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ARTICLE

Eucynodont teeth from the Late Triassic of Krasiejów, Southern Poland

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ABSTRACT

Recent discoveries of Mammaliamorph teeth in the Keuper of southern Poland have extended the global record of eucynodonts in the Late Triassic and revealed a significant diversity of the group at that time. Here, we expand on this record with the description of new cynodont postcanine teeth from the Krasiejów bone bed. They show the dental morphology typical for Dromatheriidae, with a single root and crown without cingulum. We assigned them to *Polonodon woznikensis*, described from Woźniki. None of the 38 teeth from Krasiejów and Woźniki exhibit signs of serious wear, potentially indicating a very fast rate of tooth replacement in *Polonodon*.

Introduction

The specialised dentition was one of the key features of the mammalian origin and their diversification (Kühne 1958; Clemens 1980, 1986, 2011; Sigogneau-Russell 1989; Sigogneau-Russell and Hahn 1994; Godefroit and Battail 1997; Soares et al. 2011; Debuysschere et al. 2015; Martinelli et al., 2016; Martinelli et al. 2017a, b). In the evolution of therapsids, teeth differentiated into incisors, canines, and postcanines early (Kemp 1982). One of the crucial aspect of the evolution of dentition, in evolution to cynodonts, is the subdivision of originally single cusps in the postcanine teeth to the multicusps crown of premolars and molars. Prozostrodonts (Kemp 1982, 1988) is characterised by features pointing towards mammaliaforms in cranial and postcranial skeleton (Rubidge and Sidor 2001). Eucynodonts especially Probainognathia (e.g., *Prozostrodon*, therioherpetids, dromatheriids, brasilodontids) showing a mediolaterally compressed, single-rooted tricuspid or tetracuspid postcanines, are known from numerous sites restricted to the late Middle and Late Triassic (Hahn et al. 1984, 1994; Datta et al. 2004; Heckert 2004; Bonaparte et al. 2003, 2005; Bonaparte 2013; Soares et al. 2014; Abdala and Ribeiro 2010; Kligman et al. 2020, Martinelli et al., 2016, Emmons 1857, Marsola et al. 2018).

Fossil dromatheriids are mostly represented by isolated teeth, although known from some isolated dentaries (e.g., *Dromatherium sylvestre* Emmons 1857, *Microconodon tenuirostris* Osborn 1886; see Simpson 1926; Sues 2001). They are known from the Carnian-Norian strata of India, North America, and from the Norian-Rhaetian of Europe (Kielan-Jaworowska et al. 2004). The Dromatheriidae was recently considered to include *D. sylvestre, M. tenuirostris, Pseudotriconodon wildi* Hahn et al. (1984), *Therioherpeton cargnini* Bonaparte and Barberena (1975), *Tricuspes* spp., and *Meurthodon gallicus* Sigogneau-Russell and Hahn (1994) (see Hahn et al. 1984, 1994; Godefroit and Battail 1997), but other authors recognise the validity of the Therioherpetidae family (see Oliveira 2006; Bonaparte and Crompton 2017; Bonaparte and Barberena 1975, 2001; also Abdala and Ribeiro 2000). Datta et al. (2004) described several isolated teeth from the Carnian Tiki Formation of India (Mukherjee et al., 2012) and included them in *Rewaconodon tikiensis* Datta et al. (2004). Bhat et al. (2020) describe the new

dromatheriid, *Inditherium floris* from the same formation. A similar isolated tooth collected from the Carnian deposits (Locality L-1312, lower Kalgary) in Texas, USA (Heckert 2004: fig., p. 34) was tentatively assigned to aff. *Rewaconodon tikiensis*).

Here, we describe 10 isolated postcanine teeth of a representative of the Dromatheriidae, which come from the Upper Triassic (Keuper) strata of the Krasiejów locality (Opole Silesia, southern Poland). They were gathered from greenish-grey lenses of mud rich in calcareous grains in the lower part of the so-called grey unit, exposed in a few places in the Krasiejów locality, which is rich in plants and small vertebrate remains. Some teeth were part of a large collection of microfossils from Krasiejów which were described recently by Kowalski et al. (2019). Teeth are, in most cases, the only record of eucynodonts that could be used in biodiversity analysis.

Institutional abbreviations. – UOPB Institute of Biology University of Opole, Opole, Poland; UFRGS Palaeontology and Stratigraphy Department of the Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil; ZPAL, Institute of Palaeobiology, Polish Academy of Sciences, Warsaw, Poland.

