

Microstructural characteristics and seasonal growth patterns observed in *Metoposaurus krasiejowensis* teeth

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The tooth microstructure of *Metoposaurus krasiejowensis* was studied to observe external morphology, internal microstructure (comprising dentine structure and directional porosity as possible predatory adaptations) and enamel/enameloid mineral composition. Scanning electron microscopy (SEM) observation and thin-section inspection by light microscope enabled us to recognize a directional porosity in the tooth cross-sections, interpreted here as a part of the labyrinthodont structure displayed by temnospondyls and related groups. This network of canals is highly complicated and reveals a three-dimensional structure. The teeth present different cross-sections based on the distance from the tip, with a wide, circular, reinforced base and lateral compressed, directional cuspidal section with cutting edge. Interestingly, the internal structure observed in *M. krasiejowensis* teeth exhibit a peculiar variation of internal structure of temnospondyl teeth, as the convoluted canal-like structure seems to be irregular and appears in the upper section of teeth, while teeth bases show a regular structure with a pulpal cavity circled by pores. Furthermore, bands of incremental growth marks interpreted as Andresen lines, characterized by pronounced colour variation, were observed with strong implications for seasonal growth patterns in dentine. Additionally, a significant proportion (1.43–2.73%) of fluoride was observed as a component of enamel by scanning electron microscopy–energy dispersive spectroscopy (SEM–EDS) point and mapping analyses, suggesting a fluorapatite mineralogy of enamel.

Key words: *Metoposaurus*, Krasiejów, teeth, adaptations, growth lines, fluorapatite.

INTRODUCTION

Due to their preservation potential, teeth are among the most frequently found fossils. They are often found loose in a deposit, away from a skeleton and sometimes comprise the only evidence of an occurrence of a given vertebrate taxon in the fossil record. Thus, teeth themselves can serve as a useful tool for taxonomic, stratigraphic and palaeoenvironmental studies (e.g., [Enault et al., 2015](#); [Hättig et al., 2019](#); [Wierzbowski et al., 2019](#); [Pawlak et al., 2022](#)). Particular attention in palaeontological studies is placed on teeth belonging to taxa with unclear affinities, because careful study of tooth microstructure may provide valuable data concerning cladistic relationships among many extinct vertebrates (e.g., [Carlson, 1990](#)). This especially concerns the clade of temnospondyls which is the most diverse group of early tetrapods, still problematic as regards systematic classification (e.g., [Laurin and Reisz, 1999](#); [Ruta et al., 2007](#); [Schoch, 2013](#)).

In general, studies of teeth can be divided into those of tooth morphology, of their internal (micro)structure and of biomineralization. Tooth biomineralization, including its structure and chemical enamel/enameloid composition, is still researched, especially in fossil taxa. This issue is particularly interesting in early tetrapods, which include the extinct temnospondyls. The type of bioapatite that makes up enamel in tetrapods allows us to trace the evolutionary lineages of vertebrates and their affinities as well as to track diagenetic changes ([Keenan, 2016](#)). So far, studies on biomineralization of enamel/enameloid have revealed that modern Lissamphibia exhibit partially fluoroapatitic enameloid in life ([Fincham et al., 1999](#)).

Temnospondyl remains are one of the groups of fossils which are characterized by their internal folding, comprising a network of canals inside the teeth, and termed labyrinthodont structure or plicidentine ([MacDougall et al., 2014](#)). This trait is sported by lobe-finned fish and temnospondyls, among other groups, functioning as internal support for the teeth ([Romer and Parsons., 1986](#)), by transporting exterior pressures through the whole volume of the teeth. Temnospondyl tooth structure has been extensively studied in the past ([Owen, 1842](#); [Pander, 1860](#); [Credner, 1893](#); [Bystrow, 1938, 1939](#); [Parsons and Williams, 1962](#); [Chase, 1963](#); [Peyer, 1968](#); [Schultze, 1969](#); [Warren and Davey, 1992](#); [Warren and Turner, 2005](#); [Rinehart and Lucas, 2014](#)). Since the times of [Owen \(1842\)](#), who described

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the folded structure of *Mastodontosaurus* (described by him under the name of *Labyrinthodon jaegeri*) the subject of labyrinthodont structure has fascinated many palaeontologists. It was further explored by Credner (1893), who described the structure of primitive tetrapod teeth in detail, exploring the characteristics of dentine, enamel and dental pulp. Bystrow (1938, 1939), studied the variation of internal dental structure of labyrinthodonts, discovering that the internal porosity is correlated with tooth age and maturity. Chase (1963) described the primitive condition of labyrinthodont dentition as a relatively small number of teeth on the marginal tooth row of the premaxilla and maxilla, with a stout tusk pair and number of denticles on the palate. Schultze (1969) worked on the variation within the main groups of vertebrates with folded teeth, creating a classification of folded teeth of labyrinthodonts with three types: dendrodont, eusthenodont and polyplacodont. Warren and Davey (1992) described the internal structure of *Metoposaurus* sp. teeth, discovering that small vomerine teeth are characterized by a lesser number of infolds than massive palatal tusks. They also noted that, generally, infolding rate increases with the size of the teeth.

The material studied here are teeth derived from one cranium of *Metoposaurus krasiejowensis* Sulej, 2002, obtained for research by courtesy of Prof. Jagt-Yazykova (Opole University). The species studied represents the Late Triassic metoposaurid temnospondyl, widespread around the world (Fraas, 1913; Chowdhury, 1965; Dutuit, 1976; Sengupta, 1992; Hunt, 1993; Jalil, 1996). While the general morphology of *M. krasiejowensis* is well recognized (Sulej, 2007), current research focuses on exploring histological and biomechanical aspects of the anatomy (Konietzko-Meier and Sander, 2013; Gruntmejer et al., 2016; Teschner et al., 2018; Antczak and Bodzioch, 2018; Gruntmejer et al., 2019). A distinctive skull with a compressed anterior segment and rich skin ornamentation, equipped with an impressive set of teeth and multiple rows of predatory denticles (Konietzko-Meier and Wawro, 2007), makes this taxon a graceful subject for biomechanical, palaeoecological or histological studies, also in terms of tooth structure studies. The material studied, yielded from an extinct species, provides a unique opportunity, since in many modern

amphibian taxa there has been a reduction in dentition (Paluh et al., 2021), sometimes complete, in adult forms. This condition arises because the teeth of modern amphibians are not used for grinding food, which is swallowed whole with the help of strong palatal muscles, as in toads. In this research, the general dental microstructure and histology of *M. krasiejowensis* are explored in an order to infer possible mechanical shape adaptations for predatory behaviour, while the incremental growth lines visible in cross-sections are examined as a possible indicator of seasonal influence on this taxon's biology. Furthermore, the analysis of enamel (*sensu* Rinehart and Lucas, 2014) chemical composition, was carried out to assess whether the teeth studied show specific features, such as possible biofluorapatite enamel.

GEOLOGICAL BACKGROUND

The fossil material was originally acquired at the Krasiejów palaeontological site (50°39'54" N, 18°16'33" E), a former open clay pit located in the village of the same name (gmina Ozimek, Opole county, Opolskie voivodship; Fig. 1) and then housed at Opole University. The Krasiejów Lagerstätte is a well-known site in southwestern Poland, renowned for its varied assemblage of Upper Triassic vertebrate fossils. The first lithostratigraphic description was by Bilan (1976), who named the Grabowska Formation, of Rhaetian age, from the Olkusz-Chrzanów region. The most recent description of the lithostratigraphy of Krasiejów is by Szulc and Racki (2015) who assigned the deposits exposed in the quarry to the Patoka Member of the Grabowa Formation. This fossil lagerstätte was described as an accumulation of vertebrate fossils by Dzik et al. (2000). The Krasiejów clay pit is characterized by deposits of the Upper Silesian Keuper in the form of variegated clays and mudstones, often marly, with bodies of sandstone and conglomerate. Most importantly, it represents the only exposure of the Krasiejów bone-bearing horizon (Szulc and Racki, 2015) with its unique vertebrate assemblage.

