



The westernmost occurrence of *Gnathorhiza* in the Triassic, with a discussion of the stratigraphic and palaeogeographic distribution of the genus

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Abstract. The paper refines the taxonomic assignment of the only representative of the dipnoan genus *Gnathorhiza* from the Lower Triassic of Poland. It is assigned here to *Gnathorhiza otschevi* on the basis of morphological and biometrical similarity with the tooth plates from coeval strata of the European part of Russia. The material is comprised solely of tooth plates, both the upper and the lower ones. It comes from karst deposits of the Czatkowice 1 locality (southern Poland) dated to late Olenekian, Lower Triassic. The presence of *G. otschevi* in southern Poland widens its palaeobiogeographic Triassic record by more than 2000 km to the west. Czatkowice 1 locality is the only known occurrence of gnathorhizids within the Germanic Basin. *G. otschevi* from Czatkowice 1 shows petrodentine in the tooth plate. Its presence is proved for the first time in a Triassic gnathorhizid. *Gnathorhiza* was most widely distributed during the Permian and restricted to Europe in the Triassic. Tooth plates of both Early Triassic European and Late Permian Brazilian gnathorhizids are more similar to each other than to Permian-Carboniferous American ones.

1 Introduction

Gnathorhiza Cope, 1883 is so far the only dipnoan genus known from both Palaeozoic and Mesozoic sediments. This genus is of great interest due to its supposed close affinities with lepidosirenids (Romer and Smith, 1934) and aestivation capability (Campbell and Barwick, 1988). *Gnathorhiza* is known from the Upper Carboniferous to Lower Triassic strata of various localities around the world (Schultze, 1992, 2004). The Late Carboniferous and Early Permian fossils of this genus were found at different localities in the

USA (Dalquest et al., 1989), Germany (Boy and Schindler, 2000) and Oman (Schultze et al., 2008). In the Late Permian, *Gnathorhiza* occurred in Russia (Minikh, 1989; Minikh and Minikh, 2006) and Brazil (Toledo and Bertini, 2005). The youngest fossils of *Gnathorhiza* are known from the Lower Triassic freshwater sediments of Russia (Minikh, 1977, 2000; Minikh and Minikh, 2006; Newell et al., 2010) and Poland (Borsuk-Białynicka et al., 2003).

The Polish findings of *Gnathorhiza* come from karst deposits of the Czatkowice 1 locality situated near Cracow, southern Poland. The sediments were deposited just before the Röt transgression (Paszowski, 2009), and their age is estimated at early late Olenekian (Shishkin and Sulej, 2009). The dipnoan material comprising of four tooth plates (Fig. 1) was found together with remains of other fishes, procolophonids, temnospondyls, stem frogs, archosauriforms, lepidosauromorphs and kuehneosaurids (Borsuk-Białynicka et al., 1999). The tooth plates have been so far assigned to *Gnathorhiza* sp. (Borsuk-Białynicka et al., 2003). The present study provides their detailed morphological description and their specific assignment. The first evidence of the presence of petrodentine in a Triassic gnathorhizid is provided here for *Gnathorhiza* from Poland.

Czatkowice 1 in southern Poland is the westernmost occurrence of *Gnathorhiza* known so far from the Triassic. The tooth plates belong to a species known until now only from uppermost Permian and Lower Triassic sediments of Russia (Minikh, 1977; Minikh and Minikh, 1997, 2006). The Polish material and tooth plates of other known members of *Gnathorhiza* are compared. This brings new insight to the systematic affinities of the genus members. The geographic and stratigraphic distribution of *Gnathorhiza* was never sub-

ject to a broad study, and therefore the present revision may serve as a useful background for further studies.

2 Geological setting

The active Czatkowice quarry of Lower Carboniferous limestones, situated in the Cracow region (southern Poland), has revealed numerous karst forms of different ages (Paszkowski and Wieczorek, 1982). They were created during two phases of karstification – the first one between Late Carboniferous and Röt transgression and second one between Late Triassic and Callovian transgression (Paszkowski and Wieczorek, 1982). The largest of the karst fissures, named Czatkowice 1, is interpreted as a fragment of a cave formed in the first karstification phase (Paszkowski and Wieczorek, 1982). Paszkowski (2009) described the few metres thick filling consisting of yellow sands and silts in its upper part and green-brownish cave loams with Mississippian material and Lower Permian speleothems. The bone breccia formed the lowest 0.7 m of the sequence and “was filled with fine cross-bedded calcareous sandstone as well as by spar-cemented layers and discrete lenses of bone breccia” (Paszkowski, 2009, p. 11). The bones of vertebrates from Czatkowice 1 are disarticulated and often broken but show little or no abrasion. The taphonomic studies revealed that the bone breccia was deposited in a low-energy environment, with little transport but with several cycles of reworking (Borsuk-Białynicka et al., 1999; Cook and Trueman, 2009). No remains of an animal larger than 1 m have been found so far (Borsuk-Białynicka et al., 1999). The Czatkowice 1 fauna dwelled near or in a shallow freshwater pool, which had been forming an oasis in arid environment of circum-equatorial belt of northern Pangaea (Borsuk-Białynicka et al., 1999). On the basis of the geological premises and composition of the Czatkowice 1 fauna – the dominance of terrestrial reptiles and presence of a stem frog – it was assumed that during Early Triassic this locality was located on an upland (Shishkin and Sulej, 2009).

Paszkowski and Wieczorek (1982) interpreted the karst forms of Czatkowice 1 to have been deposited during the first karstification phase. Study of tetrapods specified the dating of Czatkowice 1 to be of Early Triassic age (Borsuk-Białynicka et al., 1999). The next dating was based on *Gnathorhiza* and procolophonids as index fossils (Borsuk-Białynicka et al., 2003). The heterodont dentition of the procolophonids from Czatkowice 1 gave reason to estimate the age of this sediment as younger than the Induan (Borsuk-Białynicka et al., 2003). In the Vettulian stage (Induan and early Olenekian) *Gnathorhiza* was the only dipnoan known from the European part of Russia, whereas in the late Olenekian, corresponding to the Yarenskian stage, modern dipnoans (*Arganodus*, *Ceratodus* and *Ptychoceratodus*) appeared to coexist with *Gnathorhiza* (Minikh, 1995; Minikh and Minikh, 2006). Thus, the Cza-

tkowice 1 age was estimated as early Olenekian (Borsuk-Białynicka et al., 2003). However, on the basis of typical late Olenekian temnospondyl genera, the capitosaurid *Parotosuchus* and the brachyopid *Batrachosuchoides* (members of the Yarenskian *Parotosuchus* fauna), the age of Czatkowice 1 has been refined to be early late Olenekian (Shishkin and Sulej, 2009). The dating was based on a comparison with the eastern European faunal succession (Shishkin et al., 2000). The most probable age of Czatkowice 1 thus corresponds to Fedorovskian Gorizont (sensu Minikh and Minikh 1997, 2006). *Gnathorhiza otschevi* Minikh, 1977 is one of three gnathorhizid species characteristic of the early late Olenekian of the pre-Uralian region (Minikh, 1977), so the assignment of gnathorhizid tooth plates from Czatkowice 1 to this species is consistent with the latter dating. In late late Olenekian (Gamskian Gorizont) localities *Gnathorhiza* remains are sparse and represented by only one subspecies, *G. triassica baskunchakensis* Minikh, 1977, which is outnumbered by more derived dipnoan species (Minikh, 1977; Minikh and Minikh, 1997).