Geology

The strata exposed in Krasiejów belong to the Patoka Member of the Grabowa Formation which is considered to be Late Carnian (Dzik and Sulej 2007, 2016, Pacyna 2014) or Early Norian (Szulc et al. 2015a, b), and correspond to the uppermost part of the middle Keuper deposits of the Germanic Basin (e.g. Szulc et al. 2006; Franz 2008; Bodzioch and Kowal-Linka 2012).

The exact age of the deposits from Krasiejów is difficult to establish. There is no locality in Poland with complete sequence of the Upper Triassic sediments that could be used for correlation of more or less uniform siltstone and mudstone successions (Figure 1). Nevertheless, lithostratigraphic approach points to the Norian age of the locality, based on presence of evaporites (Szulc et al. 2015). On the other hand, previously done biostratigraphy studies suggest a Carnian age for Krasiejów sediments, based on presence of several groups including charophythes, vascular plants,
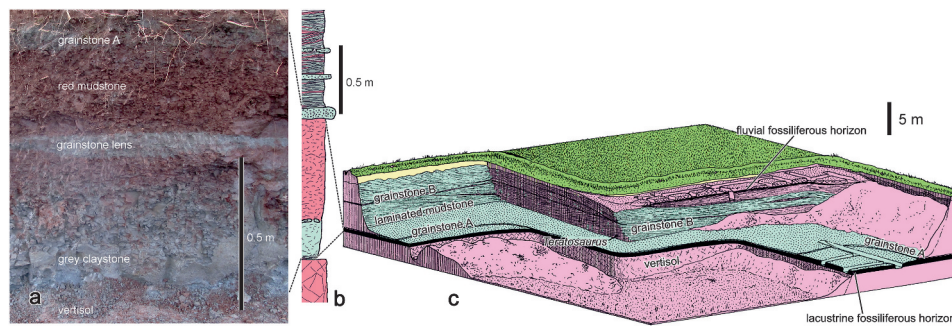
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Figure 1. Krasiejów clay pit yielding eucynodont teeth. **A**. photograph of the wall with exposed fossiliferous lower horizon. **B**. stratigraphic section in the part of outcrop with fossiliferous lower horizon. **C**. diagrammatic representation of the NW corner of the quarry with location of fossiliferous horizons (after Dzik 2003).

spinicaudatans and the large vertebrate *Parasuchus* (Dzik and Sulej 2007, 2016; Butler et al. 2014; Kozur and Weems 2010, Pacyna et al. 2014; Pacyna 2019; Zatoń et al. 2005).

Krasiejów is the most famous for the abundant and well-preserved remains of large vertebrates, representing both terrestrial and amphibious or aquatic tetrapods (Dzik et al. 2008; Niedźwiedzki et al. 2011, 2012). Among the animals connected with aquatic environment, the most frequent are remains of the temnospondyls *Metoposaurus krasiejowensis* and *Cyclotosaurus intermedius* and less numerous phytosaur *Parasuchus* sp. (Sulej 2002, 2007; Sulej and Mayer 2005; Dzik and Sulej 2007). Common are also dental plates and scales of the dipnoan fish *Ptychoceratodus roemeri* (Skrzycki 2015). Among the terrestrial fauna probably the best known is the herbivorous dinosauriform *Silesaurus opolensis* – possible ancestor of ornithischian dinosaurs (Dzik 2003; Piechowski and Dzik 2010; Piechowski et al. 2014, 2019; Piechowski and Tałanda 2020). Dominant are remains of the omnivorous aetosaur *Stagonolepis olenkae* (Pseudosuchia), which probably was a prey for the carnivorous rauisuchid *Polonosuchus silesiacus* (Pseudosuchia), known from a partially preserved skull, mandible, cervical and caudal vertebrae (Sulej 2005, 2010; Brusatte et al. 2009; Antczak 2015; Dróżdż 2018). Recently the list of the Krasiejów animals expanded with the discovery of the gliding animal *Ozimek volans*, similar to *Sharovipteryx* (Dzik and Sulej 2016). Tałanda (2016) identified a probable new species of a rhynchocephalian. Coprolites also present in the locality, were described by Qvarnström et al. (2019).

The vertebrate microfossils from Krasiejów, similarly to other Keuper bone-bearing sites in the Germanic Basin, consist primarily of aquatic animals remains, among which the most abundant are scales and teeth of the actinopterygian fishes (e.g. Antczak and Bodzioch 2018), along with teeth and dermal denticles of small sharks (Kowalski et al. 2019). These authors described also teeth of archosaurs and sphenodonts.

