

PRELIMINARY REPORT ON THE MICROVERTEBRATE FAUNAL REMAINS FROM THE LATE TRIASSIC LOCALITY AT KRASIEJÓW, SW POLAND

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Abstract: Fossil vertebrate remains from the Keuper unit in the vicinity of the village of Krasiejów have been analyzed for almost two decades. However, the main goal of these works was focused mainly on large vertebrates. Here the authors present the first description of microvertebrate fossils from that site. The collection of around 5,000 specimens is mainly comprised of teeth and scales. The most numerous remains belong to osteichthyans: dipnoans (*Ptychoceratodus* and cf. *Arganodus*), palaeoniscids, semionotids, redfieldiids and chondrichthyans, such as *Lonchidion* sp., which is the first indisputable record of that genus in the Upper Triassic of Poland and the first shark at the Krasiejów locality. Tetrapod fossils consist of temnospondyl amphibians, rhynchocephalian lepidosauromorphs and archosauromorphs. Among them, temnospondyl amphibian remains are the most numerous and are represented mostly by *Metoposaurus*. However, on the basis of diversity in tooth morphotypes, the occurrence of other taxa cannot be excluded. Rhynchocephalians are composed of 7 fragmentary jaw morphotypes with dentition, which could indicate high taxonomic diversity (cf. *Planocephalosaurus*, cf. *Diphydontosaurus* and cf. *Clevosaurus*). The most varied fossil group was assigned to the archosauromorphs. The authors can distinguish at least 19 teeth morphotypes, which show similarities to the dentition of: protorosaurians (cf. Tanystropheidae), pseudosuchians (cf. *Protecovasaurus*, cf. *Revueltosaurus*), early crocodylomorphs and basal sauropodomorph dinosaurs. The first occurrence of a theropod dinosaur and cynodonts at the Krasiejów locality is also recorded. However, their remains are very rare. These new records show a high taxonomic diversity at the Krasiejów locality that contributes to our deeper understanding of Late Triassic ecosystem of Poland.

Key words: Microvertebrates, archosauromorphs, fish, amphibians, Triassic, Keuper, Poland.

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INTRODUCTION

Fossil vertebrate remains of the Keuper unit from the vicinity of the village of Krasiejów located in SW Poland, have been analyzed for almost two decades. In that time, two main review papers have been published (Dzik *et al.*, 2000; Dzik and Sulej, 2007). Since then, many detailed papers and tens of conference contributions have been published. However, the main goal of these detailed articles was focused on large vertebrates, such as *Silesaurus* (Dzik, 2004; Piechowski and Dzik, 2010), *Stagonolepis* (Sulej, 2010; Antczak, 2016), *Polonosuchus* (Sulej, 2005; Bru-

satte *et al.*, 2009), *Paleorhinus* (Dzik, 2001), *Metoposaurus* (Sulej, 2002, 2007; Konietzko-Meier and Wawro, 2007; Gądek, 2012; Konietzko-Meier and Klein, 2013; Konietzko-Meier and Sander, 2013; Konietzko-Meier *et al.*, 2014, 2018; Gruntmejer *et al.*, 2016), *Cyclotosaurus* (Sulej and Majer, 2005), and large dipnoan *Ptychoceratodus* (Skrzycki, 2015). Small vertebrates from this locality, with the exception of the *Ozimek volans* (Dzik and Sulej, 2016) and isolated fish scales (Antczak and Bodzioch, 2018a), have been mentioned only in general review articles and classified as

the uncommonly occurring skeletal remains of ray-finned fishes (Palaeoniscidae), reptiles (Rhynchocephalia) and problematic bones, probably belonging to *Protorosauria* (Dzik *et al.*, 2000; Dzik and Sulej, 2007). In addition to that, a new accumulation of microvertebrate remains has been discovered and is described here for the first time. The main aim of this article is to reveal the microvertebrate taxonomic biodiversity of the Krasiejów locality. This, on the other hand, can provide valuable data for future research on the palaeoecology and palaeogeography of Late Triassic vertebrate communities and their biostratigraphy. Owing to the new observations on faunal diversity, the authors aim to present new data on the continental ecosystems of the Late Triassic.

GEOLOGICAL SETTING

The research was carried out in the clay pit at Krasiejów, SW Poland, Opole Voivodeship (50°039'54"N, 18°016'33"E). The outcrop once was an active quarry, which later was converted into a commercial theme park (JuraPark), founded by the Delta Association. The whole section (about 35 m) already has been described in the literature, which presented the lithological, sedimentological and stratigraphical framework (e.g., Dzik *et al.*, 2000; Szulc, 2005, 2007; Dzik and Sulej 2007; Gruszka and Zieliński 2008; Szulc *et al.*, 2015a, b; Jewuła *et al.*, 2019). According to these studies, two bone beds occurred in the analyzed profile. The lower one currently is well exposed and has been the subject of intensive searches. Its exact location in the succession is described below.

The succession investigated starts with reddish mudstone, representing a palaeovertilsoil (Gruszka and Zieliński, 2008), and consists of several thin layers (Fig. 1). Its upper boundary is undulating and followed by grey, muddy deposits (up to 40 cm thick), containing rhizoids, gyrogonites, unionid bivalves, often preserved in the life position, and channels with concentrations of faecal pellets, both of which were likely produced by bivalves. In the lower part of the bed, sporadically bones of large vertebrates (mostly *Stagonolepis* and *Metoposaurus*) occur. The authors interpret this unit as autochthonous marsh sediment (see Bodzioch *et al.*, 2018). Beneath these accumulations, small lenses were formed, which are composed of grey, calcareous grains and rarely, microvertebrate remains. However, the main concentration of microvertebrate fossils occurs in the upper layer. The fossils found in this dark grey sediment occur with small, irregular and poorly sorted, calcareous grains, bonded with clay. This layer is characterized by significant variations in thickness (from local absence up to 10 cm). Previous study (Szulc, 2005) and the authors' observations indicate that this layer is the product of erosion of a palaeosoil (outwash) and hydrodynamic concentration of it during redeposition. In areas, where the microvertebrate layer does not occur, the upper surface of the marsh layer is discontinuous as a result of erosion and is covered by reddish mud/clay with no internal structures. The bottom part of this reddish mud/clay layer is rich in bone accumulations, dominated by large, aquatic temnospondyl (*Metoposaurus*) and reptile (phytosaur) remains. Near the middle part of

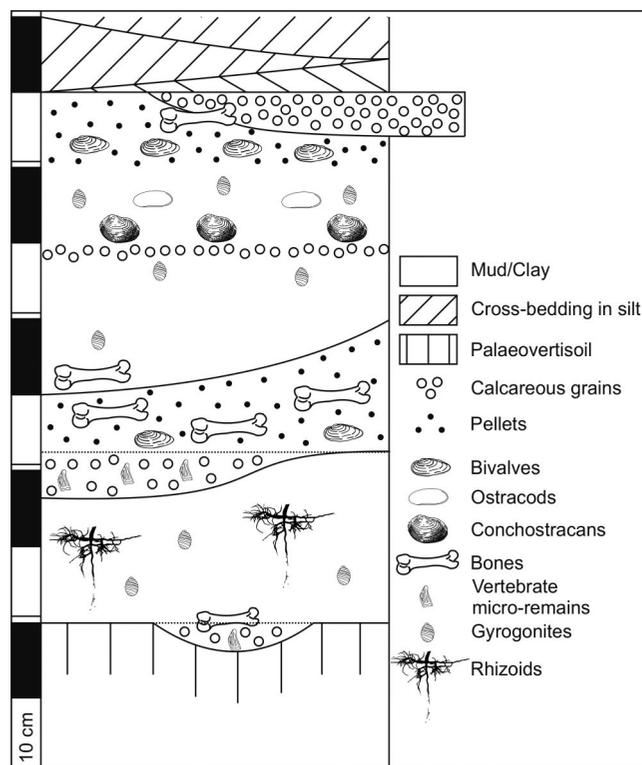


Fig. 1. Stratigraphical position of the microvertebrate-rich horizon during excavation in 2015.