In Czatkowice 1 no other dipnoan was found (Borsuk-Białynicka et al., 2003), but it is worth noting that in younger (Late Triassic–Middle Jurassic) karst forms of Czatkowice 2 locality numerous tooth plates of *Ptychoceratodus* cf. *philippsi* (Agassiz, 1838) were encountered (Paszkowski and Wieczorek, 1982). This material is currently under study and will be described elsewhere.

3 Material and methods

The dipnoan material used for this study comprises one complete and three partially complete tooth plates (Fig. 1). Only fragments of bones underlying the tooth plates are present. Tooth plates come from three different samples (Borsuk-Białynicka et al., 2003) of the Czatkowice 1 material extracted from blocks of karst deposits broken down by acetic acid (Borsuk-Białynicka et al., 1999). All specimens examined are housed in the collection of Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland (IP PAS). They are catalogued under ZPAL P. VII/5–7, 9 collection numbers. SEM images were taken at the Institute of Paleobiology PAS, Warsaw. Terminology of tooth plate characters follows Kemp (1993) and Skrzycki (2015). The measurements are made according to the method used by Vorobyeva and Minikh (1968), which was adapted for gnathorhizids by Minikh (1977) (Fig. 1k). Only ratios of one lower tooth plate is taken into account, because the first ridge rest of tooth plates is broken in our material. The Russian regional stratigraphy (see Tverdokhlebov et al., 2005, for details) is used here for Russian localities and the Czatkowice 1 site.

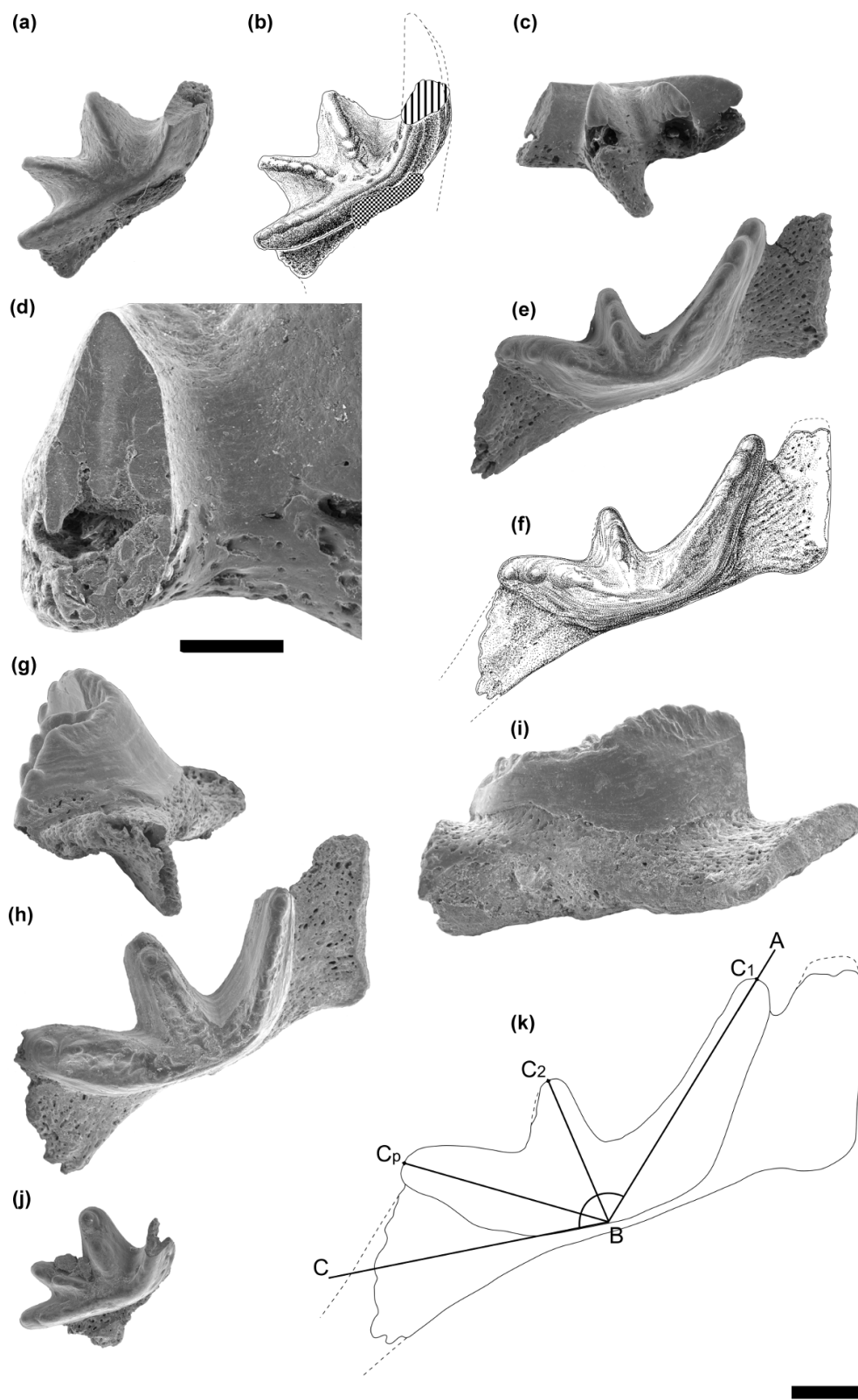


Figure 1. Tooth plates of *Gnathorhiza otschevi* from Czatkowice 1. (a, b) Upper tooth plate, ZPAL P. VII/6 in occlusal view and (c) in lateral view, and (d) a section of the first ridge; (e, f) lower tooth plate, ZPAL P. VII/7, in occlusal view and in dorsal view (g); (h) lower tooth plate, ZPAL P. VII/9, in occlusal view and (i) in medial view; (j) upper tooth plate, ZPAL P. VII/5, in occlusal view; (k) measurements of Minikh (1977) method. Scale bar for (a)–(c) and (e)–(j) 1 mm, 0.5 mm for (d).