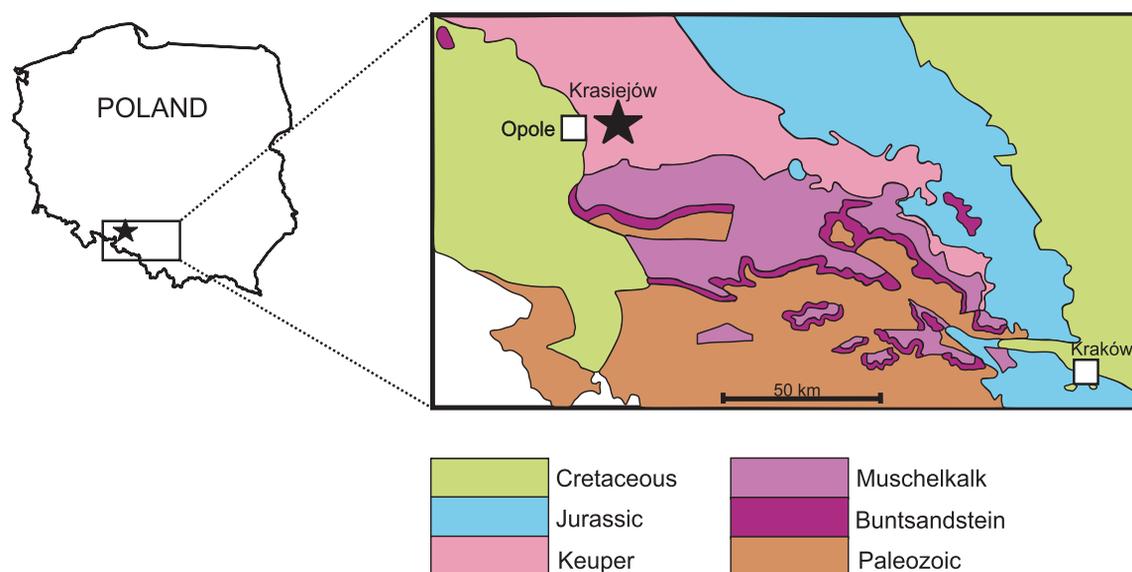


Fig. 1. Location of Krasiejów and simplified geological sketch of the area (after Dadlez et al., 2000 and Antczak and Bodzioch, 2018)

The Krasiejów assemblage biota the Metoposauridae, Captiosauria, Phytosauria, Lepidosauria and Aetosauridae families, and Archosauromorpha and Dinosauromorpha groups (Dzik, 2003; Sulej, 2005; Dzik and Sulej, 2007, 2016). Other reported vertebrate taxa include ganoid fish (Kowalski et al., 2019).

There is a general scientific consensus that the Krasiejów deposits represent a hot seasonal climate, with dry and wet seasons (Reinhardt and Ricken, 2000; Fijałkowska-Mader et al., 2015). The first interpretation of the sedimentary setting, by Bilan (1976), proposed a brackish basin environment. Dzik et al. (2000) suggested lacustrine deposition, with bone accumulation in the river delta system as a possible sedimentary setting.

By contrast, Szulc (2005) proposed dry or semi-dry conditions with episodic surface runoff as a sedimentary environment of the Patoka Member with palaeosol development at times of lower fluvial activity. Further research suggested sedimentary conditions as Szulc described (Gruszka and Zieliński, 2008; Bodzioch and Kowal-Linka, 2012). The most recent sedimentary description recognized three facies in the Carnian-Rhaetian interval: floodplain-gilgai, playa and fluvial deposits, of which Krasiejów was assigned to the first one (Jewuła et al., 2019).

Based on the presence of palygorskite, it was inferred that the area included small ephemeral ponds (Środoń et al., 2014). Lately, Jewuła et al. (2019) distinguished three lithologies encompassing the Patoka Member, as follows: massive conglomerates dominated by pedogenic nodules; massive mudstones with mm-scale calcareous clasts/nodules supported in a mud matrix; and mudstones with internal convolutions.

MATERIAL AND METHODS

A skull of *M. krasiejowensis* was obtained from the Department of Paleobiology, Opole University archival collection. The skull consisted of a separated cranium encased in a block of claystone. The monolith that contained the skull comprised fine-grained clay and marly silty mudstone with a minor sand admixture. Based on the Patoka Member lithology characterized by Jewuła et al. (2019), the monolith matrix can be described as massive mudstone with minor calcareous nodules. Following preparation, the skull sample was found to be strongly fractured and deformed, with an asymmetrical central axis (Fig. 2). The posterior ventral bones of the skull are much better preserved than the anterior ones, especially of the dorsal part. The poor preservation can be attributed to the enclosing lithology, as according to Sulej (2007) the best specimens can be found in calcareous concretions.

The tooth samples were acquired by disintegration of the matrix around the palatal tooth row (Fig. 2), and by water-washing material through a sieve. The marginal dental row was very poorly preserved, which prohibited sampling of the teeth for study. Ten teeth were sampled for this study, six for thin-section and four for SEM observations. The dental material was cut in the transverse plane and cleaned to get samples for examination, at the Institute of Geological Sciences of the Jagiellonian University in Kraków. Six teeth were cut into 30 mm sections and impregnated with resin in thin-sections. The samples were examined under a transmitted light microscope fitted with a Nikon Eclipse E600-POL camera, which enabled high-resolution photos to be taken. Thin-sections were examined at 25x and 100x magnification to observe the microstructure.



Fig. 2. Ventral view of the *M. krasiejowensis* cranium which provided the sample teeth, with locations of sampled teeth highlighted

The other tooth material, for electron microscopy, was examined using a HITACHI S-4700 scanning electron microscope with NORAN Vantage microanalysis system, which provided high-resolution observations, mainly of tooth topography and general morphology, along with EDS analysis in order to assess the chemical composition of the enamel. Well-preserved enamel was identified in samples T1 and T2. Point element analysis was run on sample T1, characterized by enamel preserved in the horizontal plane, along with mapping of the dentine layer. Sample T2 was mapped to assess the extent of lateral tooth surface with preserved enamel.

RESULTS

THIN-SECTIONS

The light microscope thin-section observations encompassed the upper sections of the teeth studied. In general, they are oval in cross-section with slight lateral compression, and taper towards a defined anterior cutting edge. These observations show a clear distinction between an outer laminated dentine layer, and massive, non-laminated internal dentine intertwinning with a pulp cavity, which is very spacious and shows signs of remineralization in all samples. The internal porosity of the teeth appears to be directional, with pores occupying more area away from the cutting edge. The samples feature a prominent network of winding internal canals, partially recrystallized (Fig. 3). The enamel layer is very thin. The internal structure shows signs of vascularization, preserved as small filaments of different coloration, which correspond to minor capillaries, meeting in larger pores that correspond to larger blood vessels (Fig. 4). Another characteristic feature is black-dotted structures interpreted here as preserved odontoblasts. The most prominent features are bands of differing colours present in the dentine layer, identified here as incremental growth lines (see Erickson, 1996; Dean, 2000; Fig. 5A, B). The teeth show an average of 7 or 8 different colour bands (Fig. 5C, D) in the outer dentine layer. Each generation of growth is characterized by deposition of a thinner dentine layer. Individual colour bands measure 20 to 100 μm and are of irregular shape, possibly as a re-

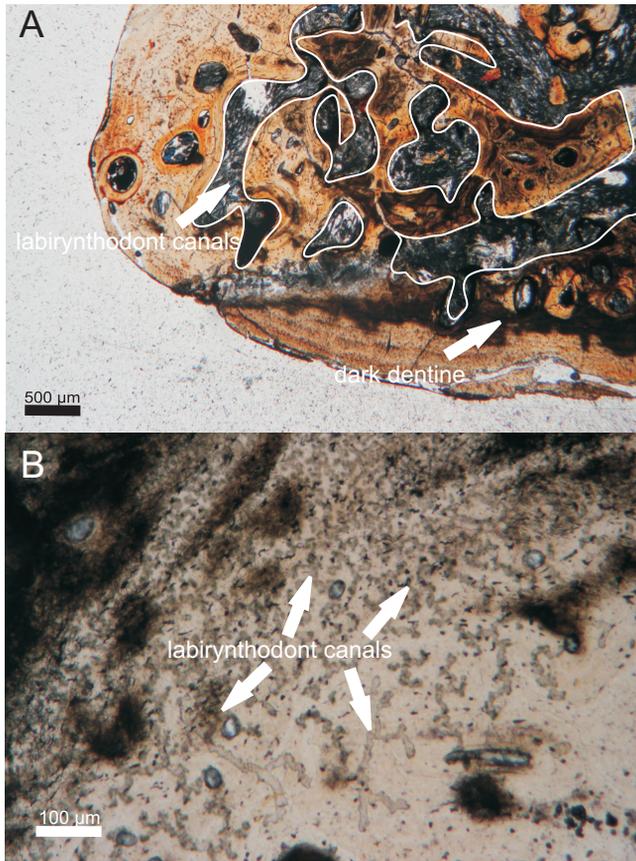


Fig. 3. Preserved labyrinthodont structure, visible as winding canals in the dentine layer

A – visible at macroscale, also with highlighted areas of dark dentine; **B** – visible at microscale

sult of internal dentine folding or diagenetic influence. The dentine colour varies independently of the layer colours, as dentine appears in lighter and darker variations in specific areas of cross-sections (compare Figs. 3A and 4).

