

Historical Biology

An International Journal of Paleobiology

ISSN: 0891-2963 (Print) 1029-2381 (Online) Journal homepage: <http://www.tandfonline.com/loi/ghbi20>

A new early Late Triassic non-mammaliaform eucynodont from Poland

Tomasz Sulej, Grzegorz Niedźwiedzki, Mateusz Tałanda, Dawid Drózdź & Ewa Hara

To cite this article: Tomasz Sulej, Grzegorz Niedźwiedzki, Mateusz Tałanda, Dawid Drózdź & Ewa Hara (2018): A new early Late Triassic non-mammaliaform eucynodont from Poland, Historical Biology, DOI: [10.1080/08912963.2018.1471477](https://doi.org/10.1080/08912963.2018.1471477)

To link to this article: <https://doi.org/10.1080/08912963.2018.1471477>



Published online: 05 Jun 2018.



Submit your article to this journal [↗](#)



View related articles [↗](#)



View Crossmark data [↗](#)

ARTICLE



A new early Late Triassic non-mammaliaform eucynodont from Poland

Tomasz Sulej^a, Grzegorz Niedźwiedzki^b, Mateusz Tałanda^c, Dawid Drózdź^a and Ewa Hara^a

^aPalaeobiology, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland; ^bDepartment of Organismal Biology, Evolutionary Biology Centre, Uppsala University, Uppsala, Sweden; ^cDepartment of Paleobiology and Evolution, Faculty of Biology, Biological and Chemical Research Centre, University of Warsaw, Warsaw, Poland

ABSTRACT

Bicuspid, tricuspid and tetracuspid postcanine teeth of a new non-mammaliaform eucynodont, *Polonodon woznikiensis* gen. et sp. nov. from the mid-late Carnian (early Late Triassic) of Woźniki clay-pit, Silesia (southern Poland) show incipient root division. They are similar to teeth of Dromatheriidae from the Carnian (early Late Triassic) to the Rhaetian (late Late Triassic) of Europe, India, and USA and the dentition of brasilodontids from the early Norian (mid Late Triassic) of Brazil. The *P. woznikiensis* teeth differ from those of the latter group mostly in the absence of cingulum. Some of the new fossils from Silesia provide the oldest Laurasian record of eucynodont teeth with the main cusp (a) anterior edge very long as the mesial cusp b is placed much lower than cusp c (distal). The contemporaneous *Alemoatherium huebneri*, from Gondwana, had similar postcanines. The findings from Poland indicate that this postcanine morphology was present in non-mammaliaform cynodonts from both hemispheres as early as the mid-late Carnian. The distal end of the humerus from the same locality is also described.

ARTICLE HISTORY

Received 24 November 2017
Accepted 27 April 2018

KEYWORDS

Polonodon;
mammaliaform;
Therapsida; Carnian; Late
Triassic

Introduction

The Triassic period witnessed the development of the crucial diagnostic aspects in the evolution of the mammalian lineage (Abdala and Gaetano 2017). The oldest known representative of Mammaliaformes is *Adelobasileus cromptoni* Lucas and Hunt, 1990, from the Late Triassic of north-west Pangea, represented by the partially preserved, posterior part of the skull without dentition (Lucas and Luo, 1993). The specialized dentition was one of the key features that attracted attention of scholars studying the mammalian origin and their Late Triassic-Early Jurassic diversification (Kühne 1958; Clemens 1980, 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, 2017a; 2017b). Teeth differentiated into incisors, canines, and postcanines early in the evolution of therapsids (Kemp 1982; Liu et al. 2009). One of the crucial aspect of dental evolution, on the mammaliaforms stem is the subdivision of the single root of the postcanine teeth into the double-rooted premolars and even multi-rooted molars. Eucynodontia (Kemp 1982, 1988) is characterized by features pointing towards mammals in dentition, cranial and postcranial skeleton (Hopson 1991, 1994; Rubidge and Sidor 2001 and Kemp 2005). In addition, in some basal cynodonts (e.g., *Thrinaxodon liorhinus* Seeley, 1894; see Abdala et al., 2013) the crown morphology of the postcanines is reminiscent of some basal mammaliaforms (e.g., *Morganucodon watsoni* Kühne, 1949 or *Hadrocodium wui* Luo, Crompton, and Sun, 2001). The discoveries of new fossils and the redescription of old collection material however, have revealed many convergences and reversals in the dentition and the jaw structure among early non-mammaliaform cynodonts (e.g., Gaetano and Rougier 2012;

Soares et al. 2014; Martinelli et al. 2016). Prozostrodonts (e.g., *Prozostrodon*, therioherpetids, dromatheriids, brasilodontids) showing a strongly mediolaterally compressed, single-rooted tricuspid or tetracuspid postcanines, are known from numerous sites restricted to the late Middle and Late Triassic (Abdala and Gaetano, 2017; Hahn et al. 1984, 1994; Bonaparte and Barberena 2001; Bonaparte et al. 2003, 2005; Datta et al. 2004; Heckert 2004; Abdala and Ribeiro 2000; Bonaparte 2013; Soares et al. 2014; Martinelli et al. 2016; Martinelli et al., 2017a, 2017b).

Fossil dromatheriids are mostly represented by isolated teeth, although some dentary fragments are also known (e.g., *Dromatherium sylvestre* Emmons, 1857 or *Microconodon tenuirostris* Osborn 1886; see Simpson, 1926; Sues 2001). Most authors agree that they have single rooted teeth, with crown consisted of one row of cusps and one or two small cuspules (Bonaparte and Barberena 1975, 2001; Datta et al. 2004; Abdala and Ribeiro 2010). They were described from the Carnian-Norian strata of North America, India and from the Norian-Rhaetian of Europe (Kielan-Jaworowska et al. 2004). Dromatheriids (e.g., *D. sylvestre* and *M. tenuirostris*) have been regarded as early mammals in the 19th century (Owen 1871; Osborn 1886, 1887), but they were later regarded as cynodonts (Simpson 1926a, 1926b; Hahn et al. 1994) or eucynodonts (Kemp 1982; Sues 2001; Martinelli et al. 2017a; 2017b), however their precise phylogenetic position still remains uncertain. They could have mammalian affinities, as suggested by Hopson and Kitching (1972) but more complete fossils are needed to accurately address this issue. The Dromatheriidae was subsequently redefined to include *D. sylvestre*, *M. tenuirostris*, *Pseudotriconodon wildi* Hahn et al., 1984, *Therioherpeton carnigini* 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 recognize the

validity of the Therioherpetidae family for *T. cargini* and *M. gallicus* (see Bonaparte and Barberena, 1975, 2001; also Abdala and Ribeiro 2010). Lucas and Oakes (1988) described the 'dromatheriid' *Pseudotricodon chatterjeei* Lucas and Oakes, 1988 from the upper Norian Bull Canyon Formation in eastern New Mexico, but its cynodont affinity has been questioned (Sues and Olsen 1990; Fraser and Sues 1997). Datta et al. (2004) described several isolated teeth from the Carnian Tiki Formation of India (Mukherjee et al. 2012) and included them in the taxon *Rewacodon tikiensis* Datta, Das and Luo, 2004. A similar isolated tooth collected from the Carnian deposits (Locality L-1312, lower Kalgary) in Texas, USA (Heckert 2004) was assigned to the same taxon (aff. *R. tikiensis*).

The brasilodontids (Bonaparte et al. 2003, 2005; Bonaparte 2013; Soares et al. 2014) is a group of relatively small eucynodonts probably of insectivorous habit, mostly known from the Late Triassic of southern Brazil (according to Bonaparte 2013). This group was postulated as the sister-group of mammaliaforms (Bonaparte et al. 2003, 2005; 2012; Luo 2007). *Brasilitherium riograndensis* is the best-known representative of the group. The holotype specimen UFRGS PV1043T shows an almost complete skull, lower jaws and a few postcranial bones, of a very well state of preservation (Bonaparte et al., 2012). Most of characters of the cranial, the lower jaw and the teeth of brasilodontids shows a *Morganucodon*-like appearance but are slightly less derived (Bonaparte et al. 2003, 2005). It seems that brasilodontids are a paraphyletic group (Bonaparte 2013; Soares et al. 2014; Martinelli et al. 2016). The most important and well dated brasilodontid fossils (*Brasilodon quadrangularis*, *Brasilitherium riograndensis* and *Minicyonodon maieri*) come from *Riograndia* Assemblage Zone of the Upper Triassic Caturrita Formation (Martinelli and Soares 2016). The age of the *Riograndia* AZ is considered early Norian (Soares et al. 2011; Martinelli et al. 2017a).

The Late Triassic-Early Jurassic record of a mammalian lineage in Poland is still poorly known. Until now, the only fossils with mammal-like, double-rooted teeth are specimens referred to *Hallautherium* sp., reported from the Upper Triassic strata exposed at Lipie Śląskie clay-pit in Lisowice (Świło et al. 2014, 2015). Moreover, Gierliński et al. (2004) described a very small pentadactyl footprint from the lowermost Hettangian (Lower Jurassic) of Sołtyków, which strongly resembles ichnites supposed to belong mammalian forms from the Lower Jurassic of New Jersey and Lesotho. Tałanda et al. (2011) described a burrow complex from Wyszyna Machorowska (Holy Cross Mountains, Poland), which might belong to cynodonts. Study of their three-dimensional architecture revealed a surprising shape. Nonetheless, at this stage it is unclear if these structures represent tetrapod burrow infillings or other biogenic or abiotic structures (ongoing study).

Here we describe isolated postcanine teeth of non-mammaliaform eucynodonts and part of a humerus collected from the Upper Triassic strata of Silesia (southern Poland). We propose for these specimens a new genus, with lower postcanines having a very long anterior edge of cusp a, and cusp b much lower than c and single conspicuous (but still incomplete) division of the single postcanine roots. All the studied fossils come from a single approximately 60 cm thick interval exposed at the clay-pit in Woźniki (Sulej et al. 2011). The locality has been dated as

mid-late Carnian (lower part of the Middle Keuper) based on associated spinicaudatan crustacean (conchostracan) fossils (Sulej et al. 2011) and shows faunistic similarity to that from the Krasiejów site (Olempska 2004; Dzik and Sulej 2007; Skawina and Dzik 2011; see also Tałanda 2015). The most complete vertebrate specimen from Woźniki belongs to a medium-sized dicynodont (Sulej et al. 2011). This locality also provided bones of temnospondyls and archosauriforms. Some characteristic Upper Triassic tetrapod tracks (Chirotheriidae indet., cf. *Brachychirotherium* isp., cf. *Grallator* isp., cf. *Atreipus* isp., possible pentadactyl synapsid prints) are associated with skeletal fossils at Woźniki (Niedźwiedzki and Sulej 2007; Gierliński et al. 2009; Sulej et al. 2011).