4 Institutional abbreviations

ZPAL – Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland

5 Systematic palaeontology

Order Dipnoi Müller, 1845

Family Gnathorhizidae Miles, 1977

Genus *Gnathorhiza* Cope, 1883

Type species: *Gnathorhiza pusilla* (Cope, 1877)

Gnathorhiza otschevi Minikh, 1977

(Fig. 1)

2003 *Gnathorhiza* sp. – Borsuk-Białynicka et al. (2003)

2010 *Gnathorhiza* – Brinkmann et al. (2010)

Type locality and horizon: Bolshoye Bogdo Mountain, southern Russia, Early Triassic, late Olenekian, Yarenskian Superhorizont, Fedorovskian Gorizont.

Referred material: ZPAL P. VII/5, P. VII/6 upper tooth plates, ZPAL P. VII/7, P. VII/9 lower tooth plates. The material comes from Czatkowice 1 locality (southern Poland), Early Triassic, early late Olenekian, Yarenskian Superhorizont, Fedorovskian Gorizont.

Emended diagnosis (modified after Minikh, 1977): Medium-sized tooth plates with an obtuse inner angle (lower about 125°, upper about 140°); radiating ridges straight, narrow and acute, originate from one point at the mediolingual junction; four ridges in upper tooth plates, three in lower ones; lingual edge slightly concave; big, cone-shaped cusps present on ridges crests; in upper tooth plates the first ridge about 2 times longer than the second and fourth ridges; in lower tooth plates the first ridge about 2 times longer than the second one, and about 1.5 times longer than the third one; pterygopalatine ascending process originates above the second ridge of the upper tooth plates, and is short and slightly curved posteriorly; prearticular sulcus single and shallow; prearticular symphysis half-oval; furrows between ridges are throughout; inter-ridge furrows very deep; occlusal pits absent; enamel to bone junction straight; tooth plates do not contact in the midline.

5.1 General description

There are two upper tooth plates and two lower ones known from the Czatkowice 1 locality (Fig. 1). All the tooth plates of *Gnathorhiza otschevi* from Czatkowice 1 are small, with the last ridge not exceeding 4 mm. They are high-crowned, triangular in outline, with an obtuse inner angle and an almost indistinguishable occlusal surface. All ridges are straight, narrow and acute, and originate medially from one point at the mediolingual junction. However, the first ridge is slightly curved posteriorly near its origin. Cusps are present on the labial part of all the ridges (Fig. 1). Inter-ridge furrows are wide, very deep and reach the mediolingual junction. There is no wear facet on the medial faces of both upper and lower

tooth plates, which indicates that they do not contact each other along the midline.

5.2 Upper tooth plates

The upper tooth plates (Fig. 1a, b, c and j) bear four ridges. The first ridge is broken in both specimens, but it seems to be the longest or as long as the last one, as similar to all other representatives of *Gnathorhiza*. The first ridge is also the highest in ZPAL P. VII/5, although in ZPAL P. VII/6 the first broken ridge is slightly lower than the second ridge. The pterygopalatine bone is thin and short. Sulci of the pterygopalatine bone are almost indistinguishable, and the ascending process originates from the bone above the second ridge (Fig. 1c). The process is short, oval in section and slightly curved posteriorly. ZPAL P. VII/5 has two big cusps on both the second and third ridge, as well as three cusps on the fourth ridge. On ZPAL P. VII/6 the cusps are nearly worn out, but few can be still observed on the second and fourth ridge. The inner angle of the upper tooth plates equals about 135° in ZPAL P. VII/5 and about 141° in ZPAL P. VII/6 (Table 1). Specimen ZPAL P. VII/5 is the smallest tooth plate from Czatkowice 1. This specimen could have belonged to a juvenile fish as can be assumed from relatively big cusps (Fig. 1j) in comparison to other specimens from the collection.

5.3 Lower tooth plates

Three ridges separated by deep furrows can be observed on each of the lower tooth plates (Fig. 1e–i). The first ridge is the longest and highest one. Only in one specimen (ZPAL P. VII/7) the first ridge is complete, and it is almost 2 times longer than the second one and 1.2 times longer than the third one (Table 1). The sulcus on the prearticular bone is single and very shallow. The symphyseal shaft of the prearticular bone is long and slightly curved medially. Despite the fact that the posterior shaft of this bone is incomplete, it is evident that it was not much longer before it broke. The prearticular symphysis is long, half-oval in section and devoid of grooves on the surface (Fig. 1i). ZPAL P. VII/9 bears five to seven cusps on each of the ridges, while ZPAL P. VII/7 has only three cusps on each ridge. On the last ridge of the latter specimen a newly formed cusp can be seen, as well as horizontal growth lines of enamel (Fig. 1g). The inner angle reaches almost 130° in both lower tooth plates (Table 1).

5.4 Microstructure

A natural section of the ridge is visible on a broken first ridge of ZPAL P. VII/6 upper tooth plate (Fig. 1d). The ridge section is roughly oval in shape. In the place where the pterygopalatine bone fuses to the tooth plate, in one-third of the section length, a small pulp cavity can be seen. The bone has a spongy appearance inside the pulp cavity. A moderately narrow core of petrodentine stretches from the pulp cavity

up to the occlusal surface of the ridge. It has a lighter colour than the surrounding dentine (Fig. 1d). The core of petrodentine has the shape of a narrow, strongly elongated triangle, broadened toward the occlusal surface of the ridge.

Petrodentine (or pleromic hard tissue of Oervig, 1967) is a specific hypermineralized dentine present in adult dipnoan tooth plates (e.g. Smith, 1984; Kemp, 2001; Reisz et al., 2004). This tissue “is formed by the continued growth of the core dentine of the cusps in the hatchling tooth plate in those species that have this tissue” (Kemp, 2001, p. 424). Due to its continuous growth, growth lines can be seen in petrodentine (Smith, 1984). This tissue is free of denteons, almost free of collagen, but rich in calcium hydroxyapatite (Lund et al., 1992). Petrodentine is clearly distinguishable from the osteodentine (trabecular dentine), because its secretion begins in the larval stages of tooth plate development (Smith, 1984). Circumdenteonal dentine does not surround petrodentine; it is enclosed in interdenteonal dentine (Kemp, 2001). Smith (1984) defined 12 characters (which were later reduced to 9 in Reisz et al., 2004) enabling distinction of petrodentine from other tissues, both in extant and extinct dipnoans. However, Lund et al. (1992) did not agree with Smith (1984) and stated that petrodentine is present only in gnathorhizid and lepidosirenid tooth plates. But Kemp (2001) showed petrodentine also in some other derived taxa (e.g. *Mioceratodus*).

Originally the term was used by Lison (1941) to describe such tissue in tooth plates of extant *Protopterus* and *Lepidosiren*, but petrodentine is present also in some extinct taxa, e.g. *Gnathorhiza* (Smith, 1984; Lund et al., 1992; Kemp, 2001). On the occlusal surface of gnathorhizid tooth plates petrodentine is visible as a hard raised dentine that encloses regions of circumdenteonal and interdenteonal dentine (Lund et al., 1992). *Gnathorhiza* has extensive masses of petrodentine similar in structure to petrodentine of *Mioceratodus* (Kemp, 2001). The petrodentine in *G. otschevi* upper tooth plate from Early Triassic Czatkowice 1 locality (Fig. 1d) presented here shows fairly comparable structure with those described earlier for Gnathorhizidae by Lund et al. (1992).