SCANNING ELECTRON MICROSCOPY

Electron microscopy was applied to assess the overall surface microtopography of the teeth to identify specific characteristics connected with the tooth morphology. The tooth bases are distinctly different in cross-section than the cuspidal section, with an oval shape and strong lateral grooving (Fig. 6). In general, the shape changes from a tapered, slightly laterally compressed tip with cutting edge to a circular base with prominent grooving (Fig. 7). The cavity observed in the dental pulp is narrow, oval and surrounded radially by canals. The enamel observed in transverse section (Fig. 8A) is very thin, measuring ~5 μm, and while the crystallites are strongly integrated into the blocky structure, the individual fibrous structure is still visible. In transverse section (Fig. 8B), the slightly irregular fibrous character of the crystallites is clearly visible. In general, the distinction between the compact outer dentine layer and the inner layer with cavities is clear. The structure of the canals observed (Fig. 9) is clearly three-dimensional, creating a complex inner labyrinth. The observable canals vary in dimensions and directions, with larger canals characterized by an internal opaque structure of dentine, while smaller canals are often superficial.

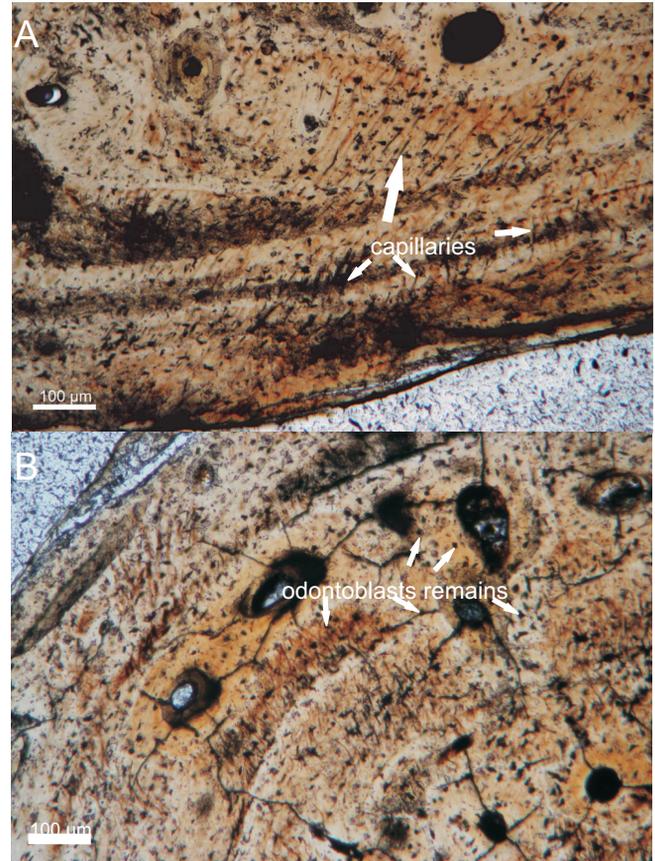


Fig. 4A – preserved capillary canals in dentine (brown or dark, hair-like short filamentary marks); B – marked miniscule dark-dotted structures interpreted as remains of odontoblasts

SCANNING ELECTRON MICROSCOPY–ENERGY DISPERSIVE SPECTROSCOPY

In the samples analysed (Fig. 10) P, Ca, and O (Table 1) are decidedly dominant components, comprising >90% of the molecular mass. In the samples studied, fluoride is present in enamel (T1_pt1–T1_pt5 and T2_pt1) but not in dentine (T1_pt6), ranging from 1.43 to 2.73 in wt.%. CaO and P₂O₅ fall into similar ranges (47.6–57.67% for CaO and 35.24–40.46% for P₂O₅) in both dentine and enamel. Similar observations can be made when comparing the content of SO₃, which are also comparable in both layers. Magnesium and sodium, other components of biomineralized tissue, are present in five samples for sodium (T1_pt1, T1_pt2, T1_pt3, T1_pt5, T1_pt6, and T2_1) and five (T1_pt1, T1_pt3, T1_pt4, T1_pt6, T2_pt1) for magnesium. Other significant components include Fe₂O₃ (0.44–1.76%), Al₂O₃ (0.19–2.99%) and SiO₂ (0.98–7.17%).

DISCUSSION

MORPHOLOGICAL CHARACTERISTICS

The peculiar shape of the teeth is characterized by longitudinal changes in cross-section, which means that the tooth bases are strongly reinforced against mechanical stress

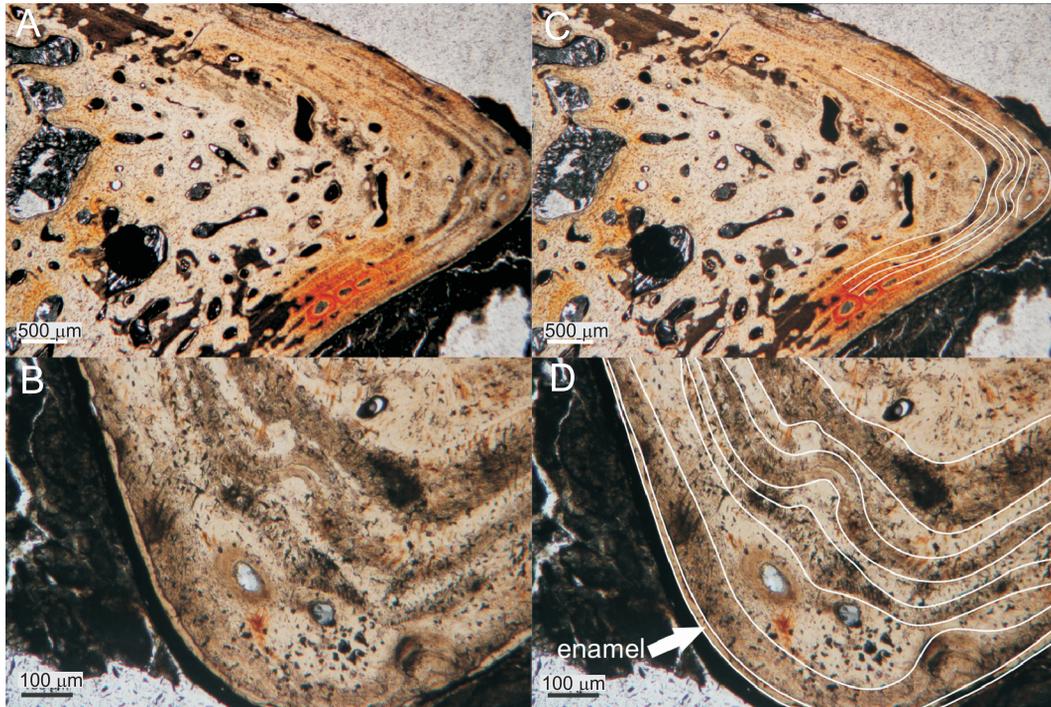


Fig. 5A, B – cross-section of a teeth of *M. krasiejowensis* with seasonal growth lines, **A** also with visible anterior cutting edge; **C, D** – growth lines highlighted, **D** also with thin layer of enamel on the tooth edges