Institutional abbreviations

GSI, Geological Survey of India in Calcutta, India; **MCZ**, Museum of Comparative Zoology, Harvard University, Bristol, USA; **MCT**, Museu de Ciências da Terra, Rio de Janeiro, Brazil; **MMACR**, Museu Municipal Aristides Carlos Rodrigues, Candelária, Brazil; **MNHN**, Paris Natural History Museum, Paris, France; **PIMUZ**, Paläontologisches Institut und Museum der Universität Zürich, Switzerland; **RBINS**, The Royal Belgian Institute of Natural Sciences, Brussels, Belgium; **SMNS**, Staatliches Museum für Naturkunde, Stuttgart, Germany; **UFRGS**, Paleontology and Stratigraphy Department of the Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil; **UFMS**, The Federal University of Santa Maria, Santa Maria, Brazil. **ZPAL**, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Geological setting

The studied locality (understanding as a town) is historically one of the oldest fossil vertebrate sites in Silesia (Roemer 1867, 1870). The lithostratigraphic position of the fossiliferous strata exposed at the Woźniki clay-pit is well-defined by characteristic underlying and overlying rock units known from the outcrop and nearby boreholes. The terrestrial deposits from the Woźniki clay-pit are similar to other Middle Keuper deposits of the Central European Basin (CEB) which were dated as Carnian (e.g. Shukla et al. 2010) or Norian (e.g. Szulc et al. 2015). The biostratigraphical evidences (e.g. unionoid bivalve, spinicaudatan crustaceans and composition of tetrapod fauna) indicate mid-late Carnian age for the Woźniki clay-pit fossiliferous levels (Sulej et al. 2011; Lucas 2015; see also below). The strata exposed in the Woźniki clay-pit are mostly red or reddish and greenish claystone and siltstone (without evaporates). Among them occur several layers of carbonate grainstone (greenish) and carbonaceous sandstone (reddish, brown and greenish). Most of the carbonate-rich beds are very thin, excepts for two thicker, lenticular and local layers. According to Szulc et al. (2015), the fossiliferous strata exposed at the Woźniki clay-pit grade upwards conformably into the crenogenic-lacustrine deposits of the Limestone Member from Woźniki ('Woźniki Limestone'), but it is not visible in the clay-pit section.

The most fossiliferous layer in the clay-pit, about seven metres below the ground level, is composed of greenish

siltstone and mudstone approximately 60 cm thick. The samples for screen-washing were taken from two different places of the middle part of the north-eastern wall (Figure 1). In this part the fossiliferous layers are represented by four thin beds of a greenish siltstone (Figure 1(b)), which are irregular and in some parts join together. The most productive were samples 1 to 3 (18 teeth) and sample 6 (Table 1). Irregular intercalations of lithified grainstone with ooid-like grains (probably redeposited calcretes) occur throughout the section. There are tetrapod footprints and trackways produced by therapsids and archosauriforms. Many of them were found in isolated slabs, which were collected on the pile outside the clay-pit.

A relatively rich assemblage of vertebrate body fossils is associated to eucynodont remains. Sulej et al. (2011) reported shark (*Nemacanthus* sp.), an indeterminate plagiosaurid, a *Cyclotosaurus*, a medium-sized kannemeyeriiform dicynodont, an indeterminate phytosaur, and a silesaurid dinosauriform. The residue with eucynodont teeth, contain also numerous teeth and bone fragments of small temnospondyls and phytosaurs, *Ozimek* sp. remains, numerous lungfish teeth, sharks teeth, and actinopterygian fish scales and teeth (see below).

Apart from the previously identified ostracods, small freshwater unionid bivalves and spinicaudatan crustaceans (Kotlicki 1974; Sulej et al. 2011), the Woźniki clay-pit invertebrate fossil assemblage includes other fossils of aquatic arthropods (on-going study). Ostracods and well preserved

Table 1. List of specimens with number of fossiliferous layers their originated (see Figure 1).

description	ZPAL V.34/	Layer on Figure 1.
Tooth	43	2
Tetracuspoid tooth from dentary.	44	2
Tetracuspoid tooth from dentary (holotype).	45	2
Tetracuspoid tooth from dentary.	46	2
Tetracuspoid tooth from dentary (paratype).	47	2
Bicuspid tooth.	48	2
Tooth	49	2
Tricuspid tooth from maxilla.	50	2
Tricuspid tooth from maxilla.	51	2
Distal part of humerus	52	2
Tricuspid tooth from maxilla.	53	3
Tooth	54	3
Tetracuspoid tooth with part of dentary	55	3
Tricuspid tooth from maxilla.	56	6
Tooth	57	6
Tooth	58	6
Tricuspid tooth from maxilla.	59	6
Tetracuspoid tooth from dentary	60	2
Tricuspid tooth from maxilla.	61	2
Tricuspid tooth from maxilla.	62	6
Tooth	63	2
Tooth	64	2
Tooth	65	1

spinicaudatan specimens (Figure 2) occur at Woźniki in a thin (approximately 20 cm thick) interval of greenish-grey claystone and mudstone with rare organic carbon nests and located about 20–30 cm below the horizon where the main accumulation of the dicynodont bones was excavated in the years 2007–2009 (see Sulej et al. 2011). Occurrences of

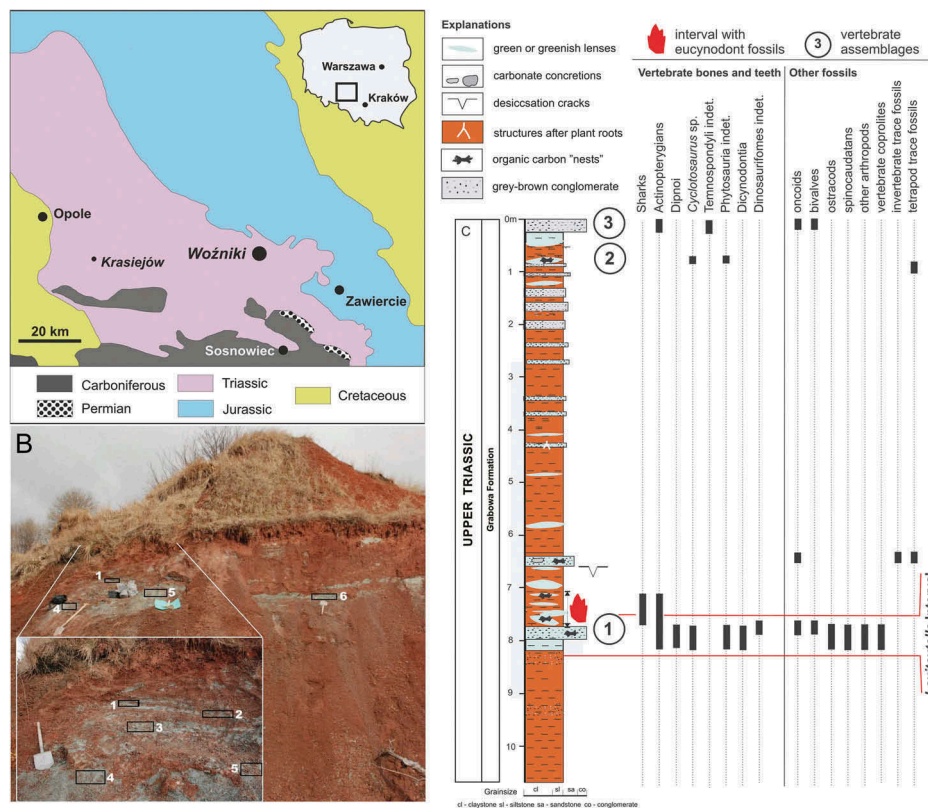


Figure 1. (a) geological sketch-map of the Upper Silesia region between Opole and Zawiercie showing the location of the bonebearing sites at Woźniki and Krasiejów; (b) the north-eastern wall of the Woźniki clay-pit with the exposure of the Upper Triassic rocks. Small shovel (the same on both pictures) is approx. 50 cm long. In frame: Close-up on the location of the most productive samples to screen-washing. the numbered samples correspond to the sample numbers in Table 1; (c) lithostratigraphic section of deposits exposed at the Woźniki clay-pit. Three vertebrate assemblages are assigned by circle with number. [planned for page width].

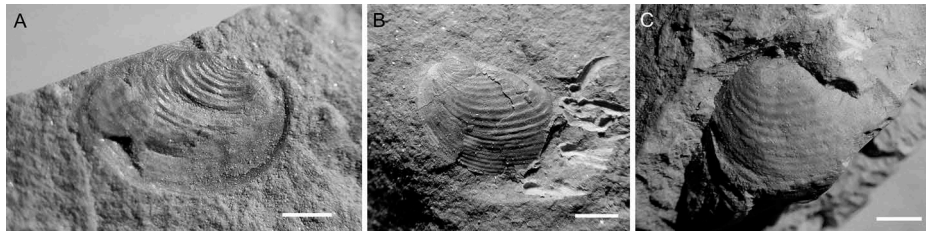


Figure 2. Conchostracan fossils from Woźniki clay-pit. (a) *Laxitextella* cf. *laxitexta* (Jones 1890), right valve ZPAL V.34/103 in lateral view; (b) *Laxitextella* cf. *laxitexta* (Jones 1890), left valve ZPAL V.34/104 in slightly oblique lateral view; (c) *Laxitextella* sp., right valve ZPAL V.34/105 in slightly oblique lateral view. Scale bar equals 1 mm. [planned for page width].

numerous ostracod carapaces were recorded in the upper part of the exposed section (Figure 1). Ostracods represent a few species of the superfamilies Darwinuloidea and Suchonelloidea. Isolated finds of spinicaudatan fossils represent mainly *Laxitextella* cf. *laxitexta* (Jones, 1890) (Figure 2), which indicates a mid–late Carnian age (from the *Anyuanestheria fimbriata*–*Laxitextella laxitexta* Zone to the *Laxitextella freybergi* Zone in the Germanic Basin; Kozur and Weems 2010; Lucas et al. 2012; Geyer and Kelber 2018). According to Lucas (2015) the genus *Laxitextella* has no Norian records, so this spinicaudatan finds at Woźniki strongly indicates a Carnian age.

In the CEB, the Carnian part of the Keuper sedimentation has a rich spinicaudatan record (Lucas et al. 2012), which is, however, restricted to some horizons of the basin margins, as the central basinal and hypersaline deposits do not contain spinicaudatan fossils. The richest spinicaudatan faunas of the Weser Formation occur in the Lehrberg Beds and their correlatives as red beds exposed at the famous locality Krasiejów (Opole Silesia, southwestern Poland) with important vertebrate fossil faunas.