this unit, small, dispersed, pedogenic grains appear. They form an amalgamated lamina with the microfossil layer just above it. Microfossils in this layer are represented by conchostracans, ostracods, and charophyte gyrogonites (e.g., Zatoń *et al.*, 2005). Towards the top, unionid bivalves preserved in the life position form a centimetre-thick layer. The section of the lower bone bed finishes at the top with mud/clay or locally with carbonate lenses, containing well preserved molluscs remains and bones. Starting from the unionid accumulation, the barite content increases, which can be interpreted as evidence of evaporation. Mineral fillings of original pore spaces in the bones showed that they come from various early diagenetic settings (aquatic, terrestrial or mixed). Therefore, their co-occurrence must be secondary and was explained as redeposition in a mud flow (Bodzioch and Kowal-Linka, 2012). Taking into account all the features listed above, the current interpretation of the section of the lower bone bed is as follows: (1) marsh development (autochthonous bones may occur); (2) outwash of soil and nearly simultaneous transportation, concentration and deposition of calcareous grains (together with microvertebrate remains), probably in local depressions; (3) generation of a mud flow (redeposition of bones representing both exhumed and superficial remains, as well as the bones of animals killed during the catastrophic events); (4) formation of a pond colonized by microorganisms; (5) colonization by an opportunistic, unionid community (ecological succession probably according to deterioration of living conditions probably caused by rise in salinity of shallow water); and (6) complete evaporation of the pond, which could be the explanation for the mass mortality of the bivalves and other

aquatic organisms. This interpretation contradicts the previously favoured hypotheses about a large lake, inhabited by aquatic animals and autochthonous, time-averaged bone accumulation (e.g., Dzik and Sulej, 2007, 2016). The data presented, as well as published comments regarding those ideas (Szulc *et al.*, 2017), palynological analyses (Fijałkowska-Mader, 2015), and a detailed palaeoenvironmental study of the Upper Silesian Keuper (Jewuła *et al.*, 2019) support this interpretation.

However, the age of the deposit is still controversial. According to biochronological concepts based on vertebrate fossils, a Carnian age was suggested (e.g., Dzik and Sulej, 2007, 2016; Lucas, 2015). However, ambiguities in the biostratigraphy of continental deposits (e.g., Becker, 2015; Szulc *et al.*, 2017), as well as the facies and event stratigraphy (Racki and Szulc, 2015; Szulc *et al.*, 2015a, b), palynology (Fijałkowska-Mader, 2015) and chemical analyses (Środoń *et al.*, 2014) indicate a Norian age.

MATERIAL AND METHODS

The fossil-bearing sediment was collected manually and then screen-washed in large, flat, plastic bowls. First, the sediments were rinsed several times with clean water and stirred to remove most of the suspended clay. After the first washing, a detergent (hydrogen peroxide or acetic acid) was added to the water. The sediment was stirred hourly and the suspension was decanted again. This procedure was repeated at least five times, depending on the sediment volume and clay cohesion. The sediment particles obtained were put on sieves with a mesh size of 2–0.125 mm and submerged in clean water for the last screening process. Afterwards, the particles were dried naturally. Macroscopical fossils were taken manually from the sieves, while the rest were separated under a stereoscopic microscope, using tweezers. The collected material resulted in nearly 5,000 specimens being prepared for palaeontological analysis. In this publication, the authors follow the definition given by Heckert, which defines microvertebrates as vertebrate remains that generally are isolated elements, including teeth, bones, and scales, smaller than approximately 12.5 mm in diameter (Heckert, 2004). The most numerous specimens are fish teeth and scales; however, amphibian and reptile teeth are also very common. Postcranial elements are much less numerous and usually badly preserved and incomplete. The specimens were documented photographically, using a microscope camera attached to the light stereoscopic microscope (Leica M205 with Leica application suite V 4.10) at the Geology Department of Torino University (Italy). The authors also used a scanning electron microscope (Hitachi TM 3000 EDS) at the Faculty of Geographical and Geological Sciences of Adam Mickiewicz University in Poznań.

RESULTS

Many of the skeletal remains belong to fishes, both Chondrichthyes and Osteichthyes, temnospondyl amphibians, sauropsid reptiles and synapsids. The following text describes the systematically identified specimens.

Chondrichthyes

The Chondrichthyes or cartilaginous fishes until now had not been described in the Norian sediment sequences at Krasiejów. However, they are known from other Upper Triassic localities of the Upper Silesia region: Lipie Śląskie (Świło, 2010; Świło and Kowalski, 2011), Poręba (Sulej *et al.*, 2012), and Woźniki (Sulej, pers. comm., 2017). From the collected skeletal remains, teeth characteristic of a primitive group of chondrichthyans (Hybodontiformes) could be distinguished. Teeth crowns recognized as belonging to the hybodonts are mesiodistally wider than high, slender and the main cusp is not well developed (Fig. 2A). From the labial side, there is a very prominent cusp process, located above the recess, being the remnant of the nutrient canal, which is typical of the genus *Lonchidion* (Estes, 1964). These teeth show morphological differences that result in a different size of the nutrient canal, the labial cusp elongation and the outline of the cutting crest. This may result from a different position occupied in the tooth row or the tooth spiral on the dentary.

Osteichthyes

The skeletal remains of the Osteichthyes or bony fishes represent over 1,500 teeth, 500 scales, some cranial fragments, gill rakers of the branchial arcs, as well as lower jaws, fins and complete skeletons. The specimens mentioned can be classified as Actinopterygii or Sarcopterygii.

Actinopterygii scale morphotypes

The scales of Actinopterygii have been classified into the family Palaeoniscidae, already identified by Dzik and Sulej (2007) in the Norian at Krasiejów. Additionally, the present authors identified scales belonging to the families Redfieldiidae and Semionotidae.

Morphotype 1. Semionotidae scales (Fig. 2B) are thick rhomboidal scales with a slight ornamentation on the outer surface. They expose a hooked process in the anterior part of the scale (which is the ending of the thin ridge on the inner surface), intermeshing with the posterior indentation of the fore-scale. It is a so-called peg-and-socket articulation (Woodward, 1885, 1890; Schulze, 1996, 2016; Heckert, 2004).

Morphotype 2. Palaeoniscidae scales are characterized by their rhomboidal shape and ornamentation on the outer surface that is formed by labyrinthically bifurcating ridges (Fig. 2C; Heckert, 2004). Additionally, in some specimens, growth rings and edge serration can be seen.

Morphotype 3. Redfieldiidae (Fig. 2D) are represented by numerous, characteristic rhomboidal scales, that are massive, flat on the outer surface, with a well-developed intermeshing (dovetailing) area (Berg, 1940; Heckert, 2004). The shape variability from rhomboidal to almost quadratic may have its origin in the different placement of specific scales in the body of the fish (Giordano *et al.*, 2016).

Morphotype 4. Ctenoid scales, which belong to a derived species of Teleostei (Mookerjee, 1948; Roberts, 1993; Benton, 2005). These scales are oval in shape. They are distinct from typical cycloidal dipnoan scales in having a posteri-