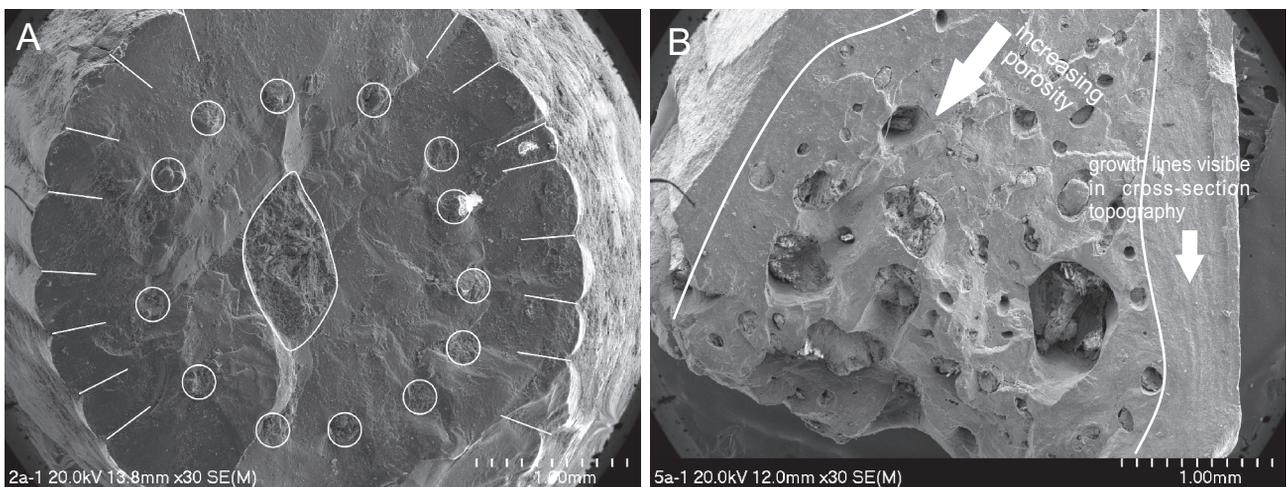


Fig. 6. High-resolution SEM image of cross-section of *M. krasiejowensis* tooth

A – basal fragment, with outer grooves and internal canals filled with sediment; **B** – upper segment, with differentiated non-layered dentine with directional porosity and outer dentine layer, with von Ebner lines visible in the tooth topography

caused by struggling prey, while the upper portion still retains an oval, slightly compressed shape with an anterior cutting edge which can be interpreted as an adaptation to increase shearing strength (Whitenack et al., 2011), providing a compromise between cutting ability and dental resistance. This characteristic is further highlighted by the lesser porosity near the anterior cutting edge.

M. krasiejowensis exhibits a labyrinthodont structure, which is typical feature for the members of the Temnospondyli, characterized in this case by the irregular network of canals, with a

clear pattern of increasing porosity towards the posterior teeth. Apart from intense diagenetic changes to the structure, the teeth in life were characterized by extensive internal cavities as result of infolding. The labyrinthodont-like structure observed in samples – a characteristic of basal tetrapods – in this case is interpreted as a reinforcing structure, which relieves external pressures caused by the act of predation and trauma induced by struggling prey, as a result strengthening the mechanical resistance of the teeth. Plicidentine is also present in non-temnospondyl predatory groups, such as varanids and ichthyosaurs

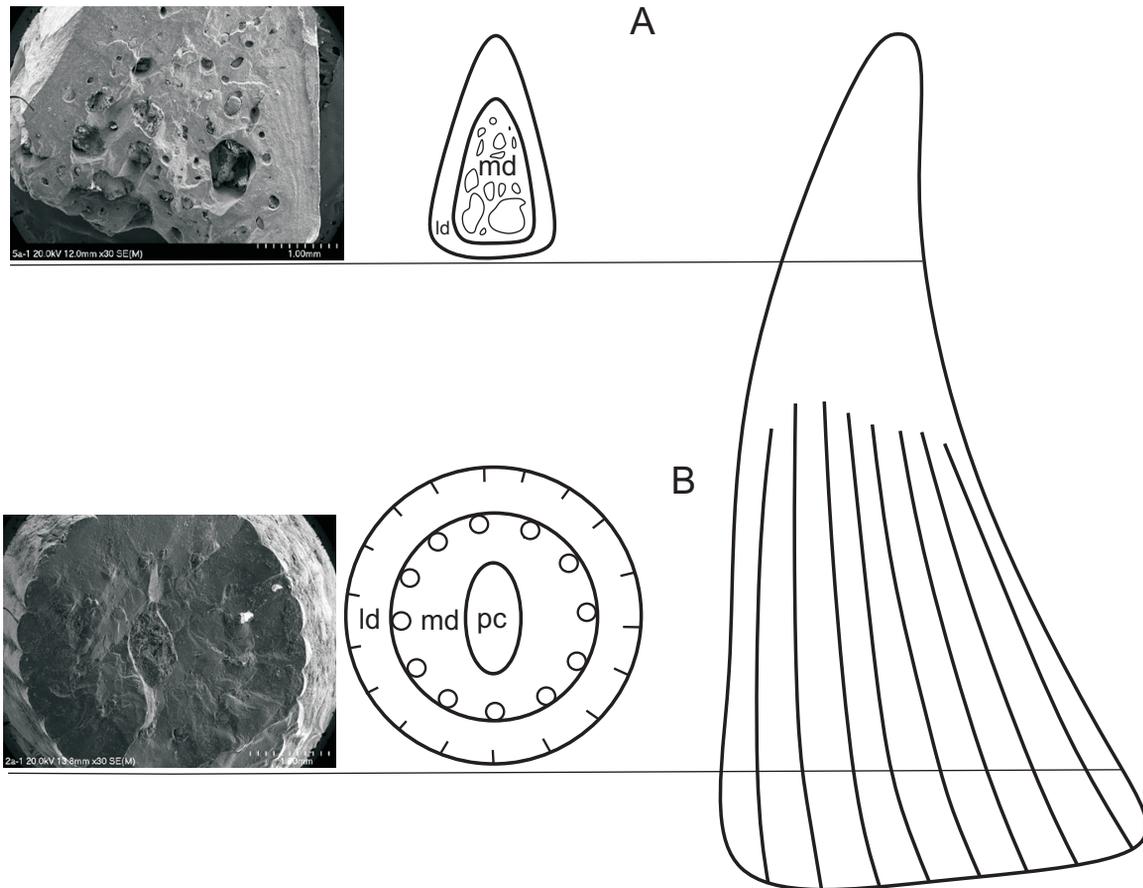


Fig. 7. Illustration of changing tooth morphology and cross-section along the vertical axis, with observed cutting edge and longitudinal grooving at base; cross-sections represent sectioning plane

A – cuspidal cross-section, with directional porosity; **B** – tooth base cross-section with rosette of internal pores; pc – pulp cavity, md – massive (non-layered) dentine, ld – layered dentine

(Schultze, 1969), providing evidence that this feature can be indeed interpreted as a predatory adaptation.

This complex network of canals was probably highly vascularized during the animal's life, as shown by prominent capillary systems, especially visible in the dentine layer. The structure observed in *M. krasiejowensis* is similar to the structure observed in *Metoposaurus* sp. by Warren and Davey (1992), and structures observed in different temnospondyl taxa (e.g., Owen, 1842; Schultze, 1969; Warren and Turner, 2005); however, it is characterized by a peculiar longitudinal variation, as the convoluted canal-like structure is rather irregular in the upper sections of the teeth, while tooth base sections feature regular structure with a pulpal cavity surrounded by a radially spaced system of pores. This petaloid, lobe-like structure, present at the bases of the teeth, can be ascribed to a different rate of packing of dentine tubules (Warren and Turner, 2005), causing the deformation in tooth structure. Furthermore, prominent grooving at the base of the teeth along with the curved outline between individual grooves can be interpreted as a strengthening structure, the presence of which relates to the internal development of the labyrinthodont structure. The internal porosity of the teeth in temnospondyls is an indicator of tooth age, as they gradually become hollower as they mature (see Bystrow, 1938). This can indicate that the teeth sampled are mostly quite

young, as their internal porosity is still not quite as developed as in truly mature teeth. This is especially visible in electron microscope samples of the tooth bases, as the internal space of the teeth is mostly solid, with small cavities filled with diagenetic mineralization. Overall, the observed structure of the tooth bases is very similar to the cross-section described by Warren and Davey (1992), but infolds are much less visible, which can be ascribed a) to preservation state, or b) age of the teeth, which influences internal folding development and/or c) tooth type, as it was noted by Warren and Davey (1992) that infolds are much more visible in palatal tusks than in smaller marginal and palatal teeth, which were sampled in this case.

