings of Maxwell et al. (2011),

who did not find evidence for incremental lines in the orthodentine of *P. australis*.

As discussed by Dean (1998, 2000) it is much debated how to identify the incremental growth marks in dentine, so that similarly spaced lines might be interpreted either as long or short period lines by different authors. Dean (1998, fig. 7) showed that in human dentine seven to eight short period lines (i.e. daily lines von Ebner spaced $<3 \mu\text{m}$ apart; after von Ebner 1902, 1906) are situated between long period lines of Andresen (after Andresen 1898), which are spaced approximately $20 \mu\text{m}$ apart. In reptiles, Erickson (1996a), when studying the dentine deposition in juvenile *Crocodylus mississippiensis* using double fluorochrome staining, found daily growth lines of von Ebner in the crocodylian dentine similar to those found in most mammals. Erickson (1996b: p. 14625) also described the presence of lines of von Ebner in dinosaur teeth, and noted that: “dinosaur incremental line widths revealed a range of $6\text{--}28 \mu\text{m}$ and mean values ranging from 10.1 to $19.8 \mu\text{m}$...” with a “...general increase in incremental line widths through ontogeny in the taxa for which multiple age specimens were available”, leading to calculated tooth replacement rates in dinosaurs between 46 and 777 days. Following Erickson’s (1996b) approach, Sereno et al. (2007) and D’Emic et al. (2009) calculated even higher tooth replacement rates for sauropod dinosaurs, based on counts of lines of von Ebner. Both works, however, did not explicitly discuss Dean’s (1998, 2000) articles and the possibility that the growth lines found in the sauropod teeth might also present long period lines instead of daily increments, in which case the replacement rate in sauropod dinosaurs would increase significantly. Based on the two sets of lines found in Bauer’s (1898) slides, we follow Dean (1998, 2000) in identifying the finer set of growth lines as lines of von Ebner, whereas the coarser set of growth lines (or rather bands) are tentatively referred to as long period Andresen lines.

The shape of ichthyosaur teeth in cross-section

Bardet (1990), who analysed characteristic dental cross-sections, indicated that a circular shape of the crown and a quadrangular outline in the lower part of the tooth root apparently unites all Cretaceous ichthyosaurs. Later, Maxwell and Caldwell (2006) noted that not only the Cretaceous *Platypterygius* and *Maiaspondylus* possess this character, but also the Upper Jurassic *Brachypterygius*, whereas the character state remained unknown in the Upper Jurassic *Aegirosaurus*. Given the fact that the series of transverse sections can be referred to *Aegirosaurus leptospondylus* (sensu Bardet and Fernández 2000), this character can also be addressed in the serial transverse sections on slides 1–7 and the longitudinal section of slide

“8”: the sections indicate that, while the crown has a circular outline, the root of the sectioned tooth did not have a quadrangular but an oval outline.

Regarding the second tooth (possibly aff. *Nannopterygius*, according to Bardet and Fernández 2000), Bauer (1898) discussed the sub-quadratic shape of the root (the shape of the external cementum) and refers to his plate 26, figure 27. Without knowing the original outer shape of the second tooth, however, the preserved longitudinal section does not yield the information necessary to address the shape of the root for this taxon.

Conclusions

Despite their advanced age, the slides prepared for Bauer’s (1898) dissertation, are in exceptionally good condition. All histological features of the ichthyosaur teeth could be studied in the slides and all slides were matched with the original figures and descriptions of Bauer. Following Bardet and Fernández (2000), the transversely sectioned tooth (slides 1–“8”; BSPG AS XIX 504a–h) belongs to the ophthalmosaurid *Aegirosaurus leptospondylus*, whereas the longitudinally sectioned tooth is derived from an indeterminate ichthyosaur close to the ophthalmosaurid *Nannopterygius*. Studying the slides with up-to-date knowledge of ichthyosaur dentition and tooth histology further led to the recognition of an exposed layer of acellular cementum (sensu Maxwell et al. 2011) at the tooth neck, and daily and long period growth lines in the orthodentine in both specimens. Some slides of the tooth of *A. leptospondylus* furthermore revealed a more oval than rectangular shape of the root and the presence of peculiar vascular canals, interpreted as secondary osteodentine deposition, in the peri-pulpal orthodentine. It is therefore documented that dental characters of advanced ichthyosaurs are taxonomically useful for distinguishing at least the genera.