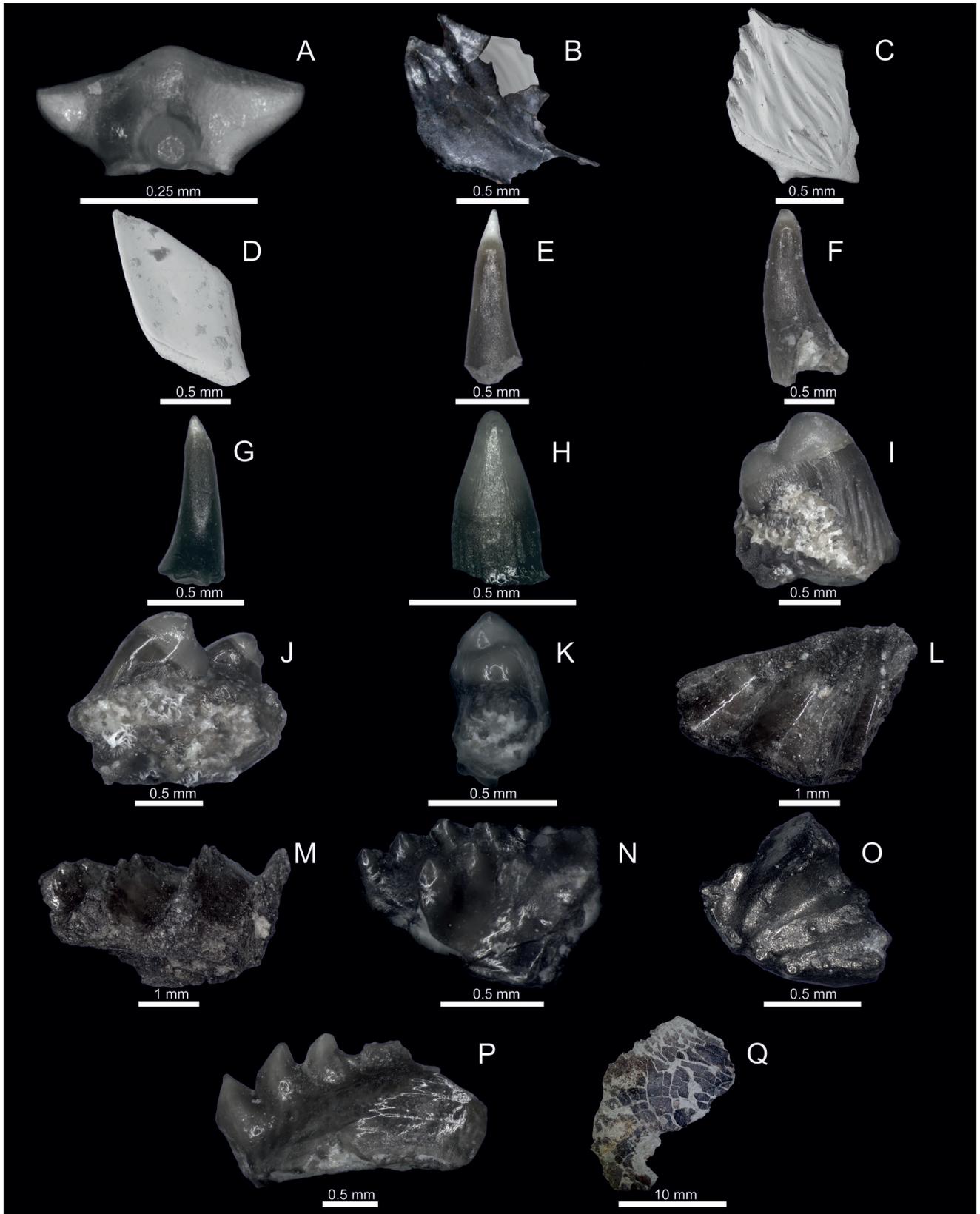


Fig. 2. Chondrichthyes and Osteichthyes elements. **A.** *Lonchidion* hybodontid tooth. **B.** Fragment of Semionotidae scale with the reconstruction (marked in grey) of original shape, based on imprint. **C.** Palaeoniscidae scale with characteristic pattern of grooves and ridges. **D.** Redfieldiidae scale with tuberculate outer surface. **E.** Actinopterygian tooth cf. *Saurichthys* (FM1). **F–G.** *Gyrolepis* sp. tooth (FM2). **H.** Actinopterygian tooth cf. *Severnichthys* (FM3). **I–J.** Indeterminate actinopterygian tooth (FM4). **K.** Actinopterygian tooth cf. Semionotidae (FM5). **L–M.** Dipnoan toothplate cf. *Arganodus*. **N.** Indeterminate dipnoan toothplate. **O.** *Ptychoceratodus* toothplate. **P.** Probable pharyngeal tooth of indeterminate dipnoan. **Q.** Dipnoan scale (posterior) fragment with distinct squamulae.

or edge serration and in their smaller size. Moreover, the growth rings are poorly visible, and posteriorly they do not occur, owing to the development of ctenii. The scales of this morphotype, discovered at Krasiejów, are referable to spinoid scales (Roberts, 1993) since they possess large, triangular spines ($\frac{1}{5}$ – $\frac{1}{6}$ of the scale length). Some of these scales have shorter, narrower spines, and these can resemble an early ontogenetic stage of the ctenii *sensu stricto*. The last characters would imply that they could be included in *Actinopterygii*. These are the earliest record of the *Acanthopterygii* fish, described in detail by Antczak and Bodzioch (2018a, fig. 6).

Actinopterygii teeth morphotypes

The teeth belonging to *Actinopterygii* have been grouped on a preliminary basis into five types (Fig. 2).

Morphotype 1 (FM1). Conical, massive teeth, slightly curved, round or oval in cross-section (Fig. 2E). The crown represents ca. $\frac{1}{3}$ of the total tooth height. Under the crown, along the entire tooth shaft, slight but very pronounced, radial striations are observed. The tip of the crown is clearly translucent. The general morphology of this type resembles the genus *Saurichthys* (Slater *et al.*, 2016; Nordén *et al.*, 2015).

Morphotype 2 (FM2). Conical, elongated and straight or slightly curved teeth, round in cross-section. The crown represents only around 25% of the total tooth height and is slightly sharpened or rounded. The tip of the crown is clearly translucent. The tooth is smooth or sometimes with a slight, transversal ornamentation (Fig. 2F, G). This morphotype resembles the teeth of *Gyrolepis* (Slater *et al.*, 2016).

Morphotype 3 (FM3). Massive tooth, cone-shaped, round in cross-section. The crown constitutes half or slightly more of the total tooth height. The apex of the crown is clearly translucent. Below the crown are visible, vertical ridges. The crown is separated from the tooth shaft by a prominent ridge (Fig. 2H). This morphotype resembles the teeth of *Severnichthys* (Storrs, 1994; Nordén *et al.*, 2015).

Morphotype 4 (FM4). Very massive and short teeth that have a dome-shaped crown with thick enamel, typical for crushing dentition. Some specimens have two cusps on the crown or one big cusp and a flat shelf. The tip of the crown is clearly translucent. Base of tooth usually has longitudinal grooves (Fig. 2I, J). Morphotype can be assigned to *Actinopterygii* indet.

Morphotype 5 (FM5). Very massive, bulbous tooth with a pyramidal crown. A clearly visible border between the tooth base and the crown. The tip of the crown is clearly translucent. Tooth base with prominent longitudinal grooves (Fig. 2K). This morphotype is similar to the dentition of representatives of the family Semionotidae (Nordén *et al.*, 2015; Slater *et al.*, 2016).

Sarcopterygii

The occurrence of *Sarcopterygii* in the Krasiejów clay pit was noted in the first palaeontological publication (Dzik *et al.*, 2000). Later descriptions mentioned large dipnoan tooth plates (Skrzycki, 2015) and scales (Antczak and Bodzioch, 2018a), as well as pharyngeal teeth and poorly preserved skull fragments (Skrzycki, 2015).

Some tooth plates with high ridges without prominent serration could represent juvenile stages of the species *Ptychoceratodus roemeri* (Skrzycki, 2015). The majority of the tooth plates in the collection described here (Fig. 2L–M) measure less than 5 mm and are represented only by fragmentary specimens. They are massive, characterized by the presence of 3–5 arms and prominent serrations along the ridges. The cusps on the ridges are sharp, laterally flattened, sometimes slightly recurved. Ventrally, large pores are visible, which are the remnants of the nutrient canal. The base of the plates is flat and wide and sometimes preserves jaw fragments. Most specimens show wear marks. The specimens described resemble *Arganodus*, known from the Late Triassic and Early Jurassic (Heckert, 2004, Heckert *et al.*, 2012); however, the possibility of inter- or intraspecific variability within *Ptychoceratodus roemeri* should be taken into consideration, as it has been demonstrated in the microscope description of the ornamentation of dipnoan scales (Antczak and Bodzioch, 2018a; Fig. 2Q).

A few specimens exhibit small (fewer than 3 mm) tooth plates with two or three distinct, robust and low ridges made by big and robust denticles (Fig. 2N). They also possess shallow furrows between the ridges. These features do not occur in *Arganodus* or *Ptychoceratodus*. This and the very fragmentary nature of the specimens impede the precise assignment of this dipnoan morphotype. In the collection, there are also fragments of probable pharyngeal teeth with multicusped, sharp edges (Fig. 2P) of a small, unidentified dipnoan.