The invertebrate and vertebrate assemblages from Woźniki show strong similarity to that from the Krasiejów site (Olempska 2004; Dzik and Sulej 2007; Skawina and Dzik 2011; Pacyna 2014). The Krasiejów vertebrate assemblage (Dzik and Sulej 2007) can be assigned to the early Adamanian (late Carnian in age) land-vertebrate faunachron (Lucas 2010, 2015). The vertebrate assemblage from Woźniki is similar to Krasiejów in the presence of a capitosaur (*Cyclotosaurus* sp.), *Ozimek* sp. (Dzik and Sulej, 2016), a silesaurid dinosauriform, rich phytosaur remains (Phytosauria indet.), and the lack of more advanced dinosaurian taxa (e.g. basal saurischians, sauropodomorphs, neotheropods), which are numerous in the early Norian to Rhaetian in the other parts of the CEB (e.g. Rauhut and Hungerbüler 1998; Heckert and Lucas 1999; Brusatte et al. 2010; Langer et al. 2010) and also in Poland (see Sulej et al., 2012; Niedźwiedzki et al., 2014). Among Silesian localities, the Woźniki fossil assemblage clearly differs from that described from Miedary, dated as late Ladinian (Sulej et al., 2014), or the late Norian to early Rhaetian from Lisowice and perhaps Zawiercie (Marciszów) (Dzik et al., 2008; Niedźwiedzki et al., 2012; Pieńkowski et al. 2014; but see Szulc et al. 2015). This suggests stratigraphical differences between Silesian vertebrate assemblages but detailed discussion on the nature of these faunal differences demands further study. The

exposure at Woźniki was repeatedly sampled for palynomorph data, but unfortunately the rocks exposed at the clay-pit section in Woźniki (similarly to Krasiejów) do not contain well preserved plant microfossils.

Material and methods

The material used for this study was gathered from the calcareous, greenish-grey claystone/siltstone beds visible in the upper part of the exposure at the Woźniki clay-pit (Figure 1). We screen-washed on fieldwork sieves about 0.5 metric ton of in situ collected rock from most promising bone-bearing levels. Most of the small rock fragments, mineral grains, larger clast and other mineral particles were removed by washing with water. The residue with the concentration of specimens was again sieved and dried in the preparatory lab at the Institute of Paleobiology, PAS and Department of Palaeobiology and Evolution, University of Warsaw (Warsaw). The obtained material was manually sorted under a binocular microscope and numerous isolated teeth or small bone fragments of temnospondyls, phytosaurs, lungfishes, sharks, and ganoid fish scales as well as teeth have been collected. Twenty two eucynodont teeth were found (Figures 3, 4), which are the subject of this paper. We consider thirteen best preserved postcanines to represent a single species. A distal part of humerus (Figure 5) was found in the same interval.

The relative position of the teeth in the postcanine row was determined by comparing them with more complete jaw or cranial remains of *Microconodon tenuirostris* (Sues, 2001) and *Brasilitherium riograndensis* (Bonaparte et al., 2005; Bonaparte and Migale, 2010; and personal observation) and other taxa. We follow the criteria used by previous workers to orientate the isolated postcanines (see Godefroit and Battail 1997; Datta et al. 2004). For the description we adopt, in part, the terminology from the paper of Datta et al. (2004) also used by other authors (e.g., Crompton, 1974; Bonaparte et al. 2003, 2005; Martinelli et al. 2005, 2016; Oliveira 2006; Soares et al. 2014).

The proportions between seven measurements of lower postcanines were calculated and compared on scatter plots (Figure 6, Table 2). The measurements were taken on enlarged photographs and compared with published drawings or photographs of several Late Triassic taxa with teeth similar to *Polonodon* gen. nov. (e.g. *Dromatherium sylvestre*, *Brasilitherium riograndensis*, *Rewaconodon tikiensis*, *Hallautherium schalchi* Clemens, 1980, *Microconodon tenuirostris* and *Meurthodon gallicus*). Many Late

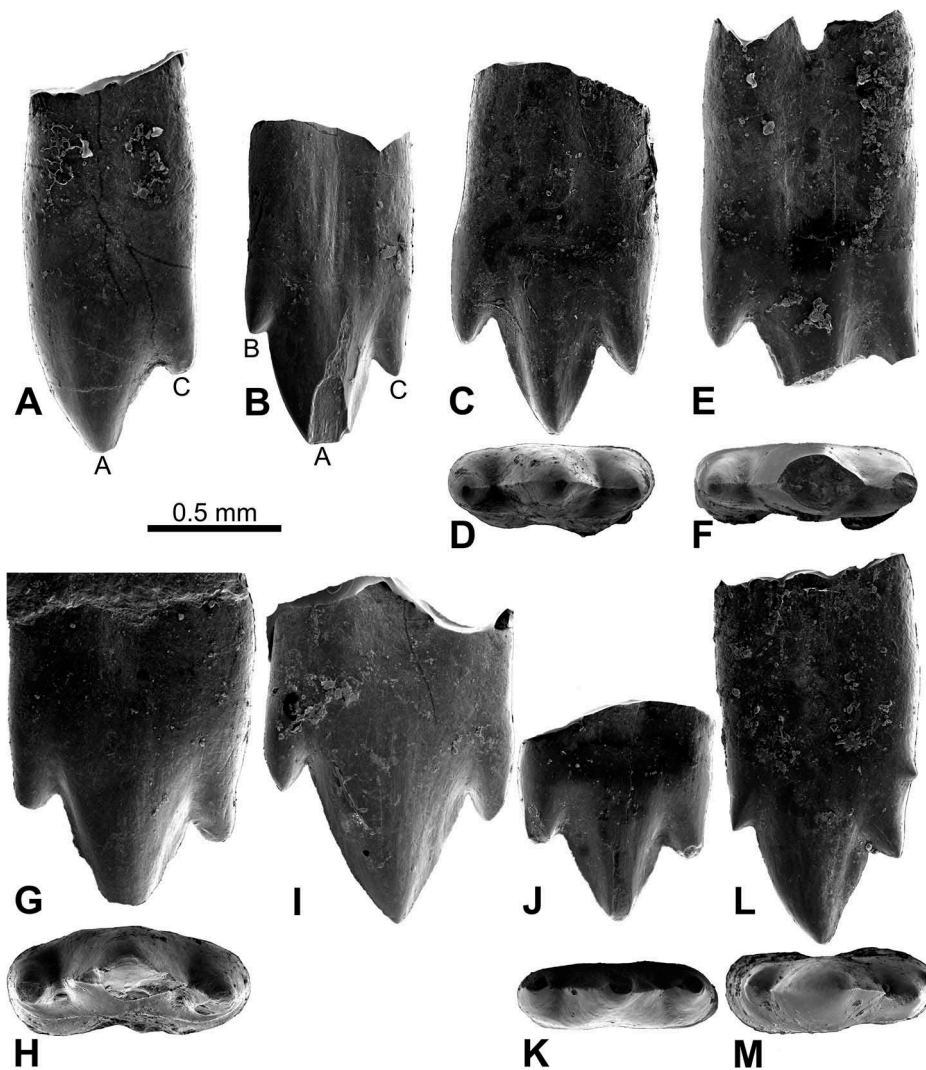


Figure 3. Two and three cuspid teeth of *Polonodon woznikiensis* gen. et sp. nov. from the mid-late Carnian of Woźniki with two or three main cusps. (a) ZPAL V.34/48; (b) ZPAL V.34/53; (c, d) ZPAL V.34/59 left; (e, f) ZPAL V.34/62 right; (g, h) ZPAL V.34/61 left; (i) ZPAL V.34/51; (j, k) ZPAL V.34/50; (l, m) ZPAL V.34/56 right. In case of A, B, I, J, K, we do not know from which side they are. The letters A-C mark the cusps. G, labial view; E, L, C lingual view. In case J, B, A, I we do not know from what view they represent. [planned for page width].

Triassic eucynodonts (e.g. *Therioherpeton*) have teeth or most of them with the tips of the cusps damaged, due to that taking all the measurements was impossible in some cases. It is reason why most species is represented on scatter-plots by singly points.

SYSTEMATIC PALAEOLOGY

Order THERAPSIDA Broom, 1905
Suborder CYNODONTIA Owen, 1861
Infraorder EUCYNODONTIA Kemp, 1982
Family DROMATHERIIDAE Gill, 1872
POLONODON gen. nov.

Etymology

The genus is named after the latin name (*Polonia*) of Poland, *odon* in Greek means tooth.

Diagnosis

As for type and only species.

POLONODON WOZNIKIENSIS gen. et sp. nov.

Holotype

ZPAL V.34/45 (Figure 4 (k– m)), a tetracuspide lower post-canine tooth with a mesiolingual and a distolingual accessory cusps, in the collection of the Institute of Paleobiology, Polish Academy of Sciences (Warsaw).

Referred Specimens

Teeth: ZPAL V.34/44 (Figure 4 (g, h)), V.34/47 (paratype Figure 4 (e, f)), V.34/46 (Figure 4 (c, d)), V.34/48 (Figure 3 (a)), V.34/50 (Figure 3 (j, k)), V.34/51 (Figure 3 (i)), V.34/53 (Figure 3 (b)), V.34/55 (Figure 4 (a, b)), V.34/56 (Figure 3 (l, m)), V.34/57, V.34/59 (Figure 3 (c, d)), V.34/60 (Figure 4 (i, j)), V.34/61 (Figure 3 (g, h)), V.34/62 (Figure 3 (e, f)).
Humerus: ZPAL V.34/52

Etymology

The species is named after the town Woźniki in Silesia where the studied material was collected (Figure 1(a)).