Materials and methods

The 10 eucynodont teeth (Figure 2, Figure 3) studied here were gathered from several greenish-grey lenses of mud rich in calcareous grains, occurring in the lower part of the fossiliferous layer (Figure 1). The lenses are composed of small limestone concretions that were apparently concentrated by winnowing. The rock samples, from which the teeth were extracted, had been collected during the excavation camps between 2014 and 2016. They were screen-washed during fieldwork and dried in the preparatory lab at the Institute of Palaeobiology, PAS and Laboratory of Palaeobiology

and Evolution in the Department of Biosystematics at the UO. Collection method is described in Kowalski et al. (2019), where microfossils from Krasiejów were described. The obtained material was manually sorted under a microscope. The specimens ZPAL AbIII/3405-3407 and UOPB-1180, UOPB–1183 were photographed under SEM housed in the Institute of Palaeobiology Polish Academy of Sciences. Based on the microtomography scans, 3D models of the teeth (UOPB-1177-UOPB-1179) were generated with free to use programs Fiji, Drishti and MeshLab (Cignoni et al. 2008; Shindelin et al. 2012; Limaye 2012). Broken specimen UOPB-1177 was digitally reconstructed in MeshLab.

Systematic palaeontology

Order THERAPSIDA Broom (1905)
    Suborder CYNODONTIA Owen (1861)
    Infraorder EUCYNODONTIA Kemp (1982)
    Family DROMATHERIIDAE Gill (1872)
    POLONODON WOZNIKIENSIS Sulej et al. (2020)
Diagnosis (after Sulej et al. 2020). Lower postcanine teeth characterised by labiolingual compressed crown with four or six cusps. Cusps a, b, c, d are aligned in longitudinally; cuspules may be present on the lingual and/or labial sides; incipient division of the root by shallow lingual and labial depressions; no bulging cingulum near the base of the crown; a constriction at the crown-root junction occurs in some teeth. *Polonodon* differs from chiniquodontids in that the primary cusps of its postcanines are not as recurved posteriorly. It differs from thrinaxodontids, chiniquodontids and probainognathids in having a more conspicuous (but still incomplete) division of the postcanine roots (Romer 1969a, 1969b, 1970; Abdala 2000; Hopson and Kitching 2001; Abdala and Giannini 2002; Martinelli et al. 2016). It differs from *Meurthodon gallicus* and *Mitredon cromptoni* in lacking the complete root divisions in the postcanines (Sigogneau-Russell and Hahn 1994; Shapiro and Jenkins 2001); differs from thrinaxodontids, *Prozostrodon brasiliensis, Brasilitherium* and tritheledontids in lacking a well-developed cingulum. It differs from Therioherpeton in having a very long anterior edge of cusp a, and cusp b much lower than c (proportion between the length of mesial and distal edges of cusp a larger than 1.5). It differs from *Alemoatherium* in lacking cingular cusps and in both surfaces lingual and labial slightly convex. It differs from *Rewaconodon* in cusp d much higher in the crown and closer to cusps c.