Amphibia

Temnospondyl amphibian remains are the second most common group after fish remains. The structure of the tooth dentine is typically labyrinthine, with visible folds on the entire crown surface or at least at its base. The major morphological differences among the recovered specimens are expressed in the crown shape and the density of labyrinthine ornamentation. The most common temnospondyl teeth belong to *Metoposaurus krasiejowensis* (Sulej, 2002; species name revised by Brusatte *et al.*, 2015), which is the most abundant, large tetrapod at the locality. The teeth are conical, massive, sometimes slightly curved. They are slightly asymmetrical. The labial surface of the crown is more rounded and convex than the lingual surface, which is much flatter. Both edges of the crown form sharp, uniform cutting edges. Most specimens are the broken, upper part of the crown without folds (Fig. 3A), but more complete teeth have visible and prominent labyrinthine folds near the base. In many specimens, there are visible signs of wear on the crown tips. Identification of these teeth was possible after comparison with metoposaur mandible fragments containing preserved dentition (Fig. 3B, C). The present authors also recognize at least 4 other different tooth morphotypes in the microvertebrate layer. These morphotypes recognised as belonging to temnospondyls are much smaller and less common. They have also various morphological structures, clearly different from typical *Metoposaurus* teeth.

Morphotype 1 (AmM1). Long, conical, elliptical or circular in cross-section, slightly bent lingually. Very delicate,

labyrinthine folds at the base of the tooth (Fig. 3D). Upper part of the crown without folding, flattened with sharp edges. In some specimens, there is a visible shallow groove at the lingual surface of the crown tip. Characteristic for this morphotype is a combination of features: dense labyrinthine folds on the basal part of the crown, together with a smooth surface of enamel on the apical part. Morphotype can be assigned to Temnospondyli indet.

Morphotype 2 (AmM2). Very robust, clearly recurved, the base circular, the crown rhomboidal in cross-section (Fig. 3E). Very prominent, parallel labyrinthine folds, continuous throughout the entire crown surface, made by irregular and strong ripples. The cutting edges at the crown apex are very weakly developed or not visible. This type is the second most common of all the amphibian morphotypes in the collection. Morphotype can be assigned to Temnospondyli indet.

Morphotype 3 (AmM3). Robust, conical tooth, circular or slightly elliptical in cross-section (Fig. 3F). Characteristic triangular shape in the lateral view. Very prominent labyrinthine folds over the whole crown surface made by densely arranged, sometimes branched, longitudinal ripples. Cutting edges not visible. Morphotype can be assigned to Temnospondyli indet.

Morphotype 4 (AmM4). Short and robust, conical, circular in cross-section. Probably represented by only the upper part of the crown (Fig. 3G). Very prominent, irregular, longitudinal or sometimes branched labyrinthine folds, which are fewer in number in comparison to other morphotypes.

Crown apex without folding, pointed and sharp, but without visible cutting edges. Very rare morphotype in the collection. Morphotype can be assigned to Temnospondyli indet.

Amniotes

Amniote remains are the most taxonomically diverse; however, they are represented predominantly by teeth. At least 300 teeth can be assigned to different morphotypes and taxonomical groups, including rhynchocephalian lepidosauromorphs, various archosauromorphs and cynodonts. Elements of skulls and postcranial skeletons are far less common.

Rhynchocephalia

The occurrence of rhynchocephalian lepidosauromorphs in the Upper Triassic of Krasiejów was reported already by Dzik and Sulej (2007), but not described in detail. The collected material includes dozens of teeth and fragmentary jaws with characteristic acrodont dentition, which is the main diagnostic feature of the sphenodonts. More basal rhynchocephalians possess pleurodont or subpleurodont dentition (Evans, 1985; Klein *et al.*, 2015). They are represented by seven different morphological groups:

Morphotype 1 (RM1). Fragments of jaw bones with subpleurodont dentition. Preserved fragments of jaws are relatively gracile and low. Teeth are very large, robust and conical, circular in cross-section, with a blunt crown tip. The surface of the teeth is smooth without any traces of grooves

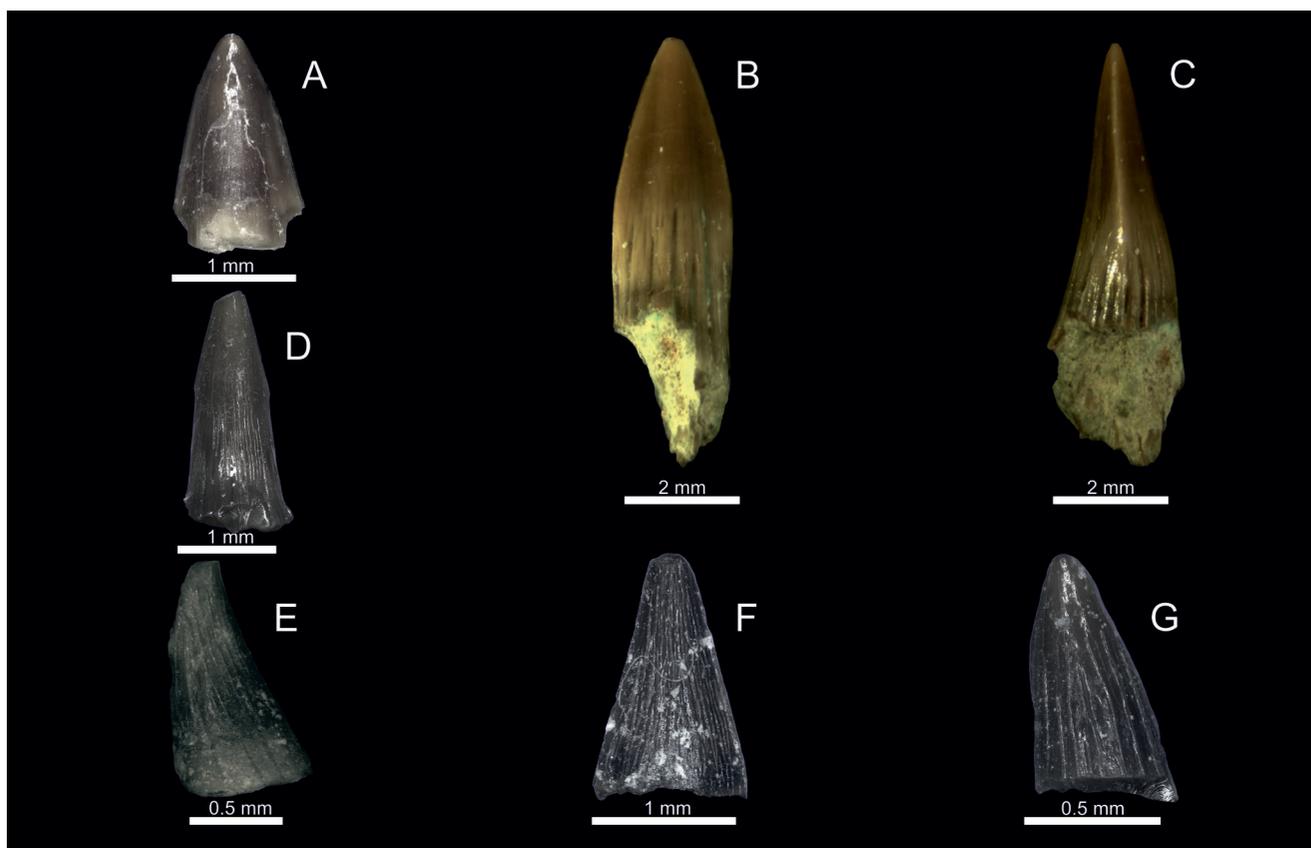


Fig. 3. Amphibian teeth. A. Upper part of *Metoposaurus* teeth. B–C. Complete *Metoposaurus* teeth. D. Temnospondyl indet. tooth (AmM1). E. Temnospondyl indet. tooth (AmM2). F. Temnospondyl indet. tooth (AmM3). G. Temnospondyl indet. tooth (AmM4).

(Fig. 4A). Morphotype can be assigned to Rhynchocephalia indet.

Morphotype 2 (RM2). Fragments of jaw bones with fully acrodont dentition. Teeth are very robust, relatively low with prominent striations made by longitudinal grooves on the lingual surface. Labial surface of the teeth is smooth without ornamentation. Teeth are circular in cross-section. The tip of the crown is slightly deflected to the lingual part of the jaw (Fig. 4B). Morphotype show similarities to *Planocephalosaurus* (Whiteside and Marshall, 2008; Whiteside *et al.*, 2017).

Morphotype 3 (RM3). Fragments of the jaws with fully acrodont dentition. Teeth on the preserved fragments are homodont lacking any ornamentation, triangular, with a sharp and pointy tip of the crown. On the lingual surface there is a singular shallow pit. The cross-section of the teeth is circular or oval. Tips of the tooth crowns are slightly recurved (Fig. 4C). Morphotype shows similarities to specimens assigned to *Diphydontosaurus* (Whiteside and Marshall, 2008).