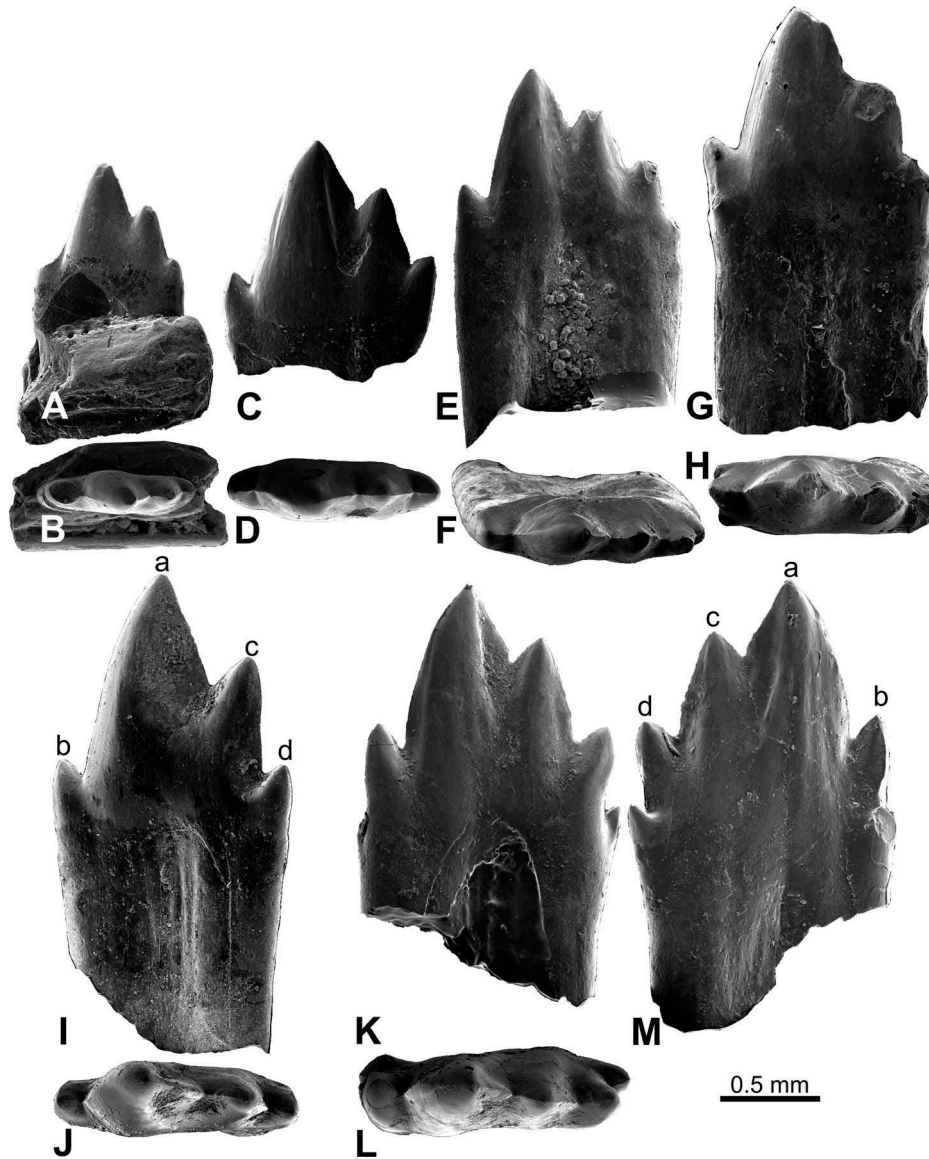


Figure 4. Lower teeth of *Polonodon woznikiensis* gen. et sp. nov. from the mid-late Carnian of Woźniki. (a, b), ZPAL V.34/55 right; (c, d), ZPAL V.34/46; (e, f) ZPAL V.34/47 left; (g, h) ZPAL V.34/44 right; (i, j) ZPAL V.34/60 right; (k–m) ZPAL ZPAL V.34/45 (holotype) left. Cusps marked with a, b, c, d, letters. E, K labial view; A, G, I, M lingual view. [planned for page width].

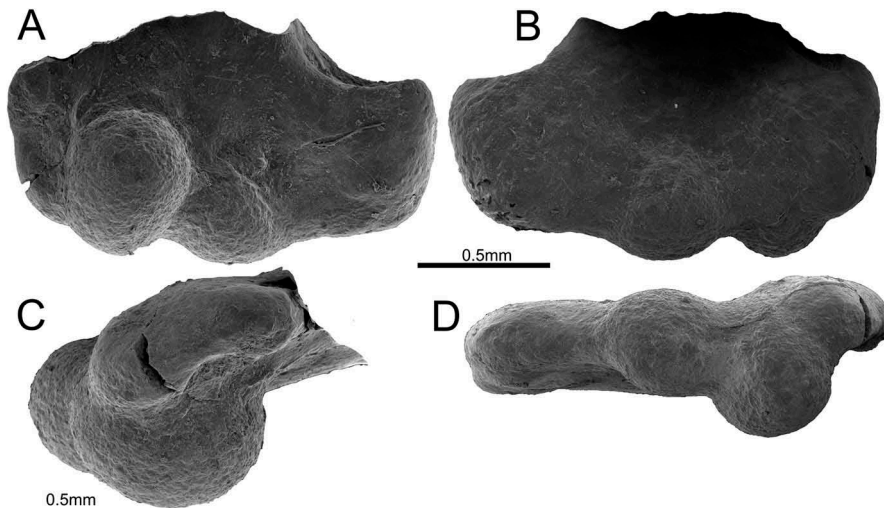


Figure 5. Distal part of the right humerus attributed to *Polonodon woznikiensis* gen. et sp. nov. from the mid-late Carnian of Woźniki, ZPAL V.34/52 in dorsal (a); ventral, (b); dorsal, (c); anterior, (d); distal view. [planned for page width].

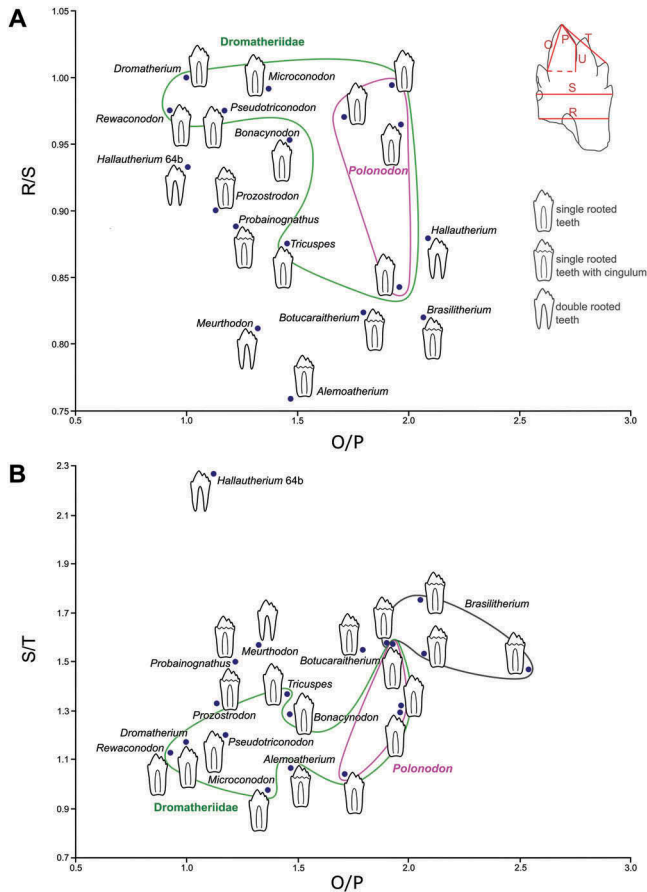


Figure 6. Scatter-plots of teeth proportions of *Polonodon* gen. nov., dromatheriid, brasilodontids and early mammaliaforms. (a) proportion between the length of mesial and distal edges of the main cusp (O/P) against proportion between the width of the crown and distance from top of the cusp a to top of the cusp d (S/T); (b) proportion between the length of mesial and distal edges of the main cusp (O/P) against proportion between the width of the crown and the width of the roots base (R/S). The measurements were taken from illustrations (photographs or drawings) published in the papers of Datta et al. (2004: Figure. 1), (*Rewaconodon*); Osborn (1887: Figure. 1 and Figure. 2), (*Microconodon* and *Dromatherium*); Soares et al. (2014: Figure. 6), (*Brasilitherium* and *Prozoostrodon*); Martinelli et al. (2017a: fig. 6), (*Alemoatherium*); Hahn et al. (1984: plate 3), (*Pseudotriconodon*); Martinelli et al. (2016: fig. 8), (*Bonacynodon*); Peyer (1956: plates 5 and 10), (*Hallautherium 64b*); Świło et al. (2014: Figure. 2), (*Hallautherium*); Hahn et al. (1994: Figure. 2, 15 and 16), (*Meurthodon* and *Tricuspes*). Measurements of *Probainognathus* (MCZ 4294) and *Polonodon woznikiensis* gen. et sp. nov. (ZPAL V.34/45,46,47 and 60) were made personally. [planned for page width].

Type Locality and Type Stratum

Clay pit in the town Woźniki near Częstochowa, southern Poland; mid-late Carnian (early Late Triassic).

Diagnosis

Lower postcanine teeth characterized 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* gen. nov. 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;

Table 2. List of specimens measured for Figure 6 and proportions of their crowns.

Name, number in collection	O/P	R/S	S/T	S/U
<i>Polonodon woznikiensis</i> ZPAL V.34/60	1.712	0.97	1.038	2.7
<i>Polonodon woznikiensis</i> ZPAL V.34/46	1.959	0.84	1.293	2.6
<i>Polonodon woznikiensis</i> ZPAL V.34/45	1.965	0.96	1.32	3
<i>Polonodon woznikiensis</i> ZPAL V.34/47	1.926	0.99	1.573	3.5
<i>Brasilitherium riograndensis</i> UFRGS-PV-0603-T (last tooth)	2.052		1.754	
<i>Brasilitherium riograndensis</i> UFRGS-PV-0603-T	2.067	0.82	1.535	
<i>Brasilitherium riograndensis</i> UFRGS-PV-0795-T	2.538		1.471	
<i>Brasilitherium riograndensis</i> UFRGS-PV-0834-T	1.9		1.577	
<i>Dromatherium sylvestre</i> lack of number	1	1	1.17	110
<i>Microconodon tenuirostris</i> lack of number	1.367	0.99	0.975	5.4
<i>Rewaconodon tikiensis</i> GSI Pal/CHQ-005	0.925	0.97	1.13	52
<i>Rewaconodon tikiensis</i> GSI Pal/CHQ-006		0.93		2.2
<i>Rewaconodon tikiensis</i> GSI Pal/CHQ-007		0.9		2.5
<i>Rewaconodon tikiensis</i> GSI Pal/CHQ-008		0.97		4.9
<i>Hallautherium</i> sp. ZPAL V.33/734	2.091	0.88		
<i>Probainognathus jenseni</i> MCZ 4294	1.222	0.89	1.5	
<i>Prozoostrodon brasiliensis</i> UFRGS-PV-0248-T	1.13	0.9	1.333	20
<i>Hallautherium schalchi</i> PIMUZ AIII-318	1.123	0.89	2.272	12
<i>Tricuspes</i> sp. indet. MNHN SNP RAS 814	1.455	0.88	1.371	8
<i>Pseudotriconodon wildi</i> RBINS R.M. 1	1.174	0.98	1.206	14
<i>Bonacynodon schultzi</i> MCT-1716-R	1.462	0.95	1.289	8.9
<i>Meurthodon gallicus</i> lack of number	1.321	0.81	1.57	13
<i>Alemoatherium huebneri</i> UFSM 11579b	1.681			
<i>Alemoatherium huebneri</i> UFSM 11579b	1.468	0.76	1.066	5
<i>Botucaraitherium belarminoi</i> MMACR-PV-003-T	1.79	0.82	1.54	

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, *Prozoostrodon 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 cups c.