Material. Eucynodont teeth from Krasiejów locality consist of five three cusped teeth: ZPAL AbIII/3405, UOPB-1179, UOPB-1180, UOPB-1182, UOPB-1183; and five with more than tree cusps: ZPAL AbIII/3406, 3407 and UOPB-1177, UOPB-1181.
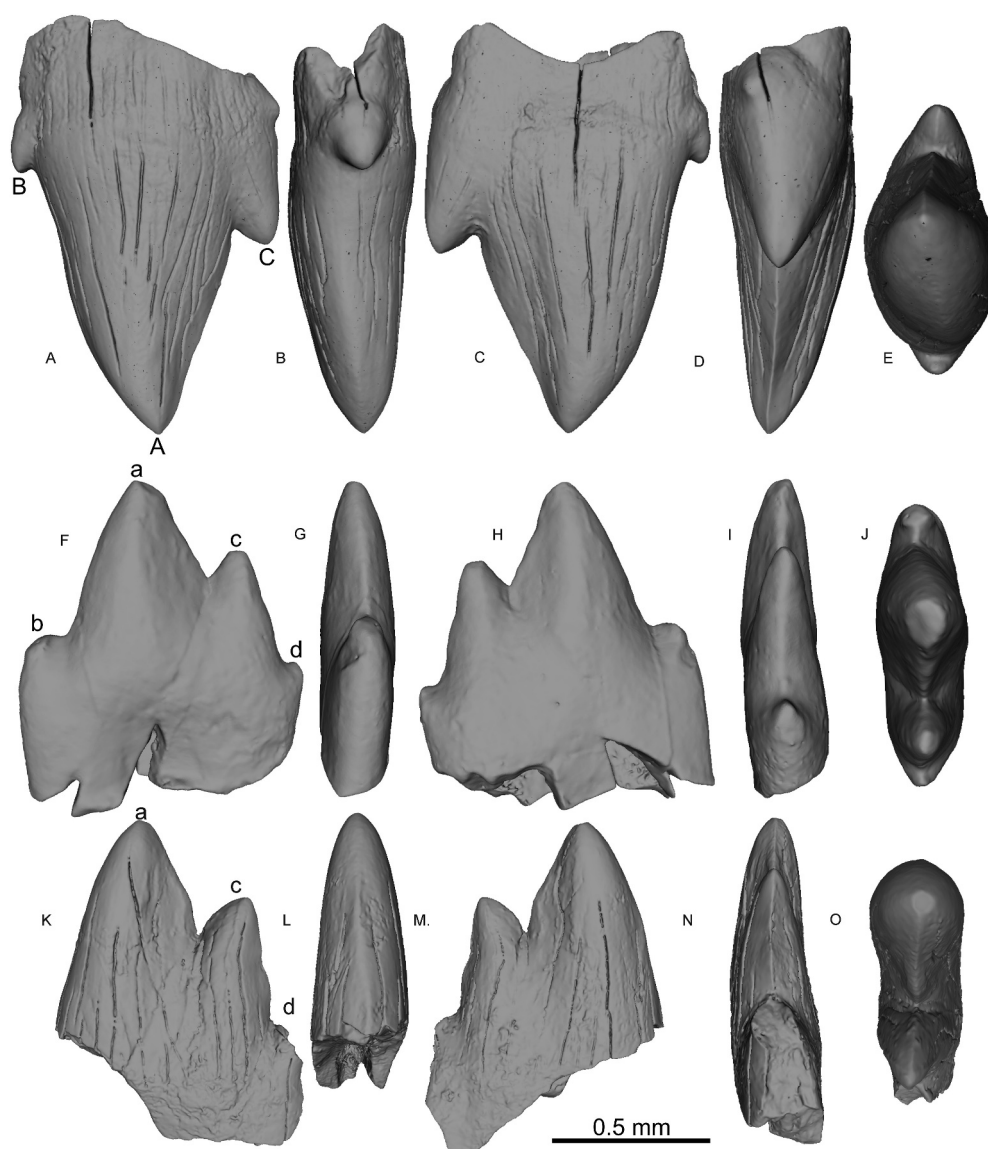
Figure 2. Eucynodont teeth of *Polonodon woznikiensis* Sulej et al. (2020) from Krasiejów. A-E, UOPB-1179; F-J, UOPB-1177; K-O, UOPB-1178. cusps marked with a, b, c, d, letters in case of lower teeth and A, B, C in case of upper teeth. A, H, M lingual view; C, F, K labial view; B, G, L mesial view; D, I, N distal view; E, J, O, occlusal view.

Most of them have broken roots and damaged crowns, but the proportion of partly preserved cusp in all postcanines are very similar to that of *Polonodon woznikiensis* (Sulej et al. 2020).

Description

The specimen UOPB-1177 (Figure 2F-J) is the smallest tetracuspid postcanine probably from the mandible. The general shape of the crown is very similar to very small ZPAL V.34/55 assigned as *P. woznikiensis* figured by Sulej et al. (2020) (compare Figure 4 M and N). Cusps a, c and d are well preserved only with broken tips, the cup b is damaged, but its position higher than the cusp d is obvious. The mesial edge of the cusp a is much shorter than in larger teeth of *P. woznikiensis*. In larger teeth of *P. woznikiensis*, the cusp b is probably larger than in ZPAL V.34/55 and UOPB-1177, but status of this character is not obvious because in UOPB-1177 only the base of cusp b is known. In distal view, the lingual side is straight or slightly concave whereas the labial side is convex (Figure 2I), what means that it is right side tooth. In occlusal view, the cusps are aligned in a row.