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References

- Abel, O. (1919). *Die Stämme der Wirbeltiere* (914 pp.). Berlin: Vereinigung wissenschaftlicher Verleger Walter de Gruyter & Co.

- Andresen, V. (1898). Die Querstreifung des Dentins. *Deutsche Monatsschrift für Zahnheilkunde, Sechzehnter Jahrgang (Leipzig)*, 38, 386–389.
- Angst, D., Buffetaut, E., Tabouelle, J., & Tong, H. (2010). An ichthyosaur skull from the Late Jurassic of Svalbard. *Bulletin de la Société Géologique de France*, 181, 453–548.
- Bardet, N. (1990). Dental cross-sections in Cretaceous Ichthyopterygia: Systematic implications. *Geobios*, 23, 169–172.
- Bardet, N., & Fernández, M. (2000). A new ichthyosaur from the Upper Jurassic lithographic limestones of Bavaria. *Journal of Paleontology*, 74, 503–511.
- Bauer, F. (1898). Die Ichthyosaurier des oberen weissen Jura. *Palaeontographica*, 44, 283–328.
- Bauer, F. (1900a). Über den Schwund der Diploe an einem Philippinenschädel. *Anatomischer Anzeiger*, 17, 58–62.
- Bauer, F. (1900b). Osteologische Notizen über Ichthyosaurier. *Anatomischer Anzeiger*, 18, 574–588.
- Bauer, F. (1901). *Ichthyosaurus bambergensis* sp. nov.—Beschreibung einer neuen *Ichthyosaurus*-Art aus dem oberen Lias von Geisfeld, nebst einigen vergleichend-anatomischen Bemerkungen über den Schultergürtel. *Bericht der Naturforschenden Gesellschaft in Bamberg*, 18, 1–56.
- Baur, G. (1887). Ueber den Ursprung der Extremitäten der Ichthyopterygia. *Berichte über die Versammlungen des Oberrheinischen Geologischen Vereines*, 20, 17–20.
- Besmer, A. (1947). Die Triasfauna der Tessiner Kalkalpen. XVI. Beiträge zur Kenntnis des Ichthyosauriergebisses. *Abhandlungen der schweizerischen Paläontologischen Gesellschaft*, 65, 1–21.
- Broili, F. (1907). Ein neuer *Ichthyosaurus* aus der norddeutschen Kreide. *Palaeontographica*, 54, 139–152.
- Buchy, M.-C., & López Oliva, J. G. (2009). Occurrence of a second ichthyosaur genus (Reptilia: Ichthyosauria) in the Late Jurassic Gulf of Mexico. *Boletín de la Sociedad Geológica Mexicana*, 61, 233–238.
- Camp, C. L. (1942). Ichthyosaur rostra from central California. *Journal of Paleontology*, 16, 362–371.
- D'Emic, M. D., Whitlock, J. A., Smith, K. M., Wilson, J. A., & Fisher, D. C. (2009). The evolution of tooth replacement rates in sauroptid dinosaurs. *Journal of Vertebrate Paleontology*, 84A (SVP Program and Abstracts Book).
- Dean, M. C. (1998). Comparative observations on the spacing of short-period (von Ebner's) lines in dentine. *Archives of Oral Biology*, 43, 1009–1021.
- Dean, M. C. (2000). Incremental markings in enamel and dentine: what they can tell us about the way teeth grow. In M. F. Teaford, M. M. Smith, & M. W. J. Ferguson (Eds.), *Development, Function and Evolution of Teeth* (pp. 119–130). Cambridge: Cambridge University Press.
- Dehm, R. (1978). Zur Geschichte von Bayerischer Staatssammlung und Universitäts-Institut für Paläontologie und historische Geologie in München. *Mitteilungen der Freunde der Bayerischen Staatssammlung für Paläontologie und historische Geologie, Sonderabdruck, München*, 1978(6), 13–46.
- Erickson, G. M. (1996a). Daily deposition of dentine in juvenile *Alligator* and assessment of tooth replacement rates using incremental line counts. *Journal of Morphology*, 228, 189–194.
- Erickson, G. M. (1996b). Incremental lines of von Ebner in dinosaurs and the assessment of tooth replacement rates using growth line counts. *Proceedings of the National Academy of Sciences USA*, 93, 14623–14627.
- Fischer, V. (2011). New data on the ichthyosaur *Platypterygius hercynicus* and its implications for the validity of the genus. *Acta Palaeontologica Polonica* (in press). doi:10.4202/app.2011.0007.