Remarks

All the teeth and the humerus are assigned to a single taxon but it is the working assumption that all cynodont material at the site represents a single taxon, pending future discoveries that might falsify or corroborate this hypothesis.

Description and comparisons

Dentition

The teeth with more than two cusps dominate in the sample. The only one two-cusped tooth (ZPAL V.34/48) is interpreted as a postcanine from anterior portion of the series. The main cusp is much larger than distal cusp (Figure 3(m)). The tooth is narrow and its root is incipiently divided by a furrow on both lingual and labial sides. The root narrows in its lower part.

Seven tricuspid teeth ZPAL V.34/50 (Figure 3 (j, k)), V.34/51 (Figure 3 (i)), V.34/53 (Figure 3 (b)), V.34/56 (Figure 3 (l, m)), V.34/59 (Figure 3 (c, d)), V.34/61 (Figure 3 (g, h)), V.34/62

(Figure 3 (e, f)) are interpreted as anterior upper postcanines, by comparison with those of *Brasilitherium riograndensis* (Bonaparte et al., 2003), *Microconodon tenuirostris* (Sues, 2001) and following the criteria of Godefroit and Battail (1997). The specimens ZPAL V.34/53, 56 and V.34/59 (Figure 3) are elements from the anterior part of the postcanine row. Their principal cusp A has a longer mesial crest. The mesial cusp (B) is much lower than the distal cusp C. The enamel is smooth. In ZPAL V.34/53 cusp A shows large abrasion. In ZPAL V.34/50, 51 and 61 cusp B is only a little lower than cusp C. An additional small cuspule is present on the distal part of the upper postcanine ZPAL V.34/56 very low on the lingual or labial side (Figure 3 (l, m)). In the upper postcanine ZPAL V.34/53, 56, 59, 62 (Figure 3) the root is incipiently divided by a furrow on both lingual and labial sides.

The holotype specimen (ZPAL V.34/45, Figure 4 (k–m)) is a left lower postcanine with the crown dominated by four main cusps (a–d) and two basal, large cuspules a mesiolingual and a distolingual one, following the criteria of Godefroit and Battail (1997). The tooth is mesiodistally longer than the others tetracuspid postcanine teeth recovered. The primary cusp a is labiolingually compressed and slightly recurved, with the mesial crest very long and curved and the distal crests straight. The mesial cusp b has a prominent mesiolingual crest, and a distal crest extending from the apex. A cuspule lies on the lingual side of the crown below cusp b, but is broken. The distal cusp c is lower than cusp a and in close proximity to it. The cusp b is smaller and much lower than cusp c. The distal cusp d is the same size as b with a rounded distal side. The distal cuspule is half the size of cusp d and occurs on the lingual side. No wear facets are present on the crown. The enamel surface slightly bulges near the crown and root junction, but there is no distinctive cingulum or constriction to separate the enamel surface of the crown from the dentine surface of the root.

Six specimens of tetracuspid teeth ZPAL V.34/44 (Figure 4(g, h)), V.34/46 (Figure 4(c, d)), V.34/55 (Figure 4(a, b)), V.34/60 (Figure 4(i, j)), V.34/47 (Figure 4(e, f)), V.34/57 are considered to be the lower posterior postcanines by comparison to those of *Microconodon tenuirostris* (Sues, 2001), *Therioherpeton cagnini* (Bonaparte and Barberena, 1975, 2001), and *Mitredon cromptoni* to a less extent (Shapiro and Jenkins 2001). They differ from holotype in the lack of large mesiolingual and distolingual cuspules basal on the crown. The specimen ZPAL V.34/60 (Figure 4(i, j)) represents a lower posterior postcanine from the right jaw, following the morphological criteria of Godefroit and Battail (1997). It has distal edge of the cusp c almost rectangular to distal edge of the root similarly to ZPAL V.34/44 and contrary to V.34/45, V.34/46, V.34/47, and V.34/55. In these teeth distal edge of the cusp c is oblique to the distal edge of the root (with exception of V.34/55 in which the root is in the mandible and its distal edge is not visible). The teeth ZPAL V.34/46 (the side is not determined; Figure 4(c, d)) and V.34/55 (it has fragment of the right mandible with probably lingual side with groove for the replacement dental lamina) have similar to holotype general proportion of cusps. The cusp a of these teeth is the largest one. Its mesial crest is much longer than the distal crest. The mesial part of cusp a

is strongly concave on both sides (lingual and labial), the distal edge is straight and very sharp. The distal cusp c is lower than cusp a and in close proximity to it, especially in ZPAL V.34/46. The mesial cusp b is similar in size to d and at the same height of the crown or slightly lower. In the tooth ZPAL V.34/44, two cuspules are on the lingual and labial sides under cusp b. In teeth ZPAL V.34/45 and ZPAL V.34/46, the distinct notch is visible between cusps a and c. The differences between all these postcanines are related probably with size and position of the tooth in the jaw. In all tetracuspid teeth the lingual and labial surfaces of the cusps a–c are slightly concave, contrary to similar postcanines of *Alemoatherium* (Martinelli et al. 2017). No wear facets are present on the crown. The enamel surface near the crown and root junction slightly bulges, but there is no distinctive cingulum. A constriction separating the enamel surface of the crown from the dentine surface of the root is visible. The specimens ZPAL V.34/46, V.34/55, V.34/60 are similar to the less well-preserved teeth (Pal/CHQ-(05) and Pal/CHQ-007) of *Rewaconodon* (Datta et al., 2004, Figure (2, 7)). They differ from *Rewaconodon* in cusp d much higher in the crown and closer to cusp c.

The roots are more or less broken in most teeth except for the tricuspid tooth ZPAL V.34/62 (Figure 3(e, f)). A shallow notch occurs between the mesial and distal thick parts of the root. The end of both parts is rather flat with rounded edges. In ZPAL V.34/61 (Figure 3(g, h)) and V.34/55 (Figure 4(a, b)) the roots are inside the bone so their shape is unknown, but the contact of the teeth with the alveolar margin is visible in those specimens. The mesial and distal edges of the roots are parallel and of the same width as the crown in most tricuspid teeth. In the lower tetracuspid teeth the upper part of the roots narrows and in the lowest part the edges are parallel (e.g. ZPAL V.34/44, Figure 4(g, h)).

Humerus

The distal end of the right humerus collected in layer 2 is well preserved (Figure 5). Both condyles are distinct. The entepicondyle is very large and has rectangular lateral edge on the distal end (Figure 5(d)). There is a small groove on its proximal surface. The ectepicondyle is curved in anterior view and forms a distinct pit on its ventral side, close to the radial condyle. The entepicondylar foramen is not visible. If it was present, it was very far from the distal end. The radial condyle has a posterior (ventral) ball-shaped part situated close to the ectepicondyle (Figure 5(a, c, d)). The trochlea for articulation with the ulna is visible on both dorsal and ventral sides of the humerus (Figure 5(d)). The trochlear surface is convex and rather small, situated in the middle part of the bone.

Discussion

The Woźniki material shows a relatively large range of sizes, especially among tricuspid teeth. It is likely that more than one generation of replacement teeth are represented in the sample; so some portion of the morphological variation may be attributed to the differences between successive

generations of teeth at the same tooth locus (Abdala et al. 2013, Datta et al. 2004; Luo et al. 2004).

The postcanines of *Dromatherium*, *Microconodon*, *Rewaconodon*, *Therioherpeton*, *Tricuspes*, *Pseudotriconodon*, and *Meurthodon* resemble *Polonodon* gen. nov. in: 1) main cusps situated in one line, 2) the root being incipiently divided by a furrow on both lingual and labial sides, and 3) very narrow crown with both sides parallel. In one tooth of *Polonodon* gen. nov. (ZPAL V.32/44) two small cusps occur on labial and lingual sides similar to the posteriormost postcanines of *Dromatherium* (Simpson, 1926; Sues, 2001). The lower postcanines of *Polonodon* gen. nov. differ from *Dromatherium*, *Microconodon*, *Rewaconodon* (only GS I Pal/CHQ-005), *Therioherpeton*, *Tricuspes*, *Pseudotriconodon*, and *Meurthodon* in the position of cusp b in relation to cusps c. We calculated the ratio (O/P) between the length of the mesial and distal edges of cusp a (the distance from the tip of cusp a to the junction of cusp a with cusp b and c; see Figure 6). This ratio was confronted to proportion between the width of the crown and distance from top of the cusp a to top of the cusp d (S/T) (Figure 6 (a)) and to proportion between the width of the crown and the width of the roots base (R/S) (Figure 6 (b)) and shown on scatter-plots (Figure 6). Unfortunately the well preserved teeth of cynodonts (which allow to make needed measurements) are very rare and most genera might be represented by single specimens. The teeth of *Polonodon* shows distinct cloud of points but also large variability on both scatter-plots. The distinct cloud means that they represent single, separate taxon and their variability might be interpreted as large differences between small and large teeth (replaced probably many times, Kielan-Jaworowska et al. 2004) which are in studied sample. In typical Dromatheriidae tetracuspoid tooth the cusp b is on the same level as cusp c and they are of similar size. Datta et al. (2004) described three teeth GS I Pal/CHQ-006, GS I Pal/CHQ-007, GS I Pal/CHQ-008 as lower posterior postcanines of *Rewaconodon*, with position of cusp b in relation to cusp c as in *Polonodon* gen. nov. (Figure 7). Some lower teeth in *Dromatherium* and *Triconodon* (Simpson, 1929) have cusp b lower than cusp c, but these teeth are tricuspid. All tetracuspoid or multi-cuspoid teeth in

Dromatherium have cusp b higher than cusp c (Osborn 1886). In *Microconodon* only two tetracuspoid teeth are preserved and in both cusp b is slightly lower than cusp c (proportions S/U are 5.4 and 10.1, S/U proportion between the width of the crown and the vertical distance from the junction of cusp a with cusp c to the junction of cusp a with cusp b for explanation see Figure 6). Similar ratios in *Polonodon* gen. nov. range from 2.56 to 3.46 and in some teeth from Rewa Formation (GS I Pal/CHQ-006, GS I Pal/CHQ-007, GS I Pal/CHQ-008) between 2.20 to 4.86. They are not shown on the scatter-plots (Figure 6), because they are incomplete and detailed measurements cannot be taken (for explanation see Figure 6 (a)), but distinction between *Rewaconodon* and *Polonodon* concerns position of cusp d.