6 Comparison with other members of *Gnathorhiza*

Tooth plates of *Gnathorhiza* from Czatkowice 1 (Fig. 1) show five gnathorhizid affinities. (1) Polish specimens share the number of ridges (four on the upper tooth plates and three on the lower ones) with other Triassic gnathorhizids. (2) Both upper and lower tooth plates do not contact each other in the midline. (3) Ridges always originate medially and usually bear few cusps on their crests. (4) The first ridge is the longest and the inner angle is considerably obtuse. (5) A short ascending process of the pterygopalatine bone and a single prearticular sulcus characterize members of *Gnathorhiza* and are also present in Czatkowice 1 specimens.

As compared to the members of the genus *Gnathorhiza* from the Lower Triassic sediments of the European part of Russia and western Kazakhstan, the tooth plates from Czatkowice 1 most closely resemble those of *G. otschevi* described from Russia by Minikh (1977) in the value of the inner angle of both upper and lower tooth plates (Table 1). The ratios of the length of first ridge to the second and the third of the lower tooth plates are similar to those given by Minikh (1977). Also, Polish specimens have only few cusps and the lower tooth plates always have three straight ridges (Fig. 1). The only differences between the specimens compared are the values of angles between the second and the last ridge (C_2BC_p angle) of both upper and lower tooth plates (Table 1). The tooth plates from Czatkowice 1 are here considered conspecific with *G. otschevi*, the mentioned differences being considered individual or ontogenetic variation.

The tooth plates from Czatkowice 1 differ from *Gnathorhiza triassica* Minikh, 1977 in most of the measurements. The ratios between the ridges of *G. triassica triassica* and the C_2BC_p angle of *G. triassica beresnikiensis* Minikh, 1977 are exceptions (Table 1). The next difference is the number of ridges on lower tooth plates, which is sometimes higher than three in *G. triassica* (Minikh, 1977), while being just three in both lower tooth plates from Czatkowice 1 (Fig. 1e, f and h). Both lower and upper tooth plates of *G. triassica baskunchakensis* Minikh, 1977 have the first ridge much shorter than the last one (BC_1/BC_p ratio much lower than 1). They also differ from other *Gnathorhiza* members in having one more ridge (Table 1). Thus, tooth plates of this subspecies do not represent a gnathorhizid type of tooth plates and can rather belong to *Ceratodus* or *Ptychoceratodus* as defined by Skrzycki (2015).

Polish specimens are much smaller than tooth plates of *Gnathorhiza lozovskii* Minikh, 1977 and *Gnathorhiza bogdensis* Minikh, 1977 (Table 1) from the Early Triassic of Russia. Lower tooth plates of those two species have a curved last ridge (Minikh, 1977), which is straight in *Gnathorhiza* from Czatkowice 1 (Fig. 1). Moreover, the biometrical values are different, except for the C_2BC_p angle and the ratio between the first and the second ridge, which are almost identical to those of *G. lozovskii* (Table 1).

The gnathorhizid tooth plates from Czatkowice 1 differ also from the latest Permian *Gnathorhiza tatarica* Minikh, 1989 in having the second and third ridges clearly developed, while they are rudimentary in the latter species. The first ridge of the *G. tatarica* tooth plates is shorter than the last one suggesting affinity with more derived genera than *Gnathorhiza*. However, *G. tatarica* is known only from one specimen, which can as well be pathological – suggesting the poorly developed second and third ridge.

The gnathorhizid from Poland has short pterygopalatine and prearticular bones (Fig. 1), in contrast to *Gnathorhiza serrata* Cope, 1883 from the Lower Permian of Oklahoma. The American species have also higher values of ratios between ridges of the lower tooth plates (Table 1). Carl-

Table 1. Measurements of different species of *Gnathorhiza*. Data from Minikh (1977), Carlson (1968) and Olson (1951). Mean values are given except for the Czatkowice 1 specimens. The range of measurement or ratio is given in brackets; “–” means lack of data in the literature.

Species	Number of ridges	BC _p	ABC angle	C ₂ BC _p angle	BC ₁ /BC _p	BC ₁ /BC ₂
Upper tooth plates						
ZPAL P. VII/5	4	2.02	134.8	74.4	broken first	broken first
ZPAL P. VII/6	4	2.62	140.8	78.7	ridge	ridge
<i>G. otschevi</i>	4	4.45	142.5	106	1.84	2.0
<i>G. triassica triassica</i>	4	3.58	120.8	82.9	0.93	1.54
<i>G. triassica beresnikiensis</i>	4	3.39	107.9	77.0	0.99	1.78
<i>G. triassica baskunchakensis</i>	4–5	3.65	90.1	60.2	0.79	1.17
<i>G. lozovskii</i>	4	5.73	129.9	91.67	1.12	2.14
<i>G. bogdensis</i>	4	7.33	133.3	102.5	1.14	1.52
<i>G. tatarica</i>	4	3.5	122	82	0.57	10.0
<i>G. serrata</i>	4	4.0	–	–	2.35	–
		(2.6–4.9)			(1.8–2.8)	
<i>G. dikeloda</i>	4	–	–	–	–	–
Lower tooth plates						
ZPAL P. VII/7	3	2.91	127.6	51.2	1.23	1.85
ZPAL P. VII/9	3	3.89	129.6	48.7	broken first	broken first
					ridge	ridge
<i>G. otschevi</i>	3	4.5	125.5	61.5	1.47	2.13
<i>G. triassica triassica</i>	3–3.5	2.66	120.3	81.2	1.22	1.83
<i>G. triassica beresnikiensis</i>	3–3.5	2.67	115.1	73.2	1.0	1.62
<i>G. triassica baskunchakensis</i>	3.5–4	2.95	98	66.8	0.8	1.23
<i>G. lozovskii</i>	3	5.82	121.3	53.1	0.97	1.85
<i>G. bogdensis</i>	3	8.7	116.6	89.8	1.03	1.47
<i>G. tatarica</i>			no lower tooth plate was found			
<i>G. serrata</i>	3	4.09	–	–	1.35	2.48
		(3–5.1)			(0.89–1.54)	(1.43–3.67)
<i>G. dikeloda</i>	3	9.4	–	–	2.36	4.17
		(9–10.2)			(2.22–2.47)	(4.13–4.2)

son’s (1968) studies of a large sample of *G. serrata* tooth plates have shown that the first ridge (Carlson’s “anterior cutting blade”) grows faster than the remaining ridges of the lower tooth plate. Carlson’s conclusion has strong implication on the taxonomic studies based solely on measurements, as the ontogeny can obviously affect the results.