HISTOLOGY AND SEASONAL GROWTH PATTERNS

The incremental growth lines, which represent the cyclic activity of odontoblasts during the formation of dentine, are an indicator of the life cycle of an individual (Erikson, 1996; Hackenberg and Rauhut, 2020), in which the rate of dentine deposition can signify the growth rate and/or nutrient availability. The *M. krasiejowensis* teeth exhibit a typical growth pattern, with wider inner rings when the dental growth rate was high, and the corresponding growth rings gradually become thinner as the growth

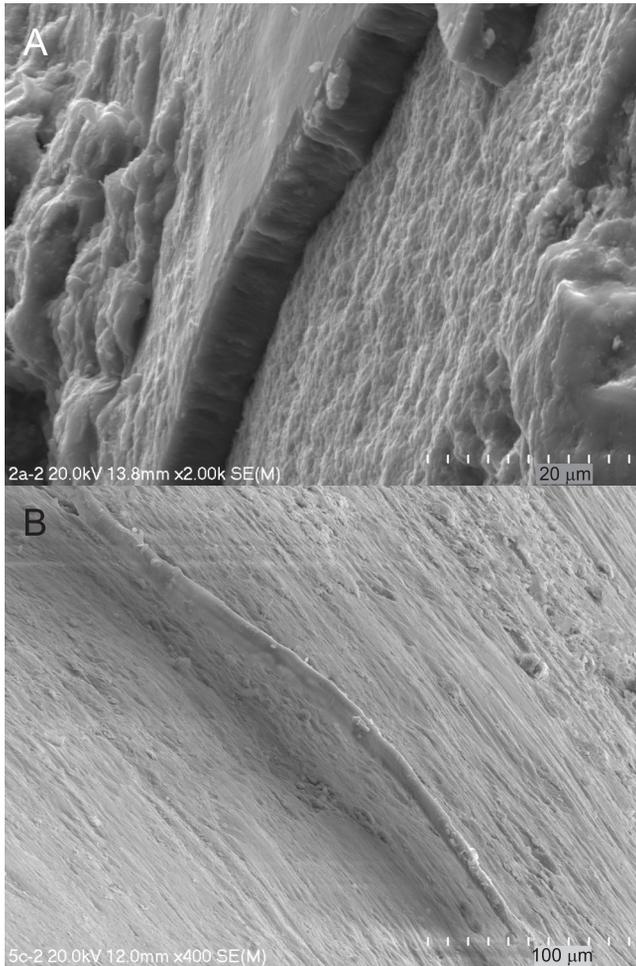


Fig. 8. Close-up view of tooth surface with visible enamel layer

A – in cross-section, with visible crystallites; **B** – slightly irregular, fibrous crystallites in longitudinal view

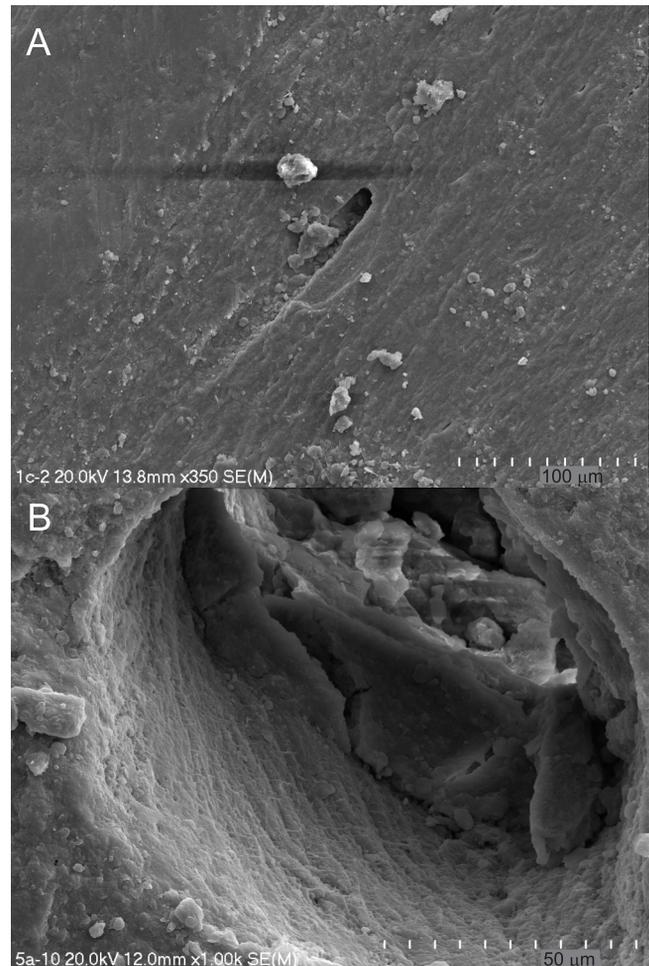


Fig. 9. Three-dimensional structure of dentary canals

A – superficial capillary canals; **B** – with oblique dentine structure

rate slowed. Compared to other predatory vertebrates, such as *Spinosaurus aegyptiacus* growth patterns (Hackenberg and Rauhut, 2020), the *M. krasiejowensis* samples examined show proportionally wide areas of growth, but fewer in number, which could mean that: a) either the growth lines were blurred by diagenetic processes, b) the growth rate was less regular, with more intensive spurts interrupted by stages of arrested growth, c) phylogenetical effects, as *M. krasiejowensis* is a member of the Temnospondyli, which are anamniotes (Konietzko-Meier et al., 2016), and current microstructure studies mostly focus on amniotes (e.g., Hackenberg and Rauhut, 2020; Owocki and Madzia, 2020), thus temnospondyl growth cycles in teeth have yet to be studied extensively.

There appears to be a differentiation in colour not explained by growth patterns. This variation can be ascribed to tight packing of dentine tubules in specific areas (Fig. 3A) as described by Warren and Turner (2005) and named by early tetrapod studies as "dark dentine". This finding is supported by the fact that darker dentine spots appear closely adjacent to visible folds of the labyrinthodont structure (Fig. 3A). Dark, dotted structures appearing throughout the dentine layer are interpreted here as remains of odontoblasts, deposited after the cyclic dentine-forming activity, which explains their presence through the

whole dentine. This structure is present in teeth in vivo as a small dots and irregular spots when the teeth are forming (see Osborn, 1981). The presence of growth bands of very different colours can be an indicator of a major change in the life conditions of an individual. Based on the development pattern present in growth lines in the samples, it can be interpreted as the influence of dry and wet seasons, the presence of which was inferred in the study area from sedimentological studies (Szulc, 2005; Jewuła et al., 2019). Longer cyclic activity in dentine formation, as described by Dean (2000), is interpreted here as Andresen growth lines, comprising long-term activity in odontoblasts, caused by endogenous biorhythms. In contrast to constant, circadian growth of von Ebner lines deposited as small scale bands (Erikson, 1996; Nanci, 2008), Andresen lines are much thicker, encompassing larger-scale trends in tooth biomineralization mode. In this case, this pattern is most probably influenced by seasonal changes, which influence tooth mineral deposition and cause strongly pronounced changes in mineral content exhibited as colour bands. Assuming that each season is represented as a colour band in the dentine layer, with an average of 7–8 bands in the teeth sampled, it can be calculated that the lifespan of the teeth sampled lasted four cycles of dry/wet seasons on average. Darker bands are interpreted here