The mesial edge of the cusp a is much longer than the distal edge and this is the main character that distinguishes *Polonodon* gen. nov. from other dromatheriids (Figure 6). In *Polonodon* gen. nov. the proportion between the length of mesial and distal edges of main cusp is larger than 1.5, in dromatheriids lower than 1.5 (see Figure 6). It makes *Polonodon* gen. nov. similar to *Brasilitherium*, *Brasilodon*, and *Botucaraitherium*. All these cynodonts have a small cusp b located below the larger cusp c. *Polonodon* gen. nov. is also similar to *Brasilitherium* in occurrence of teeth with four cusps and two cuspsules in some teeth. Postcanine teeth of *Polonodon* gen. nov. differ from those of *Brasilitherium*, *Botucaraitherium* (Bonaparte et al., 2005; Soares et al., 2014), and the tricuspid tooth from the Lehrberg Beds described by Lucas et al. (2001) in the lack of small cuspsules that forms an incipient cingulum. Figure 6(a) shows that some specimens of *Halatherium* have similar proportion to *Polonodon*, but it is probably convergence because of presence of two separate roots in *Halatherium* (Peyer 1956 and Świłło et al., 2014).

General proportions of distal end of the humerus are similar to much larger humerus of *Oligokyphus* (width of the distal end 18 mm versus 1.6 mm of ZPAL V.34/52, Kühne 1956), but cynodontian humerus from Woźniki has the entepicondyle larger and more differentiated, and its radial and ulnar condyles are connected with each other. The humerus from Woźniki differs from the traversodontid *Luangwa* (after Kemp 1980), the tritylodontid *Oligokyphus* (after Kühne, 1956), the probainognathian *Probelesodon* (after Romer and Lewis, 1973), the

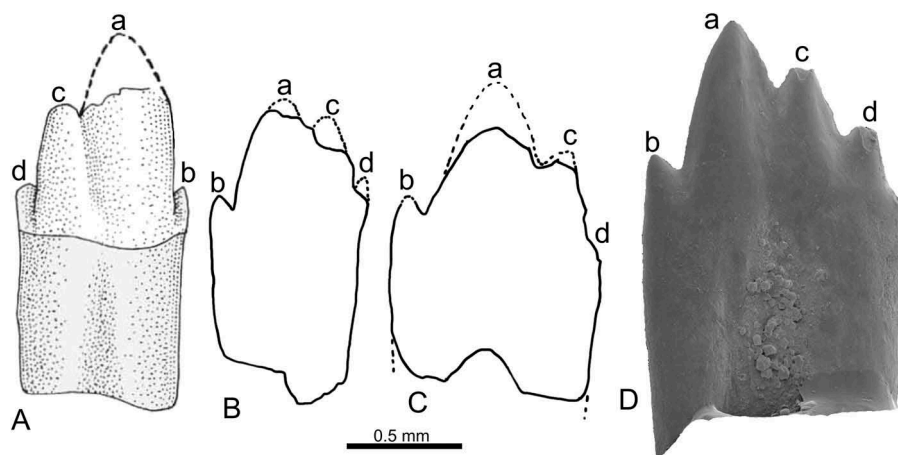


Figure 7. Some teeth from Tiki Formation (India) similar to *Polonodon woznikiensis* gen. et sp. nov. (a-c) *Rewaconodon tikiensis* (modified from Datta et al. 2004); (a) GSI Pal/CHQ-006; (b) GSI Pal/CHQ-007; (c) GSI Pal/CHQ-008; (d) ZPAL V.33/47 (paratype). [planned for page width].

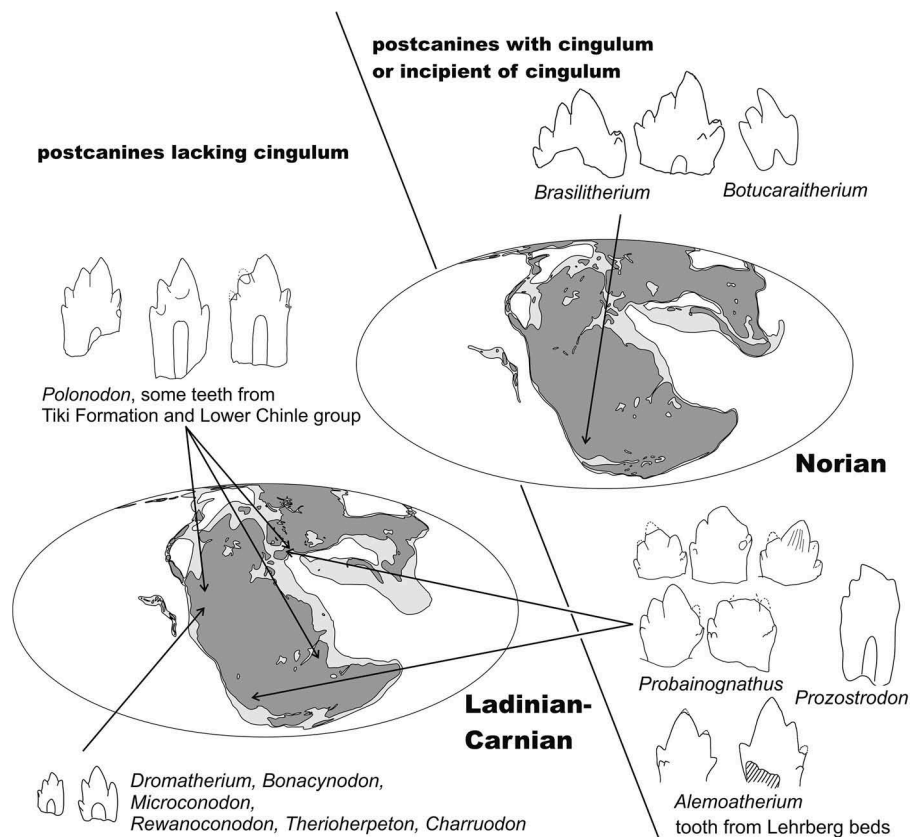


Figure 8. Examples of eucynodont teeth from Carnian and Norian of Pangea. Teeth drawings are based on Osborn (1887), Lucas et al. (2001), Soares et al. (2014), palaeogeographical reconstructions are based on Scotese Paleomap project (www.scotese.com). [planned for page width].

tritheledontid *Irajatherium* (Martinelli et al. 2005), the morgauodontid *Morganucodon* (after Jenkins and Parrington, 1976), and the cladotherian *Vincelestes* (Rougier, 1993) the radial condyle much larger than the ulnar one.

The new species from Woźniki shows that *Polonodon*, developed the postcanines with cusp b smaller and lower-positioned than cusp c at the same time as the Probainognathidae in South America (e.g. *Alemoatherium huebneri*). The next group which formed similar construction appeared in Norian. It is known from the Caturrita Formation of Brazil and is represented by *Brasilitherium*, *Brasilodon* and *Botucaraitherium* (Bonaparte et al., 2005; Soares et al., 2014). In older forms such as *Prozostrodon*, *Probainognathus*, *Bonacynodon*, *Santacruzognathus* cusp b and c are on the same level (see Figure 6).

Conclusions

The non-mammaliaform eucynodont fossils found in Woźniki, though currently represented by numerous and isolated teeth of several individuals, show strong affinities with representatives of the Dromatheriidae. The Woźniki finds also indicate that the eucynodont fossil record in the Upper Triassic of Poland is much richer than previously known.

The presence of conspicuous division of roots in postcanines in the dromatheriids and *Prozostrodon* suggests that this character developed already in the Carnian (Figure 8). Probably at that time the Dromatheriidae diverged from other eucynodonts and achieved some diversity, as represented, for example by: 1)

Rewaconodon with relatively low crown, and 2) *Dromatherium* with a very high crown, but both genera with cusp b and c on the same level in the lower tooth, 3) *Polonodon* with crown consist of more variable position of cusps.

In postcanines of *Polonodon* gen. nov. and in some postcanines from the Carnian Tiki Formation (*Rewaconodon* GS I Pal/CHQ-007, GS I Pal/CHQ-008), the crown is high and cusp b is much lower than cusp c. Moreover, in *Polonodon* gen. nov. tetracuspoid teeth with two cusps on the lingual and labial sides occur. For now it is difficult to decide, which teeth (typical dromatheriids as *Dromatherium* and *Microconodon* or *Polonodon* gen. nov.) retained a more plesiomorphic morphology. It is worth to mentioning that the crown shape similar to the *Polonodon* gen. nov. of mid-late Carnian age characterizes some early Norian eucynodonts (*Brasilitherium* and *Botucaraitherium*) from the southern part of Pangea.

Acknowledgments

The funding for this study came from a grant of National Science Centre, Poland awarded to T. S. (No 2012/07/B/NZ8/02707). The excavations and fieldworks led by the Institute of Paleobiology, PAS (Warsaw) and the Faculty of Biology of the University of Warsaw were supported from the mentioned above grant, the funds of the Institute of Paleobiology, the funds of University of Warsaw from the project of the student Scientific Circle of Evolutionary Biology, granted by The Advisory Board for The Student Scientific Movement (project No 32/II/2014). We thank the owners of the brickyard in Woźniki, Aleksandra i Mariusz Rospędek for permission to

conduct the excavations, as well as all the students, amateurs, and professionals, who participated in the field works at the Woźniki clay-pit. Writing this manuscript necessitated considerable division of labor. All authors were involved in the writing and editing of the final draft. G.N. is funded by a Wallenberg Scholarship from the Knut and Alice Wallenberg Foundation, awarded to P. E. Ahlberg (Uppsala University). Constructive criticism and improvements to the manuscript done by A. Martinelli (Universidade Federal do Rio Grande do Sul, Brazil), G. Rougier (University of Louisville, USA), and Fernando Abdala (University of the Witwatersrand) are gratefully appreciated.

Funding

This work was supported by the Narodowe Centrum Nauki 2012/07/B/NZ8/02707 [2012/07/B/NZ8/02707].