The specimens ZPAL ABIII/3406 (Figure 3D,K) and 3407 (Figure 3E,F,O) and UOPB-1178 (Figure 2K-O) are badly preserved but some characters make them similar to *P. woznikiensis*. In ZPAL ABIII/3406, the cusp a is complete with convex mesial edge and straight distal edge in labial view. This edge poses characteristic notch at the base like in some teeth of *P. woznikiensis* from Woźniki (ZPAL V.34/45, 34/46, 34/44). The cusp c is broken, but shape of its cross-section suggests that was only a little smaller than the cusp a. The cusp d is well preserved, small and conical. In ZPAL ABIII/3407 below the cusp d, there are a small cuspules on the lingual and labial side (Figure 3E,F,O), similarly as in the holotype of *P. wozni-kiensis* ZPAL V.34/45, where such cuspule is on the lingual side. The mesial part of the tooth is broken and it is not known if there was the cusp b, but the general shape of the crown is very similar to ZPAL V.34/46, which was included in *P. woznikiensis* based on the position of cusp b. Although this part of the tooth is broken, the mesial edge of the cusp a is very long like in *P. woznikiensis* and it is possible that cusp b was at the same position like in ZPAL V.34/46. Similar situation concerns UOPB-1178 (Figure 2K-O). In this tooth the cusps a and c are well preserved. The edges of cusp a are the
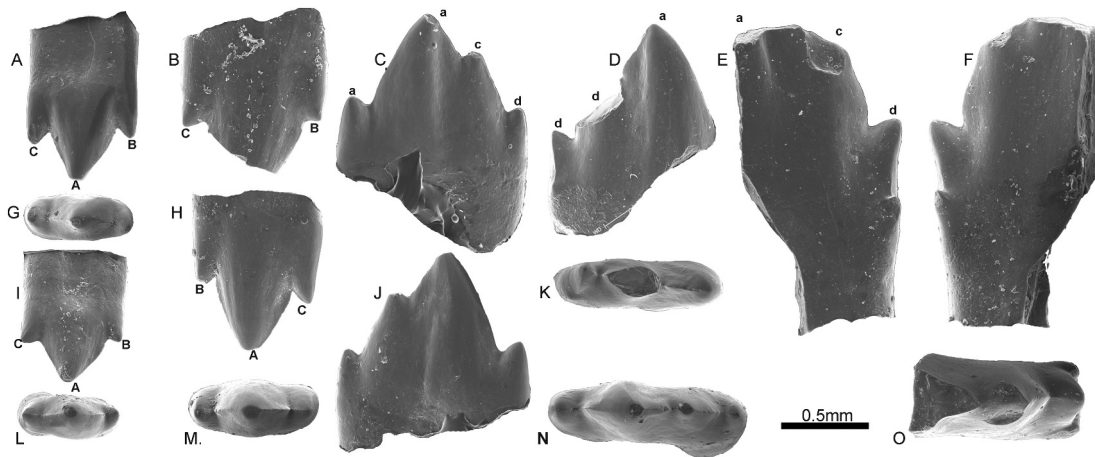
Figure 3. Eucynodont teeth of *Polonodon woznikiensis* Sulej et al. (2020) from Krasiejów. A, G, UOPB-1180; B, ZPAL AbIII/3405; C, K, N, UOPB-1181; D,K, ZPAL AbIII/3406; E, F, O, ZPAL AbIII/3407; I,L, UOPB-1183; H, M, UOPB-1182. cusps marked with a, b, c, d, letters in case of lower teeth and A, B, C in case of upper teeth. A, D, F, I labial view; B, C, E, H, J lingual view; G, K, L, M, N, O occlusal view.
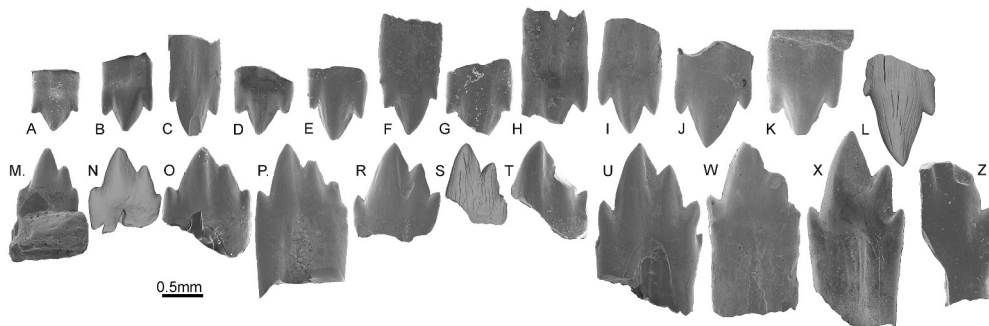