Gnathorhiza dikeloda Olson, 1951 from the Lower Permian strata of Texas has the first to last ridge ratio of lower tooth plates equal to about 2.4 (Olson, 1951) and the first to second ridge ratio is bigger than 4 (Table 1), whereas the Czatkowice 1 gnathorhizid has a relatively shorter first ridge. This American species has also markedly bigger tooth plates with a curved last ridge in the lower ones (Olson, 1951).

Tooth plates of *Gnathorhiza noblensis* (Olson, 1970) are sparse and poorly preserved; thus comparison is difficult. Olson (1970) gave measurements of only one lower tooth plate of this species. The BC₁/BC_p ratio equals 1.49, which is a little higher than in the Czatkowice 1 lower tooth plate. It also can be noted that the ascending process of the pterygopalatine bone of *Gnathorhiza* from Czatkowice 1 is posteriorly

curved (Fig. 1c), whereas it is straight in *G. noblensis* (Olson and Daly, 1972).

Comparison with *Gnathorhiza pusilla* (Cope, 1877) and *Gnathorhiza bothrotreta* Berman, 1976 is hardly possible as the tooth plates of these species are either too poorly preserved or described too superficially.

7 *Gnathorhiza* stratigraphic and palaeogeographic distribution

Gnathorhiza was a medium-sized fish measuring 5–50 cm in body length. It formed burrows. Those found in nearshore deposits are interpreted as an adaptation to living in the tidal areas (Schultze and Chorn, 1997), whereas some other findings were proposed to be evidence of gnathorhizid ability to aestivate (Carlson, 1968; McAllister, 1992).

Gnathorhiza is the only known dipnoan which crossed the Permo-Triassic boundary. However, its distribution changed at the beginning of the Mesozoic. The oldest record of this

genus comes from North American strata of Pennsylvanian age. It comprises findings from five localities (Fig. 2a): *G. pusilla* from Danville in Illinois (Cope, 1877; Case, 1915), *Gnathorhiza* sp. from freshwater strata of El Cobre Canyon in New Mexico (Berman, 1993), *Gnathorhiza* sp. from estuarine deposits of Swisshelm Mountains in Arizona (Thayer, 1985), *Gnathorhiza* sp. from Robinson and Hamilton, both in Kansas and both considered to be of marine origin (Cunningham, 1993; Chorn and Schultze, 1990). In the Early Permian, *Gnathorhiza* was still present and even more common in North America, and it appeared in other parts of the world (Fig. 2a). Five species are known from many localities in Oklahoma, New Mexico and Texas (Dalquest et al., 1989; Johnson and May, 2013), mainly from freshwater sediments. These findings are frequently encountered in aestivation burrows. Abundant material of gnathorhizids was found also in freshwater sediments of the Eskridge Formation, Nebraska (Huttenlocker et al., 2005, 2013). Numerous fossil burrows containing *Gnathorhiza* remains were also found along with abundant marine invertebrates in Kansas in the Lower Permian Speiser Shale that was deposited in a nearshore environment (Schultze, 1985; McCahon and Miller, 2015). Based on this material Schultze (1985) suggested that *Gnathorhiza* could have been salt-tolerant. All the American findings come from several localities close to the greater Permian Basin, a broad shallow shelf basin (Hills, 1972) in the middle-western part of Pangaea (Fig. 2a). Few findings are known also from the freshwater Saar–Nahe Basin in Germany (aff. *Gnathorhiza*, Boy and Schindler, 2000; Schindler, 2007) and the coastal plain of Gharif Formation in Oman (*Gnathorhiza* sp., Schultze et al., 2008) (Fig. 2a). In the Late Carboniferous and Early Permian members of other dipnoan genus, *Sagenodus* (family Sagenodontidae), occurred also in the same majority of North American localities (e.g. Case, 1915; Berman, 1968; Schultze and Chorn, 1997; Johnson and May, 2013). Noteworthy, *Sagenodus* was not found in the lacustrine Speiser Shale site (Schultze, 1985). *Gnathorhiza* is accompanied by two other gnathorhizids – *Monongahela* in localities in the Wichita Group in Texas (Johnson and May, 2013) and *Persephonichthys* in the Eskridge Formation in Nebraska (Huttenlocker et al., 2005; Pardo et al., 2014). In the Saar–Nahe Basin *Sagenodus* and *Conchopoma* (family Conchopomatidae) were found as well (Boy and Schindler, 2000; Schindler, 2007), whereas in Oman *Gnathorhiza* is the only known dipnoan.

Late Permian dipnoans were probably less diversified than in the Early Permian, as only fossils of *Gnathorhiza* were discovered from this period. One tooth plate of *G. tatarica*, one of *G. otschevi* and two of *Gnathorhiza* sp. (Minikh, 1989, 1992; Tvardokhlebov et al., 2005) were found in the uppermost Permian sediments of the Orenburg region in the European part of Russia (Fig. 2a). These sediments were formed in lakes and on flood plains in a rather dry climate (Tvardokhlebov et al., 2005). Minikh (1992) mentioned also burrows found in sediments of the same age, but none of them

contained fossils. In terms of McAllister (1992) these findings cannot be regarded as lungfish burrows if no lungfish remains were found inside. Some undetermined fossils assigned to Gnathorhizidae are known also from the continental Rio do Rasto Formation in Paraná Basin (Ragonha, 1989; Richter and Langer, 1998; Toledo and Bertini, 2005) and the shallow marine Curumbataí Formation (Toledo and Bertini, 2005), both in Brazil.

After the Permo-Triassic boundary the diversity of dipnoans rose significantly. In the Early Triassic the number of species was the highest in the whole Mesozoic (Schultze, 2004). Noticeably in the Induan the number was much smaller than in the Olenekian. In the Northern Hemisphere *Gnathorhiza* was the only dipnoan known from the lowermost Triassic. It is recorded from the European part of Russia and from Kazakhstan (Fig. 2b; Minikh, 1977, 1995; Newell et al., 2010). Its fossils were found in Induan and lower Olenekian sediments gathered in “the first ichthyofaunal complex” (sensu Minikh, 1995) and Vetlugian Gorizont (sensu Minikh and Minikh, 1997, 2006). Some skull roofing bones have accompanied the tooth plates of *G. triassica triassica* reported from sediments of Vokhminsky Gorizont (Induan) from Spasskoye locality in Nizhny Novgorod Oblast in Russia (Minikh, 2000), but so far have been undescribed. In the upper Olenekian sediments (“II ichthyofaunal complex”, Yarenskian Gorizont) of south pre-Uralian and northern Caspian region *Gnathorhiza* findings are accompanied with *Arganodus*, *Ceratodus* and *Ptychoceratodus* fossils (Minikh, 1977, 1995; Minikh and Minikh, 1997, 2006). All Lower Triassic sediments of Russia and Kazakhstan yielding gnathorhizid remains are of lacustrine–alluvial origin (Minikh, 1995; Newell et al., 2010).