ORCID

Mateusz Tałanda  <http://orcid.org/0000-0003-3358-9539>

References

- Abdala F. 2000. Catalogue of non-mammalian cynodonts in the Vertebrate Paleontology Collection of the Instituto Miguel Lillo, Universidad Nacional de Tucumán, with comments on species. *Ameghiniana*. 37:463–475.
- Abdala F, Gaetano LC. 2017. Late Triassic cynodont life: time of innovations in the mammal lineage. In: Tanner LH, editor. *The Late Triassic World: Topics in Geobiology*. 46:407–445.
- Abdala F, Giannini NP. 2002. Chiniquodontid cynodonts: systematic and morphometric considerations. *Palaeontology*. 45:1151–1170.
- Abdala F, Jasinowski SC, Fernandez V. 2013. Ontogeny of the Early Triassic cynodont *Thrinaxodon liorhinus* (Therapsida): dental morphology and replacement. *J. Vert. Paleontol.* 33:1408–1431.
- Abdala F, Ribeiro AM. 2000. A new therioherpetid cynodont from the Santa Maria Formation (Middle Late Triassic), Southern Brazil. *Geodiversitas*. 22:589–596.
- Abdala F, Ribeiro AM. 2010. Distribution and diversity patterns of Triassic cynodonts (Therapsida, Cynodontia) in Gondwana. *Palaeogeogr Palaeoclimatol Palaeoecol*. 286:202–217.
- Bonaparte JF. 2013. Una nueva especie de Triconodontia (Mammalia), de la Formación Los Alamitos, Provincia de Río Negro y comentarios sobre su fauna de mamíferos. *Ameghiniana*. 29:99–110.
- Bonaparte JF, Barberena MC. 1975. A possible mammalian ancestor from the Middle Triassic of Brazil (Therapsida-Cynodontia). *J Paleontol*. 49:931–936.
- Bonaparte JF, Barberena MC. 2001. On two advanced carnivorous cynodonts from the Late Triassic of southern Brazil. *Bull Museum Comp Zool*. 156:59–80.
- Bonaparte JF, Martinelli AG, Schultz CL. 2005. New information on *Brasilodon* and *Brasilitherium* (Cynodontia, Probainognathia) from the Late Triassic of southern Brazil. *Rev Bras Paleontol*. 8:25–46.
- Bonaparte JF, Martinelli AG, Schultz CL, Rubert R. 2003. The sister group of mammals: small cynodonts from the Late Triassic of southern Brazil. *Rev Bras Paleontol*. 5:5–27.
- Bonaparte JF, Migale LA. 2010. Protomamíferos y mamíferos Mesozoicos de América del Sur. *Museo de Ciencias Naturales Carlos Ameghino*. Mercedes. 442.
- Bonaparte JF, Soares MB, Martinelli AG. 2012. Discoveries in the Late Triassic of Brazil improve knowledge on the origin of mammals. *Historia Natural. Fundación Felix De Azara, Tercera Serie*. 2012(2):5–30.
- Broom R. 1905. On the use of the term Anomodontia. *Rec Albany Museum*. 1:266–269.
- Brusatte SL, Nesbitt SJ, Irmis RB, Butler RJ, Benton MJ, Norell MA. 2010. The origin and early radiation of dinosaurs. *Earth-Science Rev*. 101:68–100.
- Clemens WA. 1980. Rhaeto-Liassic mammals from Switzerland and West Germany. *Zitteliana*. 5:51–92.
- Clemens WA. 2011. New morganucodontans from an Early Jurassic fissure filling in Wales (United Kingdom). *Palaeontology*. 54:1139–1156.
- Crompton AW. 1974. The dentitions and relationships of the Southern African Triassic mammals, *erythrotherium parringtoni* and *megazostrodon rudnerae*. *Bulletin Of The British Museum (Natural History)*. 24:397–437.
- Datta PM, Das DP, Luo ZX. 2004. A Late Triassic dromatheriid (Synapsida: Cynodontia) from India. *Ann Carnegie*. 73:12–24.
- Debuyschere M, Gheerbrant E, Allain R. 2015. Earliest known European mammals: a review of the Morganucodonta from Saint-Nicolas-de-Port (Upper Triassic, France). *J Syst Palaeontology*. 13:825–855.
- Dzik J, Sulej T. 2007. A review of the early Late Triassic Krasiejów biota from Silesia, Poland. *Palaeontol Pol*. 64:3–27.
- Dzik J, Sulej T. 2016. An early Late Triassic long-necked reptile with a bony pectoral shield and gracile appendages. *Acta Palaeontol Pol*. 61:805–823.
- Dzik J, Sulej T, Niedźwiedzki G. 2008. A dicynodont-theropod association in the latest Triassic of Poland. *Acta Palaeontologica Polonica*. 53:733–738.
- Fraser NC, Sues HD. 1997. In the shadow of the dinosaurs: early Mesozoic tetrapods. Cambridge, United Kingdom: University Press; p. 435.
- Gaetano LC, Rougier GW. 2012. First amphiiletid from south America: a molariform from the Jurassic Cañadón Asfalto Formation, Patagonia, Argentina. *J Mamm Evol*. 19:235–248.
- Geyer G, Kelber KP. 2018. Spinicaudata (“Conchostraca,” Crustacea) from the Middle Keuper (Upper Triassic) of the southern Germanic Basin, with a review of Carnian–Norian taxa and suggested biozones. *Palaeontol Z*. (in press).
- Gierliński G, Pieńkowski G, Niedźwiedzki G. 2004. Tetrapod track assemblage in the Hettangian of Sołtyków, Poland, and its paleoenvironmental background. *Ichnos*. 11:195–213.
- Gierliński GD, Lockley MG, Niedźwiedzki G. 2009. A distinctive crouching theropod trace from the Lower Jurassic of Poland. *Geol Q*. 53:471–476.
- Gill T. 1872. Arrangement of the families of mammals with analytical tables. *Smithson misc collect*. 11:1–98.
- Godefroit P, Battail B. 1997. Late Triassic cynodonts from Saint-Nicolas-de-Port (north-eastern France). *Geodiversitas*. 19:567–631.
- Hahn G, Hahn R, Godefroit P. 1994. Zur Stellung der Dromatheriidae (Ober-Trias) zwischen den Cynodontia und den Mammalia. *Geolo et Polonica*. 28:141–159.
- Hahn GJ, Lepage C, Wouters G. 1984. Cynodontier-Zähne aus der Ober-Trias von Medernach, Grossherzogtum Luxemburg. *B Société belge de géologie*. 93:357–373.
- Heckert AB. 2004. Late Triassic microvertebrates from the lower Chinle Group (Otischalkian-Adamian: Carnian), southwestern USA. *New Mexico Museum Nat Hist Sci Bull*. 27:1–170.
- Heckert AB, Lucas SG. 1999. Global correlation and chronology of Triassic theropods (Archosauria, Dinosauria). *Albertiana*. 23:22–35.
- Hopson JA, Kitching JW. 1972. A revised classification of cynodonts (Reptilia; Therapsida). *Paleontol Africa*. 14:71–85.
- Hopson JA, Kitching JW. 2001. A probainognathian cynodont from South Africa and the phylogeny of nonmammalian cynodonts. *Bull Museum Comp Zool*. 156:5–35.
- Hopson JA. 1991. Systematics of the nonmammalian Synapsida and implications for patterns of evolution in synspsids. In: Schultze H-P, Trueb L, eds. *Origins of the Higher Groups of Tetrapods: Controversy and Consensus*. Ithaca: Comstock Publishing Associates; p. 635–693.
- Hopson JA. 1994. Synapsid evolution and the radiation of non-eutherian mammals. In: RS. Spencer (ed.), *Major Features of Vertebrate Evolution, 190–219*. The Paleontological Society, Knoxville.
- Jenkins FA, Parrington FR. 1976. The postcranial skeletons of the Triassic mammals *Eozostrodon*, *Megazostrodon* and *Erythrotherium*. *Philosophical Trans Royal Soc London B: Biol Sci*. 273:387–431.
- Jones TR. 1890. On some fossil Estheriae. *Geological Magazine, New Series*. Decada III. 7:385–390.