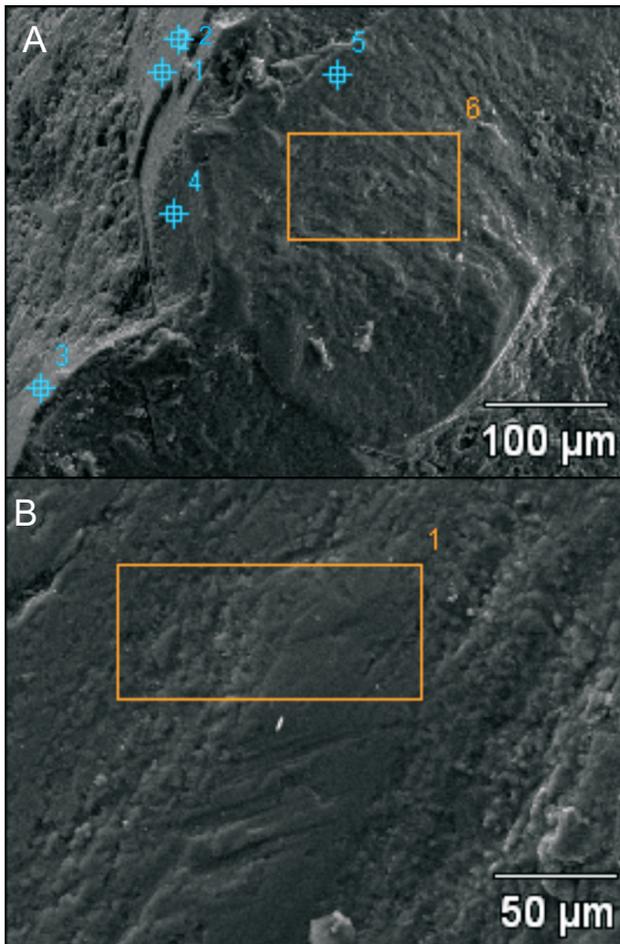


Fig. 10A – element point analysis (1–5) and mapping (6) of cross-section; B – (1) lateral surface mapping

as indicators of dry seasons, as although the incremental growth lines are irregular in form, they are mostly characterized by lesser thickness than light bands, and it is expected that during a wet season, mineral accumulation will be heightened due to increased nutrient supply, thus resulting in thicker lines during wet seasons, visible in this case as lighter bands. The discovery of a seasonal growth pattern in the teeth further establishes the influence of seasonal climate on the histology and bone ontogeny of the animal. Konietzko-Meier and Sander (2013) first described the influence of seasonal climate on bone histology, based on long-bone studies of humeral and femoral

bones; the long bones examined in cross-section showed a seasonal growth pattern based on incremental growth rings. The authors speculated that very significant changes in bone material accumulation may be associated with changes in metabolism rate, probably affected by dry/wet seasonal cycles. Those findings demonstrate the pressures of the changing palaeoenvironment at Krasiejów on animal biology, and those conditions resulted in variation in developmental processes in this taxon. In contrast to the research of Konietzko-Meier and Sander (2013), the teeth were replaced during the lifetime of the organism, so they cannot be used as an indicator of the entire lifetime of the animal, but they can visualize how a certain part of life was influenced by changing environmental conditions. Furthermore, the finding of a seasonal growth pattern in the teeth adds to knowledge of the Krasiejów palaeoenvironment, providing further palaeobiological evidence of the seasonal climate as recorded by vertebrate histology.

CHEMICAL COMPOSITION OF THE TEETH

The most striking chemical feature of the teeth studied is the presence of a significant percentage of fluoride (1.43–2.73%) in enamel. Only enamel shows the presence of this component, since the dentine mapping in T1 did not detect a significant presence of fluoride. The samples showed similar proportions of F (1.11–3.48%) as in Luebke et al. (2015). Na and Mg can be incorporated into the biological structure of apatite (LeGeros, 1980), hence, their presence is expected. The small percentage of S present in the samples is a typical element in vertebrate bones. However, the presence of Na and Mg can also be ascribed to the presence of clay minerals. Furthermore, the presence of components such as Al and Fe is strongly linked to clay minerals commonly occurring in the samples. Wide ranges of weight percentages, observed at different sampling points, can be ascribed to a different mineralization rate of these minerals, a diagenetic effect.

Based on the close taxonomic affiliation of temnospondyls with modern amphibians (Vitt et al., 2013; Benton, 2015; Schoch, 2019) it may be assumed that *M. krasiejowensis* may have had a similar composition of enamel (displayed by temnospondyls, in contrast to enameloid occurring in other taxa (e.g., Fincham et al., 1999; see Rinehart and Lucas, 2014). In general, in modern tetrapods, hydroxyapatite with carbonate substitutions at some positions, known as dahllite, is the dominant component of vertebrate enamel (LeGeros, 1981). By contrast, Chondrichthyes (Daculsi and Kerebel, 1980; LeGeros and Suga, 1980; Whitenack et al., 2011) and some Osteichthyes as well as Amphibia (Fincham et al., 1999) possess fluorapatite

Table 1

Compound percentages [in wt.%] in samples T1 and T2

Samples	F [%]	Na ₂ O [%]	MgO [%]	Al ₂ O ₃ [%]	SiO ₂ [%]	P ₂ O ₅ [%]	SO ₃ [%]	CaO [%]	Fe ₂ O ₃ [%]
T1_pt1	2.21	1.31	0.40	0.34	1.49	40.46	1.25	52.11	0.44
T1_pt2	2.74	1.32	–	0.58	2.07	38.77	1.30	52.11	1.10
T1_pt3	2.71	1.80	0.31	0.46	1.74	40.09	1.35	50.58	0.96
T1_pt4	1.75	–	0.22	0.51	0.98	37.39	1.51	57.63	–
T1_pt5	1.43	0.56	–	0.19	–	38.46	1.69	57.67	–
T1_pt6	–	0.61	0.31	0.55	1.70	38.05	1.50	56.68	0.61
T2_pt1	1.54	0.94	0.97	2.99	7.17	35.24	1.23	47.6	1.76

enameloid. Luebke et al. (2015) proposed that the high percentage of fluoride seen in different fossil groups of Sauropterygii, Lepidosauria and Archosauria, shared also with modern and fossil shark groups, is evidence of a different chemistry of the environment in the past. This claim was later debunked by de Renzi et al. (2016), who concluded that the presence of fluorapatite in the enamel of fossil tetrapods can be explained by the diagenetic replacement of the hydroxyl group by fluoride, which is also known as a well-established dating method, applied since the 19th century (Carnot, 1893). The implication is that the fluorapatite in these samples is possibly of diagenetic origin, although through a close relationship with basal tetrapods and modern Lissamphibia it is still possible for *M. krasiejowensis* teeth to exhibit fluorapatite mineralogy as an inherent trait, and this aspect requires further study.

CONCLUSIONS

Microstructural studies of teeth within palaeoecological studies can provide significant information about the biology and lifestyle of an animal. This is especially useful in species such as *M. krasiejowensis*, which are well described at the gross scale and are inferred to have inhabited turbulent environments, such as were present in the Late Triassic of the Krasiejów vicinity. Studies of histology and microstructure of vertebrate bones can be an additional proxy, providing further information as a supplement to sedimentary studies. Furthermore, exploring the palaeobiology of charismatic animals such as temnospondyls is by its nature a fascinating subject, capturing the imagination of generations of researchers since times of Sir Richard Owen.

1. The teeth of *M. krasiejowensis* examined show a morphology which can be ascribed to a predatory lifestyle, with the cutting anterior edge of the cuspidal section of the teeth and a wide basal section with reinforcement grooves. An additional aspect that protected the teeth against mechanical failure is the

internal labyrinthodont structure, which occurs in the samples in the form of a directional porosity, functioning as a stress-dispersing design;

2. *M. krasiejowensis* teeth display a characteristic labyrinthodont-like structure, with irregular, internal canals with directional porosity observed in the upper sections of teeth. The basal section is circular in shape with regular internal structure, characterised by a pulp cavity surrounded radially by prominent canals and petal-like lobes present on the surface;

3. The incremental growth lines observed in the teeth sampled reveal a clearly visible interchanging colour pattern, suggesting significant differences in dentine growth mode during tooth lifespan, interpreted as result of seasonal influence on dental histology. Based on the number of incremental growth lines, it is inferred that these teeth experienced four dry/wet seasons on average, providing further evidence that the seasonal environment of Late Triassic Krasiejów had an influence on *M. krasiejowensis* biology;

4. The enamel layer is characterized by the presence of fluoride, a sign of fluorapatite mineralogy, which is an aspect requiring further studies because while modern Lissamphibia, which are related to temnospondyls, possess at least some fluorapatite within enameloid, the presence of fluoride may be a diagenetic effect. This raises a question whether this chemical feature was an inherent characteristic of the living animal.