- Fischer, V., Clément, A., Guiomar, M., & Godefroit, P. (2011). The first definite record of a Valanginian ichthyosaur and its implications on the evolution of post-Liassic Ichthyosauria. *Cretaceous Research*, 32, 155–163.
- Fraas, E. (1891). *Die Ichthyosaurier der süddeutschen Trias- und Jura-Ablagerungen* (81 pp.). Tübingen: Laupp'sche Buchhandlung.
- Kerebel, B., Le Cabellec, M.-T., & Kerebei, L.-M. (1979). Structure and ultrastructure of intra-vitam parasitic destruction of the external dental tissue in the fish, *Anarhichas lupus* L. *Archives of Oral Biology*, 24, 147–153.
- Kiprijanoff, W. (1881). Studien über die fossilen Reptilien Russlands. I. Theil. Gattung *Ichthyosaurus* König. *Mémoires de l'Académie des Sciences de St.-Petersbourg, VIIe Série*, 28(8), 1–103.
- Koken, E. (1901). Fr. Bauer: Die Ichthyosaurier des oberen weissen Jura. (Palaeontogr. 44. 1898. 283–328. 3 Taf.). *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, II. Referate*, 1901, 476.
- Kuhn, O. (1934). Ichthyosauria. In W. Quenstedt (Ed.), *Fossilium Catalogus. I: Animalia. Pars 63* (75 pp.). Berlin: W. Junk.
- Kuhn, O. (1957). *Das Solnhofenbuch. Entstehung und Lebewelt der fränkischen Lithographieschiefer* (46 pp.). Bamberg: Bayerische Verlagsanstalt.
- Kuhn, O. (1961). *Die Tier- und Pflanzenwelt des Solnhofener Schiefers. Mit vollständigem Arten- und Schriftenverzeichnis*. *Geologica Bavarica*, 48 (68 pp.). Munich: Bayerisches Geologisches Landesamt.
- Kuhn, O. (1968). Franks Bedeutung für die Saurierforschung (Paläoherpetologie). *Bericht der Naturforschenden Gesellschaft Bamberg*, 42, 13–26.
- Kuhn, O. (1971). *Die Tierwelt des Solnhofener Schiefers. 3., neu bearbeitete Auflage. Die Neue Brehm-Bücherei*, 318 (119 pp.). Wittenberg: A. Ziemsen.
- Maisch, M. W. (2010). Phylogeny, systematics, and origin of the Ichthyosauria—the state of the art. *Palaeodiversity*, 3, 151–214.
- Maxwell, E. E., & Caldwell, M. W. (2006). A new genus of ichthyosaur from the Lower Cretaceous of western Canada. *Palaeontology*, 49, 1043–1052.
- Maxwell, E., Caldwell, M. W., & Lamoureux, D. O. (2011). Tooth histology in the Cretaceous ichthyosaur *Platypterygius australis*, and its significance for the conservation and divergence of mineralized tooth tissues in amniotes. *Journal of Morphology*, 272, 129–257.
- McGowan, C. (1976). The description and phenetic relationships of a new ichthyosaur genus from the Upper Jurassic of England. *Canadian Journal of Earth Sciences*, 13, 668–683.
- McGowan, C., & Motani, R. (2003). Ichthyopterygia. *Handbuch der Paläoherpetologie [Handbook of Paleoherpetology]*, 8, 1–173.
- Merriam, J. C. (1908). Triassic Ichthyosauria, with special reference to the American forms. *Memoirs of the University of California*, 1, 1–155.
- Owen, R. (1840–1845). *Odontography or a treatise on the comparative anatomy of the teeth, their physiological relations, mode of development, and microscopic structure in the vertebrate animals. Volume I, Text & Volume II, Atlas* (665 pp. & 150 plates). London: Hippolyte Bailliere.
- Peyer, B. (1945). Über Algen und Pilze in tierischen Hartschubstanzen. *Archiv der Julius Klaus-Stiftung. Ergänzungsband zu Bd. XX, 1945 [Festschrift für Prof. Dr. Alfred Ernst]*, 496–546. (Zürich: Art. Institut Orell Füssli A.-G.).
- Peyer, B. (1968). *Comparative Odontology* (458 pp.). Chicago: University of Chicago Press.
- Quenstedt, F. A. (1851–1852). *Handbuch der Petrefaktenkunde* (792 pp.). Tübingen: H. Laupp.
- Roux, W. (1887). Über eine im Knochen lebende Gruppe von Fadenpilzen (*Mycelites ossifragus*). *Zeitschrift für wissenschaftliche Zoologie*, 45, 227–254.