The finding of *Gnathorhiza otschevi* in Poland is the most westerly located occurrence of *Gnathorhiza* in Triassic sediments (Fig. 2b). So far, *G. otschevi* has been known only from central and southern regions of the European part of Russia from the uppermost Permian, Induan and almost whole Olenekian (except the Gamskian Gorizont) sediments (Minikh, 1977; Minikh and Minikh, 1997). In the coeval strata to Czatkowice 1, e.g. in the Holy Cross Mountains region in central Poland, only dipnoans more derived than Gnathorhizidae were found (Samsonowicz, 1929; Skrzycki, 2013). It is similar to the other parts of the Germanic Basin where *Arganodus*, *Ceratodus* and *Ptychoceratodus* remains were solely encountered (Schultze, 2004). The stratigraphically youngest fossils of *Gnathorhiza* (*G. triassica baskunchakensis*) were found in southern, central and northern regions of European part of Russia in the late Olenekian Gamskian Gorizont (Minikh, 1977). They are accompanied by numerous *Arganodus*, *Ceratodus* and *Ptychoceratodus* tooth plates (Minikh, 1977; Minikh and Minikh, 1997).

To sum up, the genus *Gnathorhiza* is known from Upper Carboniferous to Lower Triassic deposits. The palaeogeographic distribution of *Gnathorhiza* is extensive (Fig. 2) but restricted to the Northern Hemisphere with the only ex-

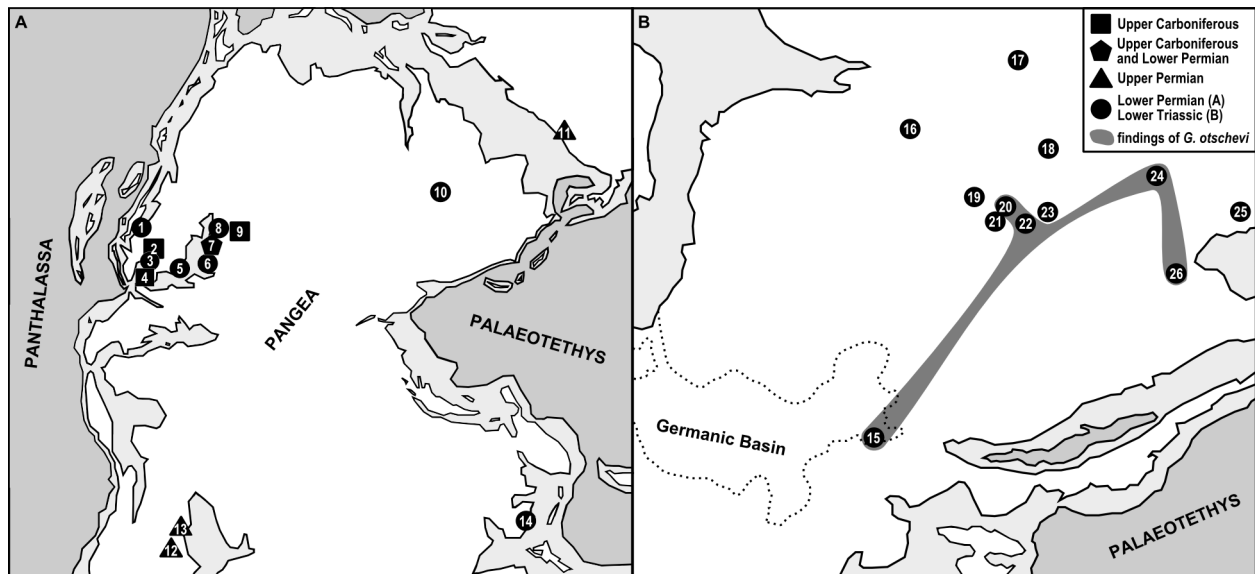


Figure 2. Palaeobiogeography of *Gnathorhiza* during Carboniferous and Permian (a) and Triassic (b). 1, *Gnathorhiza* sp.: USA, southeastern Utah, Cutler Group, Halgaito Formation (Vaughn, 1966, 1969, 1973); 2, *Gnathorhiza* sp.: USA, New Mexico, Rio Arriba County, Cutler Group (Berman, 1993); 3, *G. bothrotreta*: USA, New Mexico, Socorro County, Valencia County, Abo Formation (Berman, 1976, 1993), *Gnathorhiza* sp.: USA, New Mexico, Sandoval County, Abo Formation, San Miguel County, Sangre de Cristo Formation (Berman and Reisz, 1980); 4, *Gnathorhiza* sp.: USA, Arizona, Cochise County, Black Prince Limestone (Thayer, 1985); 5, *G. serrata*: USA, Texas, Baylor County, Lauders Formation and Wilbarger County, Arroyo Formation (Cope, 1883; Dalquest, 1968; Dalquest et al., 1989), *G. dikeloda*: Knox County, Vale and Choza Formation (Olson, 1951), *Gnathorhiza* sp.: north-central Texas, Nocona, Petrolia, Waggoner ranch Formations (Johnson and May, 2013); 6, *G. pusilla*: USA, Oklahoma, Grant County, Garber Formation (Case, 1915), *G. serrata*: Noble County, Wellington Formation (Carlson, 1968), Cleveland County, Hennessey Formation, *G. noblensis* (Olson, 1970; Olson and Daly, 1972); 7, *Gnathorhiza* sp.: USA, Kansas, Geary County, Lyon County, Speiser Shale (Schultze, 1985), Brown County, Bern Limestone Formation (Chorn and Schultze, 1990), Greenwood County, Hamilton Quarry (Cunningham, 1993), Key County, Matfield Formation (McCahon and Miller, 2015); 8, *G. serrata*, *G. dikeloda*: USA, Nebraska, Richardson County, Eskridge Formation (Huttenlocker et al., 2005, 2013); 9, *G. pusilla*: USA, Illinois, Vermillion County (Cope, 1877); 10, aff. *Gnathorhiza*: Germany, Saar–Nahe Basin (Boy and Schindler, 2000; Schindler, 2007); 11, *G. tatarica*, *G. otschevi*: Russia, Orenburg region, Kutulukskaya Svita (Minikh, 1989, 1992), *Gnathorhiza* sp.: Kulchumovskaya Svita (Tverdokhlebov et al., 2005); 12, *Gnathorhiza* sp.: Brazil, Sao Paulo State, Corumbatai Formation, Paraná State, Rio do Rasto Formation (Toledo and Bertini, 2005); 13, *Gnathorhiza* sp.: Brazil, Rio Grande do Sul State, Rio do Rasto Formation (Ragonha, 1989; Richter and Langer, 1998); 14, *Gnathorhiza* sp.: Oman, Al Wusta region, Gharif Formation (Schultze et al., 2008); 15, *Gnathorhiza otschevi*: Poland, Czatkowice 1, karst fillings (this paper); 16, *G. triassica triassica*, *G. triassica baskunchakensis*, *G. triassica beresnikiensis*: Russia, Arkhangelsk Oblast (Minikh, 1977); 17, *G. triassica triassica*: Russia, Komi Republic (Minikh, 1977); 18, *G. triassica triassica*, *G. triassica baskunchakensis*: Russia, Kirov Oblast (Minikh, 1977); 19, *G. triassica triassica*, *G. triassica beresnikiensis*, *G. lozovskii*, *G. bogdensis*: Russia, Vologda Oblast (Minikh, 1977); 20, *G. otschevi*, *G. triassica triassica*, *G. triassica beresnikiensis*, *G. bogdensis*: Russia, Kostroma Oblast (Minikh, 1977); 21, *G. triassica triassica*, *G. lozovskii*: Russia, Yaroslavl Oblast (Minikh, 1977; Novikov and Sennikov, 1997); 22, *Gnathorhiza otschevi*: Russia, Vladimir Oblast (Newell et al., 2010); 23, *G. triassica triassica*: Russia, Nizhny Novgorod Oblast (Minikh, 1977, 2000); 24, *G. otschevi*, *G. triassica triassica*, *G. triassica beresnikiensis*, *G. triassica baskunchakensis*, *G. lozovskii*: Russia, Orenburg Oblast (Minikh, 1977; Minikh and Minikh, 1997); 25, *G. triassica triassica*, *G. triassica baskunchakensis*: Kazakhstan, Atyrau Oblast (Minikh and Minikh, 1997); 26, *G. otschevi*, *G. triassica baskunchakensis*, *G. bogdensis*: Russia, Bolshoye Bogdo Mountain (Minikh, 1977; Minikh and Minikh, 1997). Numbers not in stratigraphic order. Lower Permian and Early Triassic palaeogeographic maps modified from <http://cpgeosystems.com/paleomaps.html>.