Morphotype 4 (RM4). The most common rhynchocephalian morphotype in the collection. Fragments of jaw bones and separated teeth. Dentition fully acrodont. Teeth on preserved fragments are triangular, pyramidal in shape, circular or slightly oval in cross-section. Delicate longitudi-

nal arranged grooves are visible on both tooth surfaces (Fig. 4D). Morphotype shows similarities to some specimens assigned to *Planocephalosaurus* (Whiteside and Marshall, 2008).

Morphotype 5 (RM5). Single specimen, right dentary with two fully acrodont teeth, slightly similar to morphotype 4, but much more gracile than specimens of similar size assigned to RM4, with proportionally larger dentition, flattened and oval in cross-section. Teeth low, triangular. Front edge of the teeth slightly concave, rear edge convex. There are visible, longitudinally arranged grooves, but only on the lingual surfaces of teeth (Fig. 4E). Morphotype can be assigned to Sphenodontia indet.

Morphotype 6 (RM6). Single specimen, fragmentary dentary bone with a few attached and broken, fully acrodont teeth. Dentary very robust. Dentition unusually small, teeth with blunt low crown, circular in cross-section with no grooves (Fig. 4F). Morphotype can be assigned to Rhynchocephalia indet.

Morphotype 7 (RM7). Single specimen, fragmentary and poorly preserved dentary with four broken teeth. Dentary very robust. Dentition fully acrodont. Teeth preserved only as the crown base, circular or slightly oval in cross-section. Preserved fragment is almost 2 cm long, which leads

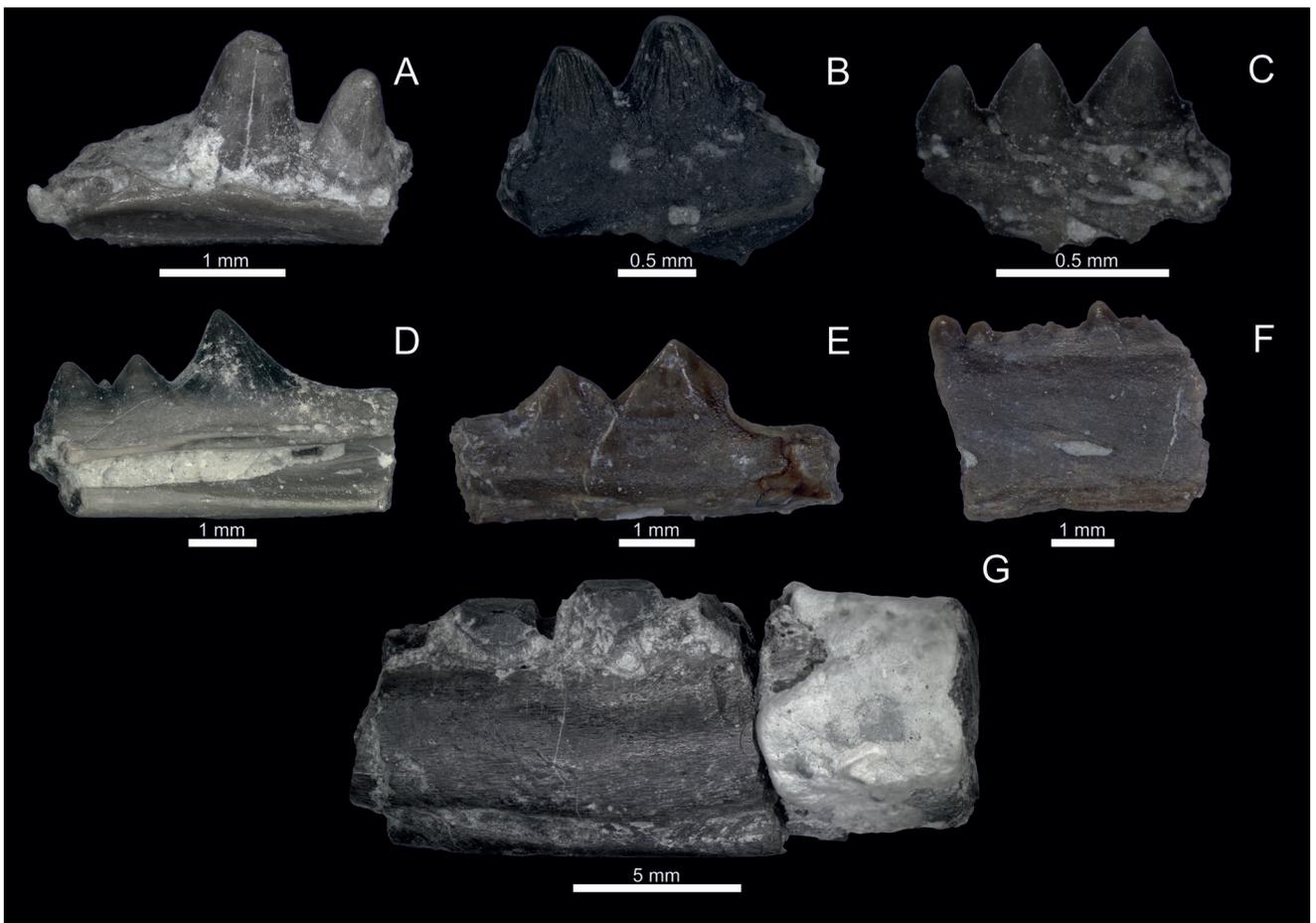


Fig. 4. Rhynchocephalian lepidosauromorphs jaw fragments with dentition. A. Rhynchocephalia indet. jaw fragment with teeth (RM1). B. Jaw fragment with teeth (RM2) – cf. *Planocephalosaurus*. C. Jaw fragment with teeth (RM3) – cf. *Diphydontosaurus*. D. Fragmentary dentary with teeth (RM4) – cf. *Planocephalosaurus*. E. Fragmentary Sphenodontia indet. dentary with teeth (RM5). F. Rhynchocephalia indet. jaw fragments with teeth (RM6). G. Fragmentary dentary (RM7) – cf. *Clevosaurus*.

to conclusion that it is the largest rhynchocephalian from the Krasiejów Quarry thus far (Fig. 4G). Morphotype show similarities to *Clevosaurus* (e.g., Heckert, 2004).

Archosauromorpha

Archosauromorphs were the main component in all Late Triassic terrestrial faunas. This group during the Triassic period diversified rapidly, owing to adaptive radiation. They occupied many different ecological niches, which resulted in a different morphological structure of dentition. There are at least 19 different tooth morphotypes in the collection at present with various characteristic features. Most of them probably belong to archosauromorphs from different groups, especially to protorosaurs and more advanced archosaurs, like pseudosuchians, crocodylomorphs and dinosauromorphs (Heckert, 2004).

Morphotype 1 (ArM1). Very common morphotype at the locality. Teeth are tall, triangular in shape, laterally compressed and lack enamel. Some specimens are gently recurved. Several specimens bear resorption pits. These teeth represent indeterminate archosauromorph (Fig. 5A). On the basis of previous studies by Heckert (2004), they may be interpreted as digested teeth. However, the abrasive effect of transportation should be taken into account.

Morphotype 2 (ArM2). Tall, spatulate in shape, laterally compressed and lacking enamel with a prominent pocket in the anterior part, near the tooth base. Visible resorption pits. Most probably, they represent shed and abraded (digested), archosauromorph teeth (Fig. 5B).

Morphotype 3 (ArM3). Tall, lanceolate in shape, laterally compressed and lacking enamel. Front edge of the crown concave, rear edge straight. Visible resorption pits. Most probably, they represent shed and abraded (digested), archosauromorph teeth (Fig. 5C).

Morphotype 4 (ArM4). Relatively short teeth, asymmetrical and gently recurved in shape. This morphotype bears small anterior and posterior flanges without serration. On the enamel, visible, longitudinal striations on labial surface of tooth (Fig. 5D). This morphotype shares some morphological features, observed in tanytropheid protorosaurian dentition, such as *Tanytrachelos* (Heckert, 2004).

Morphotype 5 (ArM5). Very tall, recurved teeth, with clearly visible serrations at the posterior edge of the crown. Anterior edge of the crown in some specimens also could have visible serrations, although less developed. The crown bears characteristic, longitudinal striations on both lingual and labial surfaces (Fig. 5E). Morphotype can be assigned to Archosauriformes indet.