Figure 4. Teeth of *Polonodon woznikiensis* from Woźniki (C, D, F, H, I, J, K, M, P, R, U, W, X) and Krasiejów (A, B, E, G, L, N, O, S, T, Z) ordered accord size. in upper row (A-L) postcanines from maxilla, in lower row (M-Z) postcanines from dentary. A. UOPB-1182; B. UOPB-1180; C. ZPAL V.34/53; D. ZPAL V.34/50 (reversed); E. UOPB-1183; F. ZPAL V.34/56 (reversed); G. ZPAL AbIII/3405; H. ZPAL V.34/62; I. ZPAL V.34/59; J. ZPAL V.34/51 (reversed); K. ZPAL V.34/61; L. UOPB-1179; M. ZPAL V.34/55; N. UOPB-1177; O. UOPB-1181; P. ZPAL V.34/47; R. ZPAL V.34/46; S. UOPB-1178; T. ZPAL AbIII/3406 (reversed); U. ZPAL V.34/45 (holotype); W. ZPAL V.34/44; X. ZPAL V.34/60; Z. ZPAL AbIII/3407.

same like in previous tooth with a characteristic notch between cusp a and c. Cusp d and part of the tooth with cusp b are broken, but the length of the mesial edge of cups suggest that this tooth was similar to ZPAL V.34/46.

The specimen ZPAL AbIII/3407, consists of only part of the crown (Figure 3E,F,O). The largest cusp is broken and only a fragment of its base is visible. We preliminary identify it as the cusp a. Close to it and very high in the crown is a complete base of a broken cusp c. The conical cusp d is complete and occurs much lower in the crown. Lower to it, there are two cuspules on the lingual and labial sides of the teeth. Among teeth described as *P. woznikiensis* from Woźniki, there is one tooth ZPAL V.34/44 with two conical cuspules on lingual and labial sides of the teeth but on its mesial edge. In ZPAL AbIII/3407 they occur probably on the distal edge, however their general shape and position on the crown is very similar to ZPAL V.34/44 and thus we preliminarily assign ZPAL AbIII/3407 to cf. *Polonodon*. Unfortunately, most of the described teeth are incomplete and it is not possible to compare proportions of their cusps (see Sulej et al. 2020) to the known specimen of *P. woznikiensis* from Woźniki.

Five tricuspid teeth represent different morphologies. All probably are upper postcanines. UOPB-1180, 1182, 1183 (Figure 3) are almost complete, only their roots are broken, whereas ZPAL AbIII/3405 (Figure 3B) has the cusp A broken and the cusps B and C well preserved, which are at the same level and have similar size. All teeth are symmetrical labiolingually. In UOPB-1181, ZPAL AbIII/3405 the cusps B and C are almost the same size, whereas in UOPB-1180, 1182 the cusp B is more distant from the top of cusp A than cusp C (Figure 3). The shape of UOPB-1179 is more complex (Figure 2, A-E). The crown is complete and the cusp A is much larger then B and C (Figure 2B). Based on Hahn et al. (1994) we identify the cusp which is closer to the cusp A as cusp C and the second one as cusp B. The cusp B is smaller than cusp C. The mesial edge of cusp A is very long and strongly curved, whereas the distal edge is almost straight and slightly concave. In mesial view the cusp A is inclined lingual with labial side convex and lingual side concave what suggests that it is right tooth. Surface of the crown is covered by long and numerous deep cracks. A small cuspule occurs in the lower part of cusp C close to the root. Based on close similarity to the tricuspid teeth of *P. woznikiensis* (ZPAL V.34/50, V.34/51, V.34/53, V.34/59, V.34/61, V.34/62) we assign all the tricuspid teeth from Krasiejów to *Polonodon woznikiensis* (Sulej et al. 2020, Figure 3). Although also *Rewaconodon* (Daata 2004), *Brasilodon* and *Botucaraitherium* (Martinelli et al. 2016) have similar anterior

postcanines, we consider geographic proximity, faunal similarity and geological age of the type locality of Woźniki to Krasiejów to suggest that the new material described is *Polonodon woznikiensis*.