ception of Brazilian (Toledo and Bertini, 2005) and Omani records (Schultze et al., 2008). The distribution of the group had been changing through time. Since its first appearance in the Late Carboniferous, *Gnathorhiza* diversified during the Early Permian into five species – all known from western part of North America (Dalquest et al., 1989; Berman, 1993; Huttenlocker et al., 2005) (Fig. 2a). It is also known from the Lower Permian of Germany (Boy and Schindler,

2000) and Oman (Schultze et al., 2008), but sparse remains enabled identification only to genus level. In the Upper Permian, *Gnathorhiza* was recorded only in Russia (Minikh, 1989, 1992) and Brazil (Ragonha, 1989; Richter and Langer, 1998; Toledo and Bertini, 2005) (Fig. 2a). The Russian material belongs to two species, whereas the Brazilian is still undetermined. Then, in the Early Triassic *Gnathorhiza* is represented by four species, one of them divided into four

subspecies, inhabiting Poland, the European part of Russia and western Kazakhstan (Minikh, 1977; Minikh and Minikh, 1997; Borsuk-Białynicka et al., 2003; this paper) (Fig. 2b). This Triassic species abundance as well as wide geographic distribution of *Gnathorhiza* ends with its last appearance in the European part of Russia in the uppermost Olenekian (Minikh and Minikh, 2006). *Gnathorhiza* was there already outnumbered by other dipnoan species belonging to *Arganodus*, *Ceratodus* and *Ptychoceratodus* (Minikh, 1977; Minikh and Minikh, 1997) and possibly replaced, as in other parts of the world, by these more derived forms. During the Late Carboniferous and Early Permian *Gnathorhiza* inhabited freshwater, transitional and marine environments (e.g. Schultze and Chorn, 1997). This suggests that most probably it was a euryhaline lungfish (Schultze, 1985). Moreover, to migrate from North America to Eurasia *Gnathorhiza* might have had to cross the sea (Fig. 2a), which was much easier being salt-tolerant. Then, it became exclusively a freshwater fish in the Triassic.

8 Discussion

The Czatkowice 1 dipnoan material consists only of tooth plates (Fig. 1) and lacks skull roofing bones. Tooth plates are regarded to be informative enough for specific and generic determinations as they have several taxonomically valid characters (Kemp, 1993, 1997; Skrzycki, 2015). Based on comparison of tooth plates anatomy with literature data the dipnoan remains from Czatkowice 1 are here assigned to *Gnathorhiza otschevi*. It is the first and so far the only Triassic record of a gnathorhizid in the Germanic Basin. It is probable that during the Early Triassic *Gnathorhiza* migrated from freshwaters of the European part of Russia toward the south-west to another habitat within the Germanic Basin.

Unfortunately, some *Gnathorhiza* members (e.g. Russian single finding of *G. tatarica*, or American *G. pusilla*) are poorly preserved, which makes it difficult to trace relationships within the genus. Many North American findings are still unstudied and so far lack the species determination. The relationships within the genus *Gnathorhiza* were studied briefly and separately for American and Russian species, whereas no contribution focused on relations between all *Gnathorhiza* members (with exception of Minikh, 1977). Studies of gnathorhizids concern mostly their affinities to one of two extant dipnoan families – the Lepidosirenidae (e.g. Carlson, 1968).

Previous works regarding relationships of members of *Gnathorhiza* showed that *G. serrata* and *G. dikeloda* differ in tooth plate morphology and skull roof composition (Olson, 1951; Carlson, 1968). Details of skull roof pattern enable to distinguish *G. noblensis* from *G. serrata*, two closely related species with almost identical tooth plates (Olson and Daly, 1972). *G. bothrotreta* have skull roofing bones arranged in similar way to other *Gnathorhiza* species, but the supraor-

bital and part of the main canal open to the surface as few large pores, which was never observed in any other dipnoan (Berman, 1976). In 1977 Minikh described tooth plates of *Gnathorhiza* from the Lower Triassic in European Russia and Kazakhstan and compared them briefly to Permian representatives of this genus known from North America. He found some resemblance of *G. triassica* to *G. serrata* and *G. pusilla*, of *G. lozovskii* to *G. dikeloda* and of *G. bogdensis* to *Proceratodus favosus*, although he did not discuss them. Lower tooth plates of *G. triassica triassica* have in fact a similar value of BC_1/BC_p ratio as *G. serrata*, but the BC_1/BC_2 is markedly higher in the latter species (Table 1). *G. lozovskii* has lower values of both ratios between ridges in comparison with *G. dikeloda* (Table 1). *Proceratodus favosus* belongs to the Sagenodontidae and is regarded as a problematic form (Romer and Smith, 1934; Schultze and Chorn, 1997), and, as it is known from one incomplete tooth plate, no certain comparison can be made. The general resemblance of American and Russian tooth plates of *Gnathorhiza* supports their correct gathering in the same genus, but detailed morphological features clearly show that they represent different species.