Morphotype 6 (ArM6). Moderately tall, robust and asymmetrical tooth. Triangular in shape, oval in cross-section. Delicate serration on the upper half of the posterior edge of the crown. Anterior edge without serrations. The crown

bears characteristic, longitudinal striations on both surfaces, but much more prominent on lingual surface (Fig. 5F). Morphotype can be assigned to Archosauriformes indet.

Morphotype 7 (ArM7). Moderately tall, very robust teeth, anteriorly convex, slightly backward recurved. Teeth asymmetrical, the crown tip bowed lingually. On the anterior tooth edge, numerous denticles can be seen. No denticles on the rear edge of the teeth. On the lingual surface, shallow groove running from the base to the top of the crown is visible. Wear signs are often on the crown tip and denticles (Fig. 5G). Morphotype can be assigned to Archosauriformes indet.

Morphotype 8 (ArM8). Very rare. Low and robust, laterally compressed teeth, with strong, prominent denticles on both edges. The teeth are slightly asymmetrical in occlusal view, with crown tip bowed lingually. On the lingual surface, shallow grooves running from the base to the top of crown are visible. The crown surface possesses striations (Fig. 6H). Morphotype can be assigned to Archosauriformes indet.

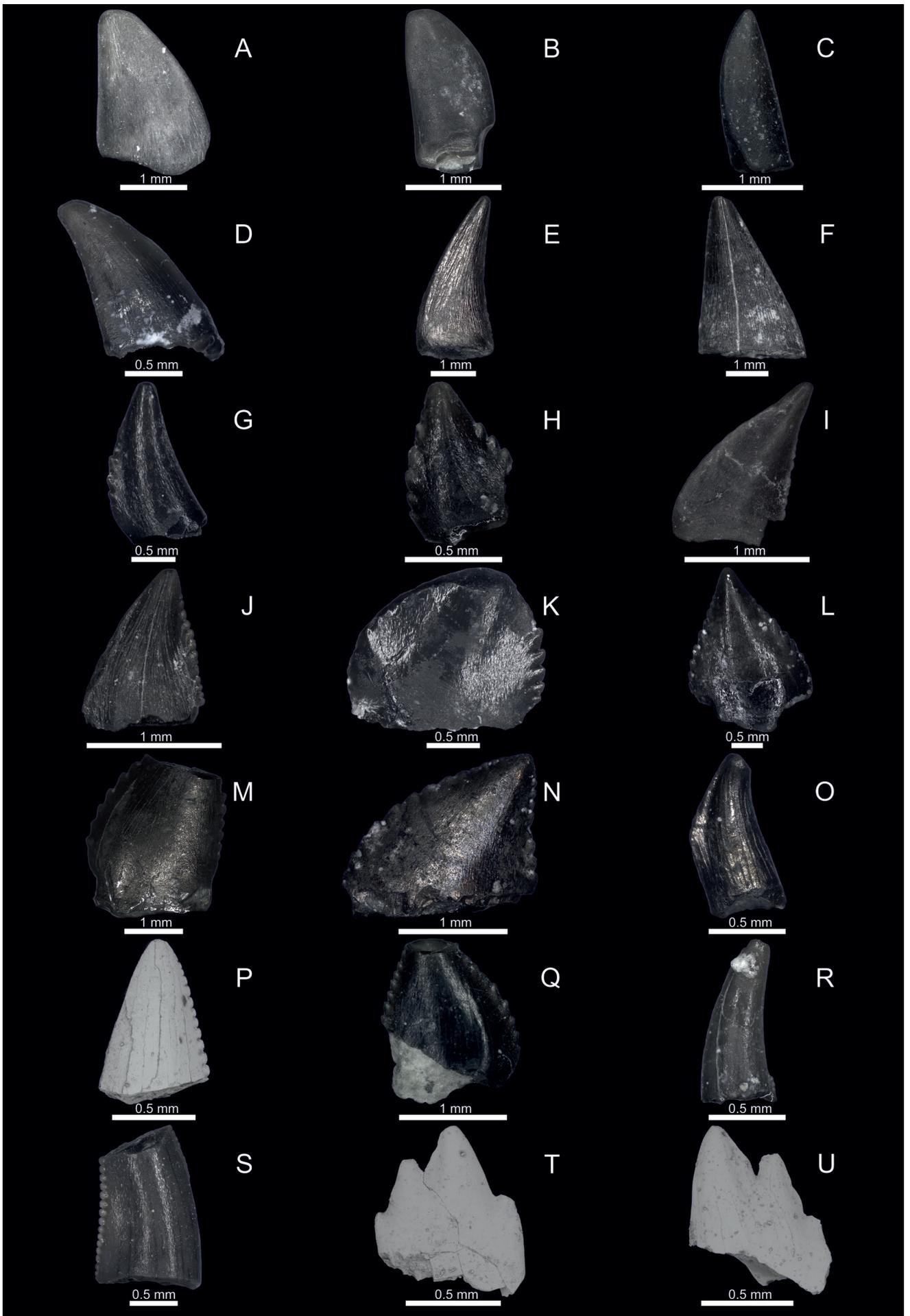
Morphotype 9 (ArM9). Very rare. Tall and gracile teeth with backswept orientation, laterally compressed, with long and thin crown apex. The teeth are asymmetrical in occlusal view, with crown tip slightly bowed lingually. There are visible denticles on both edges, often with strong signs of wear, especially on the anterior edge of the tooth. Some specimens have delicate striations on the lingual surface of the crown (Fig. 5I). This morphotype shows some similarities to dentition, assigned to *Protocovasaurus* (Heckert, 2004).

Morphotype 10 (ArM10). Very rare. Moderately tall, robust teeth, triangular in shape, slightly backswept. The teeth are asymmetrical in occlusal view, with crown tip slightly bowed lingually. There are very prominent and strong denticles on the posterior edge of the tooth. The anterior edge possesses longitudinal flange without denticles. Both surfaces of the crown with prominent, longitudinal striations (Fig. 5J). This morphotype shares some similarities with basal crocodylomorph teeth (Heckert, 2004).

Morphotype 11 (ArM11). Very rare. Low and long tooth, strongly laterally compressed, semicircular in shape, with strong signs of wear on anterior edge and upper part of the crown. On the posterior edge, very prominent and strong denticles are visible. On the anterior edge, denticles strongly abraded, but still visible (Fig. 5K). Morphotype can be assigned to Pseudosuchia indet.

Morphotype 12 (ArM12). Quite common. Moderately tall, leaf-shaped, asymmetrical and slightly backswept teeth. The crown tip slightly bowed lingually. Both edges of the crown with prominent row of denticles. Anterior denticles sometimes with signs of wear. On lingual surface of the crown, longitudinal shallow groove runs from base to the tip of the crown (Fig. 5L). The base of the tooth is rounded on

Fig. 5. Sauropsid (A–S) and Synapsid (T–U) teeth morphotypes. **A–C.** Probably digested reptilian teeth (ArM1, ArM2, ArM3). **D.** cf. Tanytropheidae tooth (ArM4). **E.** Archosauriformes indet. tooth (ArM5). **F.** Archosauriformes tooth (ArM6). **G.** Archosauriformes tooth (ArM7). **H.** Archosauriformes tooth (ArM 8). **I.** cf. *Protocovasaurus* tooth (ArM9). **J.** cf. basal Crocodylomorpha tooth (ArM10). **K.** *Pseudosuchia* indet. tooth (ArM11). **L.** Pseudosuchia indet. tooth (ArM12). **M.** cf. Sauropodomorpha tooth (ArM13). **N.** Pseudosuchia indet. tooth (ArM14). **O.** Archosauriformes tooth (ArM15). **P.** Fragmentary crown of Archosauriformes tooth (ArM16). **Q.** cf. *Reuelto-saurus* tooth (ArM17). **R.** Archosauriformes tooth (ArM18). **S.** Basal theropod tooth (ArM17) **T–U.** Cynodont molar teeth.



both edges. This morphotype shows some similarities to the dentition assigned to *Ornithischia* (Heckert, 2004). However, the latest works suggest that the dentition of some Late Triassic pseudosuchians has morphology convergent with early ornithischian dinosaurs; therefore, the authors assign this morphotype to *Pseudosuchia* indet. (Irmis *et al.*, 2007).