- Schmidt, W. J. (1954). Über Bau und Entwicklung der Zähne des Knochenfisches *Anarrhichas lupus* L. und ihren Befall mit "Mycelites ossifragus". *Zeitschrift für Zellforschung*, 40, 25–48.
- Sereno, P. C., Wilson, J. A., Witmer, L. M., Whitlock, J. A., Maga, A., Ide, O., & Rowe, T. A. (2007). Structural extremes in a Cretaceous dinosaur. *PLoS ONE*, 2(11), e1230, 1–9. doi: [10.1371/journal.pone.0001230](https://doi.org/10.1371/journal.pone.0001230).
- Tomes, C. S. (1876). *A Manual of Dental Anatomy: Human and Comparative* (406 pp.). London: J. & A. Churchill.
- von Ebner, V. (1902). Histologie der Zähne mit Einschluss der Histogenese. In J. Scheff (Ed.), *Handbuch der Zahnheilkunde* (pp. 243–299). Vienna: A. Holder.
- von Ebner, V. (1906). Über die Entwicklung der leimgebenden Fibrillen, insbesondere im Zahnbein. *Sitzungsberichte der Mathematisch-Naturwissenschaftlichen Klasse der Kaiserlichen Akademie der Wissenschaften in Wien*, 115(Abteilung 111), 281–347.
- von Huene, F. (1922). *Die Ichthyosaurier des Lias und ihre Zusammenhänge* (VIII + 114 pp.) Berlin: Gebrüder Borntraeger.
- Wagner, A. (1853a). Die Charakteristik einer neuen Art von *Ichthyosaurus* aus den lithographischen Schiefen und eines Zahnes von *Polyptychodon* aus dem Grünsandsteine von Kelheim. *Gelehrte Anzeigen der königlich bayerischen Akademie der Wissenschaften*, 36(3), 25–32.
- Wagner, A. (1853b). Beschreibung einer fossilen Schildkröte und etlicher anderer Reptilien-Überreste aus den lithographischen Schiefen und dem grünen Sandstein von Kehlheim. *Abhandlungen der mathematisch-physikalischen Classe der königlich bayerischen Akademie der Wissenschaften*, 7(1. Abtheilung), 239–264.