The present study shows that the tooth plates of North American species have higher values of ratios between the ridges than European ones; especially there is a marked difference in BC_1/BC_2 ratios (Table 1). The morphological difference results from the fact that the first ridge is markedly longer than the rest of the ridges in North American gnathorhizids. Thus, near the Permo-Triassic boundary one can observe both the distributional change and morphological modification within this group. Noticeably tooth plates from Upper Permian of Brazil (Richter and Langer, 1998; Toledo and Bertini, 2005) resemble those of Early Triassic European gnathorhizids more than the North American ones. Crests of Brazilian tooth plates have few cusps or are devoid of them, they show a developed occlusal surface and are relatively big, which make them similar to Early Triassic *G. lozovskii* and *G. bogdensis*. The Brazilian Late Permian material is important to understand the changes that occurred between Early Permian and Early Triassic gnathorhizids. It is abundant and preserved well enough to make a detailed study. Many gnathorhizid findings need to be redescribed in a modern way to enable further studies of the relationships between species of *Gnathorhiza*.

According to Schultze (1992) Gnathorhizidae consist of two more members: *Palaeophichthys (Monongahela)* and *Beltanodus*. Eastman (1908) described a partly complete specimen of *Palaeophichthys* from Late Carboniferous of Mazon Creek in Illinois. Numerous tooth plates described by Lund (1970, 1973) from Upper Carboniferous and Lower Permian freshwater limestones of Pennsylvania as *Monongahela* were synonymized with *Palaeophichthys* by Schultze (1992). Kemp (1998) did not accept this due to poor preservation of the tooth plates of the two known specimens of *Palaeophichthys*. She suggested separation of *Monongahela* and *Palaeophichthys* until new material becomes avail-

able (Kemp, 1998). Tooth plates illustrated by Lund (1973) are similar to those of *Gnathorhiza*, but they slightly differ in arrangement of the most posterior ridges of upper tooth plates. Miles (1977) and Schultze and Chorn (1997) showed that *Palaeophichthys* is closely related to *Gnathorhiza*. Tooth plates of the other genus, *Beltanodus*, are not preserved and only one skull of this genus was found in Lower Triassic deposits of Madagascar (Schultze, 1981). The skull roof of this dipnoan differs from known skulls of *Gnathorhiza* species only in proportions of the skull bones and by the probable presence of the Z bone. In most phylogenetic analyses *Beltanodus* and *Gnathorhiza* are the closest relatives (e.g. Schultze, 2004; Criswell, 2015). Kemp (1993) described a single skull of *Nematozodia pitikanta* from the Lower Triassic of Australia and included this new genus into Gnathorhizidae. In the recent analysis of Schultze (2004) it belongs to Ceratodontidae. However, the pattern of skull roofing bones of *Nematozodia* is more like *Gnathorhiza* than members of Ceratodontidae by having a paired C bone and anterior part of supraorbital canal being present on anterior median bone (with the exception of *Microceratodus*, which shows the latter feature). More material, including also tooth plates, could help to clarify affinities of this genus. Recently described *Persephonichthys chthonica* Pardo et al. (2014), assigned previously to *Monongahela* (Huttenlocker et al., 2005), is also related to *Gnathorhiza* as noted by Pardo et al. (2014). Arrangement of the skull bones and the morphology of dentition of *P. chthonica* suggest its affinity to Gnathorhizidae.

Kemp (1997) stressed the impact of ontogenetic changes on the taxonomy of tooth plates. This has also been observed in *Gnathorhiza*. Carlson (1968) showed that the first ridge grows faster than other ridges of lower tooth plates of *G. serrata*. On the other hand, Lund (1973), based on a study of *Palaeophichthys* tooth plates, wrote that angles between tooth furrows do not change during ontogeny. According to Minikh (1977), in *G. bogdensis*, the occlusal surface broadens and cusps get worn out as the tooth plates become bigger. Because of sparse and incomplete material from Czatkowice 1, the ontogeny cannot be studied and therefore the use of metric data is strongly limited.

9 Conclusions

The dipnoan tooth plates material from the Olenekian Czatkowice 1 site described here is assigned to *Gnathorhiza otschevi* (Minikh, 1977; Minikh and Minikh, 1997). Czatkowice 1 is the westernmost occurrence of this species known previously only from Russia, and it is the only gnathorhizid finding from the area of the Germanic Basin (Fig. 2b). Tooth plates of *G. otschevi* from the Polish site have petrodentine. This tissue is recorded for the first time in a Triassic gnathorhizid.

The Early Triassic Czatkowice 1 assemblage is comparable to other vertebrate communities of that time (Borsuk-Białynicka et al., 1999), mostly to those known from European Russia (Shishkin and Sulej, 2009). The presence of *Gnathorhiza* in the southern Polish locality strengthens this similarity, as gnathorhizids are also known from Lower Triassic outcrops in Russia (e.g. Minikh, 1977). The most recent dating of the karst sediments of the Czatkowice 1 site (early late Olenekian; Shishkin and Sulej, 2009) is supported by the presence of *G. otschevi* in the material.

So far, relationships within the genus *Gnathorhiza* have been poorly studied. The present contribution attempts to briefly revise the systematic affinities of the genus members, as a base for future studies. In order to make a comprehensive study, all *Gnathorhiza* members were taken into consideration, which resulted in two conclusions: (1) tooth plates of American Late Carboniferous to Early Permian gnathorhizids have a relatively longer first ridge in comparison to the remaining ridges than the European *Gnathorhiza* members show; (2) Late Permian gnathorhizids from Brazil have tooth plates more similar to the European species than to North American ones.

The palaeobiogeographic study of all *Gnathorhiza* members shows marked shifts in distribution of this genus across its Upper Carboniferous to Lower Triassic fossil record. While the Late Palaeozoic occurrences are mostly known from the USA, the Early Mesozoic ones are restricted to eastern Europe (Fig. 2). However, new findings from Brazil, Germany and Oman (Ragonha, 1989; Richter and Langer, 1998; Boy and Schindler, 2000; Toledo and Bertini, 2005; Schultze et al., 2008) show that the distribution of *Gnathorhiza*, especially in the Permian, was markedly wider and that it spread in various directions during this period.

During the Early Triassic, *Gnathorhiza* was widely distributed across European Russia (Fig. 2b). There it coexisted (but only as late as in the late Olenekian) with members of *Arganodus*, *Ceratodus* and *Ptychoceratodus* (e.g. Minikh, 1977), whereas *Gnathorhiza* is the only known dipnoan in the Czatkowice 1 assemblage (Borsuk-Białynicka et al., 2003; this paper). Moreover, there is no gnathorhizid record in the Lower Triassic sediments of the Holy Cross Mountains, the other Polish region yielding dipnoans from Mesozoic strata (Samsonowicz, 1929; Skrzycki, 2013).

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