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REFERENCES

- Antczak, M., Bodzioch, A., 2018.** Ornamentation of the dermal bones of *Metoposaurus krasiejowensis* and its ecological implications. *PeerJ*, **6**: e5267.
- Benton, M.J., 2015.** Vertebrate Palaeontology. John Wiley and Sons, Bristol.
- Bilan, W., 1976.** The stratigraphy of the Upper Triassic deposits of the eastern margin of the Upper Silesian Coal Basin (in Polish with English summary). *Zeszyty Naukowe AGH, Geologia*, **2**: 4–73.
- Bodzioch, A., Kowal-Linka, M., 2012.** Unraveling the origin of the Late Triassic multitaxic bone accumulation at Krasiejów (S Poland) by diagenetic analysis. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **346**: 25–36.
- Bystrow, A.P., 1938.** Zahnstruktur der Labyrinthodonten. *Acta Zoologica*, **19**: 387–425.
- Bystrow, A.P., 1939.** Zahnstruktur der Crossopterygier. *Acta Zoologica*, **20**: 286–338.
- Carlson, S.J., 1990.** Vertebrate dental structures. In: *Skeletal Biomineralization: Patterns, Processes and Evolutionary Trends* (ed. J.G. Carter), **5**: 235–260. Wiley.
- Carnot, M.A., 1893.** Recherches sur la composition générale et la teneur en fluor des os modernes et des os fossiles des différents âges. Ch. Dunod.
- Chase, J.N., 1963.** The labyrinthodont dentition. *Breviora*, **187**: 1–13.
- Chowdhury, T.R., 1965.** A new metoposauroid amphibian from the Upper Triassic Maleri Formation of Central India. *Philosophical Transactions of the Royal Society London, B*, **250**: 1–52.
- Credner, H., 1893.** Zur Histologie der Faltenzähne paläozoischer Stegocephalen. *Abhandlungen der Königlich-Sächsischen Gesellschaft der Wissenschaften*, **33**: 475–555.
- Daculsi, G., Kerebel, L.M., 1980.** Ultrastructural study and comparative analysis of fluoride content of enameloid in sea-water and fresh-water sharks. *Archives of Oral Biology*, **25**: 145–151.
- Dadlez, R., Marek, S., Pokorski, J., 2000.** Geological map of Poland without Cenozoic sediments in scale 1:1000 000. Polish Geological Institute, Warszawa.
- De Renzi, M., Manzanares, E., Marin-Monfort, M.D., Botella, H., 2016.** Comments on "Dental lessons from past to present: ultrastructure and composition of teeth from plesiosaurs, dinosaurs, extinct and recent sharks" by A. Lübke, J. Enax, K. Loza, O. Prymak, P. Gaengler, H.-O. Fabritius, D. Raabe and M.

- Epple, RSC Advances, 2015, **5**: 61612. RSC Advances, **6**: 74384–74388.
- Dean, M.C., 2000.** Incremental markings in enamel and dentine: what they can tell us about the way teeth grow. In: Development, Function and Evolution of Teeth (eds. M.F. Teaford, M.M. Smith and M.W.J. Ferguson). Cambridge University Press, Cambridge.
- Dutuit, J.M., 1976.** Introduction à l'étude paléontologique du Trias continental marocain. Description des premiers Stegocephales recueillis dans le couloir d'Argana (Atlas occidental). Mémoires du Muséum National d'Histoire Naturelle, Paris, Series C, **36**: 1–253.
- Dzik, J., 2003.** A beaked herbivorous archosaur with dinosaur affinities from the early Late Triassic of Poland. Journal of Vertebrate Paleontology, **23**: 556–574.
- Dzik, J., Sulej, T., 2007.** A review of the early Late Triassic Krasiejów biota from Silesia, Poland. Palaeontologia Polonica, **64**: 1–27.
- Dzik, J., Sulej, T., 2016.** An early Late Triassic long-necked reptile with a bony pectoral shield and gracile appendages. Acta Palaeontologica Polonica, **61**: 805–823.
- Dzik, J., Sulej, T., Kaim, A., Niedźwiedzki, R., 2000.** Late Triassic graveyard of large Triassic tetrapods in the Opole Silesia (in Polish with English summary). Przegląd Geologiczny, **48**: 226–235.
- Enault, S., Guinot, G., Koot, M.B., Cuny, G., 2015.** Chondrichthyan tooth enameloid: past, present, and future. Zoological Journal of the Linnean Society, **174**: 549–570.
- Erickson, G.M., 1996.** Incremental lines of von Ebner in dinosaurs and the assessment of tooth replacement rates using growth line? Proceedings of the National Academy of Sciences, **93**: 14623–14627.
- Fijałkowska-Mader, A., Heunisch, C., Szulc, J., 2015.** Palynostratigraphy and palynofacies of the Upper Silesian Keuper. Annales Societatis Geologorum Poloniae, **85**: 637–661.
- Fincham, A., Moradian-Oldak, J., Simmer, J.P., 1999.** The structural biology of the developing dental enamel matrix. Journal of Structural Biology, **126**: 270–299.
- Fraas, E., 1913.** Neue Labyrinthodonten aus der schwäbischen Trias. Palaeontographica (1846–1933): 275–294.
- Gruntmejer, K., Konietzko-Meier, D., Bodzioch, A., 2016.** Cranial bone histology of *Metoposaurus krasiejowensis* (Amphibia, Temnospondyli) from the Late Triassic of Poland. PeerJ, **4**: e2685.
- Gruntmejer, K., Konietzko-Meier, D., Bodzioch, A., 2019.** Morphology and preliminary biomechanical interpretation of mandibular sutures in *Metoposaurus krasiejowensis* (Temnospondyli, Stereospondyli) from the Upper Triassic of Poland. Journal of Iberian Geology, **45**: 301–316.
- Gruszka, B., Zieliński, T., 2008.** Evidence for a very low-energy fluvial system: a case study from the dinosaur-bearing Upper Triassic rocks of Southern Poland. Geological Quarterly, **52** (3): 239–252.
- Hättig, K., Stevens, K., Thies, D., Schweigert, G., Mutterlose, J., 2019.** Evaluation of shark tooth diagenesis-screening methods and the application of their stable oxygen isotope data for palaeoenvironmental reconstructions. Journal of the Geological Society, **176**: 482–491.
- Heckeberg, N.S., Rauhut, O.W., 2020.** Histology of spinosaurid dinosaur teeth from the Albian-Cenomanian of Morocco: implications for tooth replacement and ecology. Palaeontologia Electronica, **23**: a48.
- Hunt, A.P., 1993.** Revision of the Metoposauridae (Amphibia: Temnospondyli) and description of a new genus from Western North America. Museum of Northern Arizona Bulletin, **59**: 67–97.
- Jalil, N.E., 1996.** Les Vertébrés permien et triassiques de la Formation d'Argana (Haut Atlas occidental): liste faunistique préliminaire et implications stratigraphiques. In: Le Permien et le Trias du Maroc: état des connaissances (ed. F. Medina): 227–250. Editions Pumag, Marrakesh, Morocco.
- Jewuła, K., Matysik, M., Paszkowski, M., Szulc, J., 2019.** The late Triassic development of playa, gilgai floodplain, and fluvial environments from Upper Silesia, southern Poland. Sedimentary Geology, **379**: 25–45.
- Keenan, S.W., 2016.** From bone to fossil: a review of the diagenesis of bioapatite. American Mineralogist, **101**: 1943–1951.
- Konietzko-Meier, D., Wawro, K., 2007.** Mandibular dentition in the Late Triassic temnospondyl amphibian *Metoposaurus*. Acta Palaeontologica Polonica, **52**: 213–215.
- Konietzko-Meier, D., Sander, M., 2013.** Long bone history of *Metoposaurus diagnosticus* (Temnospondyli) from the late Triassic of Krasiejów (Poland) and its paleobiological implications. Journal of Vertebrate Paleontology, **33**: 1003–1018.
- Konietzko-Meier, D., Shelton, C.D., Sander, P.M., 2016.** The discrepancy between morphological and microanatomical patterns of anamniotic stegocephalian postcrania from the Early Permian Briar Creek Bonebed (Texas). Comptes Rendus Palevol, **15**: 103–114.
- Kowalski, J., Bodzioch, A., Janecki, P., Ruciński, M., Antczak, M., 2019.** Preliminary report on the microvertebrate faunal remains from the Late Triassic locality at Krasiejów, SW Poland. Annales Societatis Geologorum Poloniae, **89**: 291–305.
- Laurin, M., Reisz, R.R., 1999.** A new study of *Solenodonsaurus janenschii*, and a reconsideration of amniote origins and stegocephalian evolution. Canadian Journal of Earth Sciences, **36**: 1239–1255.
- LeGeros, R.Z., Suga, S., 1980.** Crystallographic nature of fluoride in enameloids of fish. Calcified Tissue International, **32**: 169–174.
- Luebke, A., Enax, J., Loza, K., Prymak, O., Gaengler, P., Fabritius, H.O., Raabe, D., Epple, M., 2015.** Dental lessons from past to present: ultrastructure and composition of teeth from plesiosaurs, dinosaurs, extinct and recent sharks. RSC Advances, **5**: 61612–61622.
- MacDougall, M.J., LeBlanc, A.R.H., Reisz, R.R., 2014.** Plicidentin in the Early Permian Parareptile *Colobomycter pholeter*, and its phylogenetic and functional significance among coeval members of the clade. PLOS One, **9**: e96559.
- Nanci, A., 2008.** Ten Cate's oral histology: development, structure and function. Seventh Edition. Elsevier Health Sciences, St Louis.
- Osborn, J.W., 1981.** Dental Anatomy and Embryology, 1. Blackwell Scientific Publications, Oxford, Boston.
- Owen, R., 1841.** On the teeth of species of the genus Labyrinthodon (*Mastodonsaurus salamandroides*, and *Phytosaurus* (?) of Jäger) from the German Keuper and the sandstone of Warwick and Leamington. Proceedings of the Geological Society of London, Volume 3. London.
- Owoczek, K., Madzia, D., 2020.** Predatory behaviour in mosasaurid squamates inferred from tooth microstructure and mineralogy. Cretaceous Research, **111**: 104430.
- Paluh, D.J., Riddell, K., Early, C.M., Hantak, M.M., Jongmsa, G.F., Keeffe, R.M., Silva, F.M., Nielsen, S.V., Vallejo-Pareja, M.C., Stanley, E.L., Blackburn, D.C., 2021.** Rampant tooth loss across 200 million years of frog evolution. eLife, **10**: e66926.
- Pander, Ch.H., 1860.** Über die Saurodipteren, Dendrodonten, Glyptolepiden und Cheirolepiden des Devonischen System. Buchdruckerei der kaiserlichen Akademie der Wissenschaften, St. Petersburg.
- Parsons, T.S., Williams, E.E., 1962.** The teeth of amphibia and their relation to amphibian phylogeny. Journal of Morphology, **110**: 375–389.
- Pawlak, W., Rozwalak, P., Sulej, T., 2022.** Triassic fish faunas from Miedary (Upper Silesia, Poland) and their implications for understanding paleosalinity. Palaeogeography, Palaeoclimatology, Palaeoecology, **590**: 110860.
- Peyer, B., 1968.** Comparative Odontology. The University of Chicago Press.
- Reinhardt, L., Ricken, W., 2000.** The stratigraphic and geochemical record of Playa Cycles: monitoring a Pangaean monsoon-like system (Triassic, Middle Keuper, S. Germany). Palaeogeography, Palaeoclimatology, Palaeoecology, **161**: 205–227.
- Rinehart, L., Lucas, S., 2014.** Tooth form and function in temnospondyl amphibians: relationship of shape to applied stress.