Discussion

The material from Krasiejów consists of 10 teeth closely similar to 28 teeth of *Polonodon woznikiensis* from Woźniki, its type locality of probably the same age (Sulej et al. 2020). In both localities the teeth were found in thin lenses of mud enriched hydrodynamically in calcareous grains. The teeth from both localities represent post-canines from both the mandible and skull. They are of various size; in both localities small and large teeth are present. Possibly, they all represented populations of the same species. The largest specimens (the complete one – ZPAL V.34/60 – the length of mesial edges of the main cusp 1.05 mm) represented in the collections were almost two times larger (Figure 4) than the smallest ones (ZPAL V.34/55 – the length of mesial edges of the main cusp 0.48 mm). Probably they represent various generations of the replacement teeth probably from a few individuals (it is not possible to determine how many). Because there are no distinct differences between teeth of various size there is no possibility to find any classes of size and count their quantity in the collection. There is also possibility that we do not have all size classes.

The posteroanterior alternate postcanines replacement was iden-tified in well-preserved skulls and mandibles of cynodonts such as *Thrinaxodon* (Abdala et al. 2013), *Galesaurus* (Norton et al. 2020) and eucynodontia such as *Brasilitherium* and *Brasilodon* (Martinelli and Bonaparte 2011, Schultz 2020). In case of series of isolated teeth, it is difficult to prove replacement of teeth. The only character that can be used is the size of teeth, but in all described skulls and mandibles of cynodonts, the variability of size of postcanines is very high. The largest postcanines in the same mandible may be two times larger than the smallest one (Abdala et al. 2013). This may also be the case in populations of *Polonodon woznikiensis* from Woźniki and Krasiejów. The teeth may represent different stages of the ontogeny of individuals as well as various generations of teeth.

Among cynodonts there are many reports on worn postcanines. They were described Eucynodontia such as *Brasilitherium* and *Brasilodon* (as a result of precise occlusion Bonapate et al. 2005, Martinelli and Bonaparte 2011) or *Probainognathus* (Abdala et al 2013, Martinelli at al. 2016). In case of *Brasilodon*, Martinelli and Bonaparte (2011) stated that the replacement was slow enough to permit an extremely strong wear of postcanines in the skull. In a sample of 32 teeth from Krasiejów and Woźniki (Figure 4 plus not figured), plus six newly collected teeth of *Polonodon woznikiensis* from Woźniki (unillustrated specimens ZPAL V.34/86- 99) no teeth with strong wear has been found. Perhaps there is a slight apical wear on cusps, unless they were not abraded during transport. The lack of significant wear was noticed also in *Inditherium floris* from India, a species having teeth similar to *P. woznikiensis* (Bhat et al. 2020). The simplest cause that the teeth does not show wear facet, is that there was no postcanine occlusion. But wear might be also the result of food consumption (Martinelli et al. 2016). In that case, it seems possible that in *P. woznikiensis* the postcanines replacement was very fast and the teeth were lost before they experienced any wear. In some mandibles of *Brasiliterium* all teeth are without any trace of wear (UFRGS-PV- 0785 T – personal observations of TS); also the postanines of *Thrinaxodon* (Abdala et al. 2013) has no worn tooth. The probainognathids teeth without distinct traces of wear were presented by Soares et al. (2014) and Martinelli et al. (2017a, b). The alternative explanation is that the food of *P. woznikiensis* and other small cynodonts was soft enough to not leave traces on normally replaced postcanines.

The postcanines described in *Brasilitherium* and *Brasilodon* (Martinelli and Bonaparte 2011) and many other Probainognathidae (Martinelli at al. 2016, Pacheco et al. 2017) have multicusp (more than 3 cusps) crowns of the mandibular postcanines and postcanines with three cusp in maxilla. Santana et al. (2011) showed that such morphology of crown with presence of crests might be defined as a low complexity morphology and is specialised for shearing insect cuticle characteristic for insectivore and omnivore molars in bats. Thus, the shape of the crown rather excludes a soft food as the explanation of the lack of wear in *P. woznikiensis*.