- Kemp TS. 1980. Aspects of the structure and functional anatomy of the Middle Triassic cynodont Luangwa. *J Zool.* 191:193–239.
- Kemp TS. 1982. Mammal-like reptiles and the origin of mammals. London, United Kingdom: London Academic Press; p. 363.
- Kemp TS. 2005. The Origin and Evolution of Mammals. Oxford, UK: Oxford University Press.
- Kemp TS. 1988. Interrelationships of the Synapsida. In: Benton MJ, editor. The Phylogeny and Classification of the Tetrapods: Mammals Vol. 35B, Chapter 2. Oxford: Systematics Association; p. 1–22.
- Kielan-Jaworowska Z, Cifelli RL, Luo ZX. 2004. Mammals from the Age of Dinosaurs. Origins, Evolution, and Structure. New York: Columbia University Press; p. 630.
- Kotlicki S. 1974. Stratigraphic position of the Triassic sediments in the Upper Silesian region. *B Acad Pol Sci.* 22:161–166.
- Kozur HW, Weems RE. 2010. The biostratigraphic importance of conchostracans in the continental Triassic of the northern hemisphere. *Geol Soc London Spec.* 334:315–417.
- Kühne WG. 1956. The Liassic therapsid *Oligokyphus*. London, United Kingdom: British Museum; p. 149.
- Kühne WG. 1958. Rhaetische Triconodonten aus Glamorgan ihre Stellung zwischen den Klassen Reptilia und Mammalia und ihre Bedeutung für die Reichert'sche Theorie. *Paläont Z.* 32:197–235.
- Langer MC, Ezcurra MD, Bittencourt JS, Novas FE. 2010. The origin and early evolution of dinosaurs. *Biol Rev.* 85:55–110.
- Liu J, Rubidge B, Li J. 2009. New basal synapsid supports Laurasian origin for therapsids. *Acta Palaeontol Polonica.* 54(3):393–400.
- Lucas SG. 2015. Age and correlation of Late Triassic tetrapods from southern Poland. *Ann Soc Geol Pol.* 85:627–635.
- Lucas SG, Heckert AB, Harris JD, Seegis D, Wild R. 2001. Mammal-like tooth from the Upper Triassic of Germany. *J Vert Paleontol.* 21:397–399.
- Lucas SG. 2010. The Triassic timescale based on nonmarine tetrapod biostratigraphy and biochronology. In: Lucas SG, editor. The Triassic timescale: Geological Society Vol. 334. London: Special Publication; p. 447–500.
- Lucas SG, Luo Z. 1993. *Adelobasileus* from the Upper Triassic of West Texas: the oldest mammal. *J. Vert. Paleontol.* 13:309–334.
- Lucas SG, Oakes W. 1988. A Late Triassic cynodont from the American South-West. *Palaeontology.* 31:445–449.
- Lucas SG, Tanner LH, Kozur HW, Weems RE, Heckert AB. 2012. The Late Triassic timescale: Age and correlation of the Carnian–Norian boundary. *Earth-Science Rev.* 114:1–18.
- Luo ZX. 2007. Transformation and diversification in early mammal evolution. *Nature.* 450(7172):1011–1019.
- Luo ZX, Kielan-Jaworowska Z, Cifelli RL. 2004. Evolution of dental replacement in mammals. in: *Fanfare for an Uncommon Paleontologist Festschrift in Honor of Dr. Malcolm C. McKenna*, (MR Dawson, and JA Lillegraven, eds.). Carnegie Museum Nat Hist Bull. 36:159–175.
- Martinelli AG, Bonaparte JF, Schultz CL, Rubert R. 2005. A new tritheledontid (Therapsida, Eucynodontia) from the Late Triassic of Rio Grande do Sul (Brazil) and its phylogenetic relationships among carnivorous non-mammalian eucynodonts. *Ameghiniana.* 42:191–208.
- Martinelli AG, Eltink E, ÁAS D-R, Langer MC. 2017a. A new cynodont from the Santa Maria formation, south Brazil, improves Late Triassic probainognathian diversity. *Pap Paleontology.* 3.3:401–423.
- Martinelli AG, Soares MB. 2016. Evolution of South American cynodonts. *Contrib Mus Argent Cienc Nat “Bernardino Rivadavia”.* 6:183–197.
- Martinelli AG, Soares MB, de Oliveira TV, Rodrigues PG, Schultz CL. 2017b. The Triassic eucynodonts *Candelariodon barberenai* revisited and the early diversity of stem prozostrodontians. *Acta Palaeontol Pol.* 62:527–542.
- Martinelli AG, Soares MB, Schwanke C. 2016. Two New Cynodonts (Therapsida) from the Middle-Early Late Triassic of Brazil and Comments on South American Probainognathians. *PLoS ONE.* 11(10):e0162945.
- Mukherjee D, Ray S, Chandra S, Pal S, Bandyopadhyay S. 2012. Upper Gondwana Succession of the Rewa Basin, India: Understanding the Interrelationship of Lithologic and Stratigraphic Variables. *J Geol Soc India.* 79:563–575.
- Niedźwiedzki G, Brusatte SL, Sulej T, Butler RJ. 2014. Basal dinosauriform and theropod dinosaurs from the middle-late norian (Late Triassic) of Poland: implications for Triassic dinosaur evolution and distribution. *Palaeontology.* 57:1121–1142.
- Niedźwiedzki G, Sulej T. 2007. Tropy kręgowców w górnym triasie Polski. Granice Paleontologii, XX Konferencja Naukowa Paleobiologów i Biostratygrafów PTG, Św. Katarzyna pod Łysicą, 10–13 September 2007: 97.
- Niedźwiedzki G, Sulej T, Dzik J. 2012. A large predatory archosaur from the Late Triassic of Poland. *Acta Palaeontologica Polonica.* 57:267–276.
- Olempska E. 2004. Late Triassic spinicaudatan crustaceans from south-western Poland. *Acta Palaeontol Pol.* 49:429–442.
- Oliveira EV. 2006. Reevaluation of *Therioherpeton cargnini* Bonaparte & Barberena, 1975 (Probainognathia, Therioherpetidae) from the Upper Triassic of Brazil. *Geodiversitas.* 28:447–465.
- Osborn HF 1886. Observations upon the Upper Triassic mammals, *Dromatherium* and *Microconodon*. Proceedings of the Academy of Natural Sciences of Philadelphia. p. 359–363.
- Osborn HF 1887. The Triassic mammals, *Dromatherium* and *Microconodon*. Proceedings of the American Philosophical Society. 24:109–111.
- Owen R. 1861. Palaeontology, or a Systematic Summary of Extinct Animals and their Geological Relations. Second ed. Edinburgh: Adam and Charles Black; p. 420.
- Owen R. 1871. Monograph of the fossil Mammalia of the Mesozoic formations. Vol. 24. London, United Kingdom: Palaeontographical Society; p. 115.
- Pacyna G. 2014. Plant remains from the Polish Triassic. Present knowledge and future prospects. *Acta Palaeobotanica.* 54:3–33.
- Pieńkowski G, Niedźwiedzki G, Brański P. 2014. Climatic reversals related to the Central Atlantic magmatic province caused the end-Triassic biotic crisis – Evidence from continental strata in Poland. In Keller G, Kerr A, editors. Volcanism, Impacts, and Mass Extinctions: Causes and Effects. Geological Society of America Special Papers 505. p. 263–286
- Rauhut OWM, Hungerbühler A. 1998. A review of European Triassic theropods. *Gaia.* 15:75–88.
- Roemer F. 1867. Neuere Beobachtungen über die Gliederung des Keupers und ihn zunächst überlagernden Abteilung der Juraformation in Oberschlesien und ihn den angrenzenden Theilen von Polen. *Z Dtsch Geol Ges J Ger Geol Soc.* 19:255–269.
- Roemer F. 1870. Geologie von Oberschlesien. Breslau: Kingdom of Prussia: Nischkowsky; p. 587.
- Romer AS. 1969a. Cynodont reptile with incipient mammalian jaw articulation. *Science.* 166(3907):881–882.
- Romer AS. 1969b. The Brazilian Triassic cynodont reptiles *Belesodon* and *Chiniquodon*. *Breviora.* 332:1–16.
- Romer AS. 1970. The Chanares (Argentina) Triassic reptile fauna VI. A chiniquodontid cynodont with an incipient squamosal-dentary jaw articulation. *Breviora.* 344:1–18.
- Romer AS, Lewis AD. 1973. The Chañares (Argentina) Triassic reptile fauna. XIX. Postcranial materials of the cynodonts *Probelesodon* and *Probainognathus*. *Breviora.* 407:1–26.
- Rougier GW. 1993. *Vincelestes neuquenianus* Bonaparte (Mammalia, Theria) un primitivo mamífero del Cretácico Inferior de la Cuenca Neuquina. Unpublished Ph.D. dissertation. 720 pp. Universidad Nacional de Buenos Aires, Buenos Aires.
- Rubidge BS, Sidor CA. 2001. Evolutionary patterns among Permian–Triassic therapsids. *Annu Rev Ecol Syst.* 32:449–480.
- Shapiro MD, Jenkins FA Jr. 2001. A cynodont from the Upper Triassic of East Greenland: tooth replacement and double-rootedness. *Bull Museum Comp Zool.* 156:49–58.
- Shukla UK, Bachmann GH, Singh IB. 2010. Facies architecture of the Stuttgart Formation (Schilfsandstein, Upper Triassic), central Germany, and its comparison with modern Ganga system, India. *Palaeogeogr Palaeoclimatol Palaeoecol.* 297:110–128.
- Sigogneau-Russell D. 1989. Haramiyidae (Mammalia, Allotheria) en provenance du Trias supérieur de Lorraine (France). *Palaeontographica Abteilung A.* 206:137–198.
- Sigogneau-Russell D, Hahn G. 1994. Late Triassic microvertebrates from Central Europe. In: Fraser NC, Sues H-D, editors. The shadow of the

- dinosaurs – early mesozoic tetrapods. Cambridge: Cambridge University Press. p. 197–213.
- Simpson GG. 1926a. Mesozoic Mammalia, IV; The multituberculates as living animals. *Am J Sci.* 63:228–250.
- Simpson GG. 1926b. Mesozoic Mammalia, V; Dromatherium and Microconodon. *Am J Sci.* 68:87–108.
- Skawina A, Dzik J. 2011. Umbonal musculature and relationships of the Late Triassic filibranch unionoid bivalves. *Zool J Linn Soc.* 163: 863–883.
- Soares MB, Abdala F, Bertoni-Machado C. 2011. A sectorial toothed cynodont (Therapsida) from the Triassic Santa Cruz do Sul fauna, Santa Maria Formation, Southern Brazil. *Geodiversitas.* 33:265–278.
- Soares MB, Martinelli AG, Oliveira TV. 2014. A new prozostrodontian cynodont (Therapsida) from the Late Triassic *Riograndia* Assemblage Zone (Santa Maria Supersequence) of Southern Brazil. *An Acad Bras Cienc.* 86:1673–1691.
- Sues HD. 2001. On *Microconodon*, a Late Triassic cynodont from the Newark Supergroup of eastern North America. *Bull Museum Comp Zoology.* 156:37–48.
- Sues HD, Olsen PE. 1990. Triassic vertebrates of Gondwanan aspect from the Richmond Basin of Virginia. *Science.* 249(4972):1020–1023.
- Sulej T, Bronowicz R, Tałanda M, Niedźwiedzki G. 2011. A new dicyodont-archosaur assemblage from the Late Triassic (Carnian) of Poland. *Earth Environ Sci Trans Royal Soc Edinburgh.* 101:261–269.
- Sulej T, Niedźwiedzki G, Bronowicz R. 2012. A new Late Triassic vertebrate fauna with turtles, aetosaurs and coelophysoid dinosaurs from Poland. *Journal of Vertebrate Paleontology.* 32:1033–1041.
- Sulej T, Niedźwiedzki G, Szczygielski T, Tałanda M. 2014. A new Triassic (Ladinian) association with a large temnospondyl, sauropterygians, a gigantic prolacertiform, and an archosauriform in Miedary (Southern Poland). 74th Annual Meeting of the Society of Vertebrate Paleontology, Berlin, Germany, November 5–8, 2014, Abstract book: 237.
- Świło M, Niedźwiedzki G, Sulej T. 2014. Mammal-like tooth from the Upper Triassic of Poland. *Acta Palaeontol Pol.* 59:815–820.
- Świło M, Niedźwiedzki G, Sulej T. 2015. Mammal-like teeth from the Upper Triassic of Poland. 13th Annual Meeting of the European Association of Vertebrate Palaeontologists, Opole, Poland, 8–12 July 2015. Abstracts: 34.
- Szulc J, Racki G, Jewuła K, Środoń A. 2015. How many Upper Triassic bone-bearing levels are there in Upper Silesia (Southern Poland)? A critical overview of stratigraphy and facies. *Ann Soc Geol Pol.* 85:587–626.
- Tałanda M. 2015. Siostra Krasiejowa – tanocenoza Woźnik. Program Konferencji – Śląskie Dinozaury (nie tylko) z Krasiejowa. V Sesja Popularnonaukowa, Instytut Nauk Geologicznych PAN, Kraków, 23.
- Tałanda M, Dzięcioł S, Sulej T, Niedźwiedzki G. 2011. Vertebrate burrow system from the Upper Triassic of Poland. *Palaios.* 26:99–105.