- New Mexico Museum of Natural History and Science Bulletin, **61**: 533–542.
- Ruta, M., Pisani, D., Lloyd, G.T., Benton, M.J., 2007.** A supertree of Temnospondyli: cladogenetic patterns in the most species-rich group of early tetrapods. *Proceedings. Biological Sciences*, **274**: 3087–3095.
- Romer, A.S., Parsons, S.T., 1986.** *The Vertebrate Body*. Saunders College Publishing, Philadelphia.
- Sengupta, D.P., 1992.** *Metoposaurus maleriensis* Roy Chowdhury from the Tiki Formation of Son-Mahanadi Valley of Central India. *Indian Journal of Geology*, **64**: 300–305.
- Schoch, R.R., 2013.** The evolution of major temnospondyl clades: an inclusive phylogenetic analysis. *Journal of Systematic Palaeontology*, **11**: 673–705.
- Schoch, R.R., 2019.** The putative lissamphibian stem-group: phylogeny and evolution of the dissorophoid temnospondyls. *Journal of Paleontology*, **93**: 137–156.
- Schultze, H.P., 1969.** Die Faltenzähne der rhipidistiiden Crossopterygier der Tetrapoden und die Actinopterygier Gattung *Lepisosteus*. *Palaeontographica Italica*, **65**: 63–137.
- Sulej, T., 2002.** Species discrimination of the Late Triassic temnospondyl amphibian *Metoposaurus diagnosticus*. *Acta Palaeontologica Polonica*, **47**: 535–546.
- Sulej, T., 2005.** A new rauisuchian reptile (Diapsida: Archosauria) from the Late Triassic of Poland. *Journal of Vertebrate Paleontology*, **25**: 78–86.
- Sulej, T., 2007.** Osteology, variability, and evolution of *Metoposaurus*, a temnospondyl from the Late Triassic of Poland. *Palaeontologia Polonica*, **64**: 29–139.
- Sulej, T., Majer, F., 2005.** The temnospondyl amphibian *Cyclotosaurus* from the Upper Triassic of Poland. *Palaeontology*, **48**: 157–170.
- Szulc, J., 2005.** Sedimentary environments of the vertebrate-bearing Norian deposits from Krasiejów, Upper Silesia (Poland). *Hallesches Jahrbuch für Geowissenschaften*, R. B, **19**: 161–170.
- Szulc, J., Racki, G., 2015.** Grabowa Formation – the basic lithostratigraphic unit of the Upper Silesian Keuper (in Polish with English summary). *Przegląd Geologiczny*, **63**: 103–113.
- Środoń, J., Szulc, J., Anczkiewicz, A., Jewuła, K., Banoe, M., Marynowski, L., 2014.** Weathering, sedimentary, and diagenetic controls of mineral and geochemical characteristics of the vertebrate-bearing Silesian Keuper. *Clay Minerals*, **49**: 569–594.
- Teschner, E., Konietzko-Meier, D., Sander, P., 2018.** Variability of growth pattern observed in *Metoposaurus krasiejowensis* humeri and its biological meaning. *Journal of Iberian Geology*, **44**: 99–111.
- Vitt, L.J., Caldwell, J.P., 2013.** *Herpetology: an Introductory Biology of Amphibians and Reptiles*. Academic Press, Cambridge, Massachusetts.
- Warren, A.A., Davey, L., 1992.** Folded teeth in temnospondyls – a preliminary study. *Alcheringa*, **16**: 107–132.
- Warren, A., Turner, S., 2005.** Tooth histology patterns in early tetrapods and the presence of “dark dentine”. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, **96**: 113–130.
- Whitenack, L., Simkins, D., Motta, P., 2011.** Biology meets engineering: the structural mechanics of fossil and extant shark teeth. *Journal of Morphology*, **272**: 169–179.
- Wierzbowski, H., Błażejowski, B., Tyborowski, D., 2019.** Oxygen isotope profiles of uppermost Jurassic vertebrate teeth and oyster shells: a record of paleoenvironmental changes and animal habitats. *Palaios*, **34**: 585–599.