Morphotype 13 (ArM13). Single, incomplete specimen. Robust and relatively big tooth, oval in cross-section, slightly backswept. With denticles on both edges of the crown. Denticles on the anterior edge are much more prominent. The base of the tooth is bulbous, with a characteristic rounded bulge on the anterior part (Fig. 5M). This morphotype shows some similarities to dentition, assigned to basal *Sauropodomorpha* (Benton *et al.*, 2000; Yates, 2003).

Morphotype 14 (ArM14). Low, very robust, strongly backswept and laterally compressed teeth. The base of tooth is massive, oval in cross-section. Both anterior and posterior edges of the teeth with prominent row of denticles along the entire length. The size of the denticles decreases from the base to the tip of the crown (Fig. 5N). This morphotype can be assigned to *Pseudosuchia* indet. (Nesbitt, 2006; Irmis *et al.*, 2007).

Morphotype 15 (ArM15). Very small, spatulate, slightly recurved and strongly asymmetrical tooth. The tip of the crown clearly bends lingually. The base is circular in cross-section. The anterior edge creates prominent flange with signs of wear on denticles. The posterior edge of the tooth is rounded without flange and denticles. Lingual surface of the crown with prominent striations, labial surface smooth (Fig. 5O). Unique traits of this morphotype prevent direct identification of this archosaur.

Morphotype 16 (ArM16). Single fragmentary tooth. The preserved fragment is conical tip of crown, symmetrical, without signs of bending. The most characteristic feature is a row of fine serration on the posterior edge of the crown. Anterior edge rounded, without any serration (Fig. 5P). Morphotype can be assigned to *Archosauriformes* indet.

Morphotype 17 (ArM17). Rare, backswept, moderately tall and leaf-shaped. Oval in cross-section. Bulbous and robust base of the crown. Both edges with carina made by prominent denticles. Anterior edge of crown with denticles, showing signs of abrasion (Fig. 5Q). This morphotype shows similarities to *Revueltosaurus* (Heckert, 2004).

Morphotype 18 (ArM18). Rare teeth, slightly recurved, tall and circular or slightly oval in cross-section. At the posterior part of the tooth near the base, small row of serration is visible, made by only few tubercles. Upper part of posterior edge smooth. The crown surface smooth, without any striations (Fig. 5R). Morphotype can be assigned to *Archosauriformes* indet.

Morphotype 19 (ArM19). Rare teeth, tall and distinctly recurved, with slightly asymmetrical crown. The base of the tooth oval in cross-section. The most characteristic feature of this morphotype is prominent serration on the posterior edge of the crown, forming fine, flattened cutting edge. Anterior edge is more rounded and bears row of serrations, but tubercles are much smaller, sometimes almost not visible (Fig. 5S). This morphotype can be assigned to the basal theropod dinosaur (Heckert, 2004; Buckley and Currie, 2014).

Cynodontia

Very important discoveries at Krasiejów site are cynodont teeth, which are rare in the Late Triassic vertebrate communities of the northern hemisphere (e.g., Bonaparte *et al.*, 2003). The main characteristic feature of cynodont and early mammal dentition is heterodonty, which means that the teeth from different parts of the jaws have different morphological structure. There are about ten specimens in the collection, which represent molar teeth. All the teeth are asymmetrical, multicusped (from 2 to 4 cusps) with different sizes of cusps. Central cusp is always the most robust and highest, sometimes with little posterior curvature. The anterior and posterior cusps are much smaller (Fig. 5T–U). All the specimens are preserved without roots. Teeth from Krasiejów show many similarities to non-mammaliform eucynodont *Polonodon*, recently described from the Woźniki locality, in Poland (Sulej *et al.*, 2018), and could represent the same or a similar taxon.

DISCUSSION

Most of the initially identified taxa from the Krasiejów locality belong to the tetrapods (temnospondyls, lepidosauromorphs, archosauromorphs). In terms of the quantity of fossils obtained, the most numerous are specimens of the morphotypes, assigned to taxa of Actinopterygii and hybodont sharks. Almost 80% of the recovered microfossils constitute the teeth and scales of various Osteichthyes and the teeth of the hybodont, *Lonchidion*. These data are consistent with previous studies, which showed that aquatic taxa compose the majority of the Upper Triassic microfossil-bearing localities (Fraser and Walden, 1983; Heckert, 2002, 2004; Heckert *et al.*, 2012; Mears *et al.*, 2016; Slater *et al.*, 2016; Landon *et al.*, 2017; Cross *et al.*, 2018). Relatively frequent finds of nearly complete fish remains or even complete, articulated skeletons at the Krasiejów Quarry (Kowalski and Janecki, in prep.) indicate the presence of at least temporary aqueous environments, such as small lakes, ponds or ephemeral rivers.

Quite remarkable is the discovery of chondrichthyan remains at the Krasiejów site, due to the fact, that in Poland they have been recognized and described from Late Triassic freshwater sediments, only in the Upper Norian deposits of Lipie Śląskie (Dzik *et al.*, 2008; Świło, 2010), which represent the upper section of the Lisowice bone-bearing bed (*sensu* Racki and Szulc, 2015; Szulc *et al.*, 2015). The presence of the *Lonchidion* hybodont is the first occurrence of this taxon in the Upper Triassic sediments of Poland, in spite of the fact that this taxon is widely distributed in other Triassic and Jurassic localities in Europe and North America (Estes, 1964; Murry, 1981; Fisher *et al.*, 2011). The validity of this genus was often under debate, as some authors (e.g., Duffin, 1985) recognized it as a synonym of *Lissodus*. However, a few other researchers acknowledge the validity of *Lonchidion* (Rees, 1998; Rees and Underwood, 2002) and the assignation to this genus still occurs in some recent papers (e.g., Heckert, 2004; Heckert *et al.*, 2007). As, the specimens of the present account are morphologically most similar to the teeth described by Heckert (2004), his assignation is used here.

On the basis of both scales and teeth, actinopterygians from the Krasiejów Quarry are very diverse and include taxa from the Redfieldiidae, Semionotidae and Palaeoniscidae. Some of the teeth have affinities to taxa, such as *Gyrolepis* and *Saurichthys*, which are widely distributed at other Late Triassic localities (e.g., Landon *et al.*, 2017; Cross *et al.*, 2018). Another notable discovery at the Krasiejów site is the oldest occurrence of rare Late Triassic forms of Teleostei with ctenoid scales (Antczak and Bodzioch, 2018a). The recorded fish fauna exhibits many similarities to those described at other localities and is comparable to ones from the sites in the Late Triassic of Europe and North America, at least to the family level. However, detailed comparison with other Polish Late Triassic localities is not possible, owing to the poor record of the fish fauna at these sites.

Dipnoans are very well represented in the microfossil collection, mainly as fragmentary tooth plates. Other skeletal elements are much less common; however pharyngeal teeth, fragments of skulls and broken fragments of scales were also found. Some specimens can be assigned to the Krasiejów lungfish *Ptychoceratodus* (Skrzycki, 2015), although their small size indicates that they belong to young individuals. However, most of the sarcopterygian remains uncovered are composed of fragmentary toothplates, quite distinct morphologically from *Ptychoceratodus*. Therefore, the present authors presume the occurrence of another taxon. The authors tentatively assign these specimens to *Arganodus*. Extant, closely related species or subspecies of dipnoans live together in small aquifers (e.g., *Protopterus* in central Africa, which usually inhabited temporary water bodies). High diversity in one (fossil) locality has been observed in the Cretaceous of South Tunisia (Fanti *et al.*, 2016: six taxa from Ain el Guettar). Thus, the large variety of dental plates and scales (Antczak and Bodzioch, 2018a) found at Krasiejów can be explained by the high taxonomic diversity of dipnoans living together in the Late Triassic.