We suggest that *Polonodon woznikiensis* had a fast rate of teeth replacement, corresponding with small difference in size between the smallest and largest postcanines in mandible (Figure 5). In *P. woznikiensis* the difference is maximum two times. This contrasts with, say, population of *Thrinaxodon* in which the largest teeth are six times larger than smallest one (Abdala et al. 2013). In case of *P. woznikiensis* it might be connected with small size of the species (the largest teeth has width approximately 1.5 mm). But the fast replacement might be also connected with fast growth of the skull during the whole life of the animal. This contrasts with, say rapid juvenile growth. A gradual evolution of mammalian growth pat-terns across the cynodont to mammaliaform transition, possibly with the origin of rapid juvenile growth preceding that of truncated, determinate adult growth was deeply discussed by O'Meara et al. (2016) with review of whole literature connected with juvenile rapid growth in cynodont, mammals and birds. The reduction in dental replacement rate across the non-mammalian cynodont lineage, with greater rates of crown extension required in most non-probai-nognathians, and slower crown extension rates permitted in mam-maliamorphs, which have reduced patterns of dental replacement in comparison with many non-probainognathians was described by O'Meara et al. (2018). Martinelli (2009) stated that the significance of interpterygoid vacuities in cynodonts and its possible re-adquisi-tion in derived forms due to heterochronic processes. These pro-cesses possible affected the cynodont skull shape that occurred in the cynodont-mammalian transitions.

The juvenile rapid growth is one of the determinants of diphyo-dont replacement observed in mammals. We speculate that it may be an expression of evolution towards diphyodont replacement of *Morganucodon* (Luo et al. 2007). It is worth consider that *Polonodon* represent stage when very small cynodont had rapid growth during whole life and in the next stages of evolution to mammas this mechanism was limited to the juvenile period of live, as a process of heterochrony which is a common phenomenon in vertebrate evolution (Klingenberd 1998).

Conclusion

The Krasiejów site is the second locality with postcanines of Dromatheriidae *Polonodon woznikiensis*. The small diversification in the size and no signs of wear of all teeth from Krasiejów and Woźniki suggest that this species had very fast rate of replacement teeth. It could indicate that the rapid growth appeared in very small cynodont for thori whole life and as result of heterochrony was passed o juvenile stages in mammaliaformes.
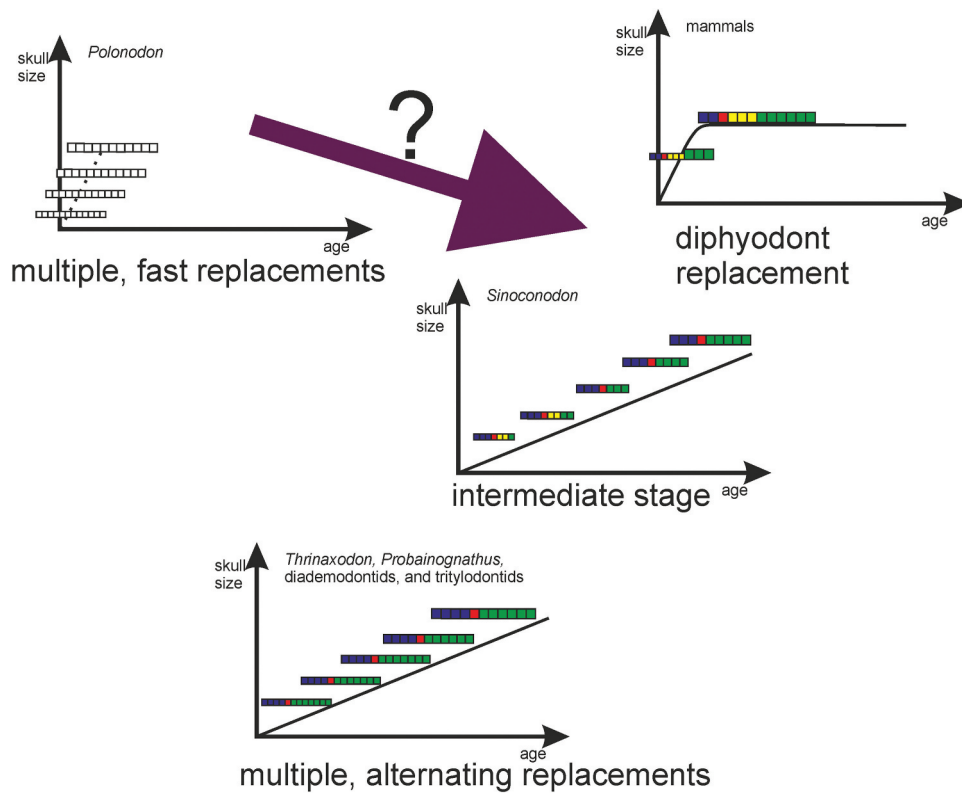
Figure 5. Schemes of various types of replacement teeth in evolution to mammals. Lines of squares shows teeth in skull, in purple: incisors, in red: canines, in yellow: postcanines, in green: molars. Based on Luo et al. 2009 and Abdala et al. (2013).

Disclosure statement

Funding

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