Remains of large temnospondyls (*Metoposaurus*, *Cycloptosaurus*) are the most common fossils of the Krasiejów macrofauna. Fossils of small amphibians in the microfossil-bearing layer are also very common. At least five different tooth morphotypes, with features characteristic for temnospondyl amphibians, could be recognized. Fragmentary teeth of the most common temnospondyl taxon at Krasiejów (*Metoposaurus*) are also dominant elements among the tetrapods in the microfossil layer and they are clearly different in shape and size from the rest of the morphotypes described. There is a possibility that some of these morphotypes belong to juvenile *Metoposaurus* individuals; nevertheless, owing to their high morphological differences, their affiliation to other taxa cannot be excluded. This presumed higher taxonomic diversity may suggest, that other temnospondyl taxa lived in different environments (as proposed by Antczak and Bodzioch, 2018b) and their remains were transported by ephemeral rivers or floods and accumulated in small depressions during a monsoon season (Bodzioch and Kowal-Linka, 2012). Isolated teeth of *Metoposaurus* from the Krasiejów locality are almost always preserved as fragments and usually they are represented by the smooth and sharp upper part of the crown. At some other Late Triassic

localities, for example, in the North American Chinle Group, various temnospondyl teeth morphotypes were described and the presence of several different taxa was suggested in a few studies (Heckert, 2002, 2004, 2005; Heckert *et al.*, 2012). Other amphibian, skeletal elements from the microfossil level are much less common, including a few small skull and jaw fragments without complete teeth and also few limb elements. All these fragments are in a poor state of preservation and for more accurate identification new finds are necessary.

Among other tetrapods found in the microfossil layer in the Krasiejów Quarry, the second most numerous and most diverse are the sauropsid reptiles. The reptilian macrofauna from this locality is dominated by both aquatic (phytosaur) and land-dwelling archosaurs (*Stagonolepis aetosaur*). Other reptilian taxa are much less common in the fossil record and include rauisuchian *Polonosuchus* and non dinosaurid dinosauromorph *Silesaurus* (the latter previously described as a possible representative of early dinosaurs) (Mazurek and Słowiak, 2009). The only small reptile taxon described from Krasiejów is *Ozimek*, which most probably belongs to the protosaurian lineage and is closely related to *Sharovipteryx* (Dzik and Sulej, 2016). Other small reptiles were not described and until now there have been only rare remains of sphenodontians mentioned in the early years of Krasiejów research (Dzik and Sulej, 2004). The microfossil layer provided a very rich collection of sauropsid taxa, distinguished by at least 26 different tooth morphotypes. Other skeletal elements, such as skull fragments, limb bones and vertebrae, are much more sparse and they are often in a very poor state of preservation. The reptilian microfossils could be divided into two groups: rhynchocephalian lepidosauromorphs and archosauromorphs. In the Late Triassic, rhynchocephalians were very common in almost all terrestrial faunal communities. They occupied niches, similar to those of extant lizards, such as small insectivores and omnivores, with a tendency to develop herbivory. The most characteristic feature of this group is the acrodont dentition – the teeth are fused with the jaw bones, creating one solid, bony element. Early forms had more primitive dentition – pleurodont or subpleurodont. At the Krasiejów Quarry, both of the more primitive rhynchocephalians and derived forms with fully acrodont dentition were found. Triassic localities, where rhynchocephalian remains were found, usually contain more than one sympatric taxon (Heckert, 2004, 2005; Klein *et al.*, 2015; Whiteside *et al.*, 2017). At Krasiejów, there are at least seven clearly different morphotypes of rhynchocephalian dentition, all of them with very characteristic features. The authors recognised that the specimens may represent at least 3 separate taxa (cf. *Clevosaurus*, cf. *Planocephalosaurus* and cf. *Diphydontosaurus*).

Other small reptile remains from the Krasiejów microfossil layer can be distinguished as various archosauromorphs, belonging to several taxonomic groups. So far, the authors have recognized at least 19 different tooth morphotypes (more than 300 specimens), which could belong to different taxa. A taxonomically rich assemblage of small archosauromorphs is observed for the first time in the Late Triassic fossil record of Poland. The only other, diverse accumulation of Triassic terrestrial reptilian microfossils

described from Poland comes from the Czatkowice Lower Triassic karst beds (Borsuk-Białynicka and Evans, 2009). However, its fossil record, represents a less taxonomically diverse community. Small archosauromorph fossils from other Late Triassic Polish localities, such as Lipie Śląskie and Woźniki, have not been described precisely; therefore, it is hard to compare the Krasiejów reptilian fauna to other Polish assemblages of similar age. On the other hand, many of the Krasiejów archosauromorph morphotypes show significant similarities to specimens from fossil localities in the USA (Chinle Group) (Heckert, 2002, 2004, 2005; Heckert *et al.*, 2012) and England (Fraser and Walden, 1983; Van der Berg *et al.*, 2012). Some specimens from the microfossil collection show traces of abrasion, which could be caused by the digestive system (indicated by the lack of enamel); a similar condition was observed in some specimens from Chinle Group (e.g., Lucas *et al.*, 2010; Heckert *et al.*, 2012). Some teeth have traces of wear from feeding or transport. Sometimes, a grated tip of the crown or denticles is seen, but with the enamel preserved. Characteristic for many archosauromorph teeth morphotypes is the presence of different types of ornamentation, serrations along the tooth edges and denticles or striations on enamel. These features could be integral to a more accurate classification of some of the specimens in future research. Teeth belonging to morphotype 4 show similarities to the dentition described as probably belonging to a small, aquatic, tanystropheid protorosaurian, such as *Tanytrachelos* (Heckert, 2004). Of particular note are the teeth of an early theropod dinosaur (ArM16; Heckert *et al.*, 2012) and morphotypes showing similarities to basal crocodylomorphs (ArM10) and basal sauropodomorphs (ArM13), that could be one of the earliest representatives of these groups in the Polish fossil record, in the case of theropoda representatives from the Late Triassic of Poland, previously described from two other localities (Niedźwiedzki, *et al.*, 2014; Skawiński *et al.*, 2017). Some of the other specimens are similar in dentition to morphotypes, which were described by Heckert (2004), as the teeth of early ornithischians (ArM12, ArM13). However, researchers in subsequent studies stated that the affiliation of these kinds of morphotypes to early dinosaurs is very dubious, therefore they might be recognised as remains of (most probably herbivorous) pseudosuchians (Parker *et al.*, 2005; Irmis *et al.*, 2007; Nesbitt *et al.*, 2007). The occurrence of other pseudosuchian reptiles with dentition similar to that of *Protecovasaurus* (ArM9) and *Reveltosaurus* (ArM11) also might be noted.

The remains of cynodonts are usually rare in Upper Triassic sediments and in Poland. They were found only at one other locality – the Woźniki clay pit, in Upper Silesia (Sulej *et al.*, 2018). More advanced synapsid remains belonging to a probable, early representative of mammaliform (*Hallatherium* sp.) was found at the Lipie Śląskie clay pit, in Lisowice (Świło *et al.*, 2014). In the collection from the Krasiejów locality, there are only 10 fragmentary specimens of molar teeth. The Krasiejów cynodont specimens show similarity to teeth of a recently described *Polonodon* (Sulej *et al.*, 2018) from Woźniki.

The taxonomic diversity presented herein corresponds with the geological setting of the Triassic at Krasiejów, which includes redeposited material after flash floods. This indicates an environment with periodic or stable water reservoirs and rivers (Szulc, 2005, 2007; Gruszka and Zieliński, 2008; Bodzioch and Kowal-Linka, 2012; Antczak and Bodzioch, 2018b). The environment of Krasiejów during the Late Triassic might have been similar to the modern gilgai relief of, for example Australia (Szulc *et al.*, 2015). Such a diverse environment was the habitat of terrestrial, semi-aquatic and aquatic animals, the remains of which were mixed and deposited or redeposited together from closer (Lucas *et al.*, 2010) and further distances (Konieczna *et al.*, 2015) after a flash-flood.

The predominant occurrence of teeth (just few bones were found – most of them fragmentary) could be an indicator of hydraulic transport, which sorted the microvertebrate remains. However, the degree of sorting was not high, as the authors found teeth of different sizes.

CONCLUSIONS

This description of microvertebrate remains depicts a remarkably diverse faunal assemblage, including a hybodont shark, palaeoniscids, semionotids, redfieldiids, dipnoans, temnospondyls, cynodonts, rhychocephalian lepidosauromorphs, and various small archosauromorphs, such as protorosaurians, pseudosuchians, theropod dinosaur and possibly a basal sauropodomorph and a crocodylomorph. Therefore, this research provides information about the occurrence of many, previously unrecorded or not well described taxa, at Krasiejów and other Polish localities. The research increases our knowledge about the Late Triassic palaeoecology of this region. These data can provide additional information, which may be helpful for the age correlation of the Krasiejów deposits.

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