New finds of Olenekian, Early Triassic, trematosaurid amphibians and prolocophonid reptiles from Poland

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The continental Lower Triassic (Middle Buntsandstein) siliciclastic deposits exposed along the margins of the Holy Cross Mountains, Poland, yield locally abundant vertebrate footprints and bones. Although the footprints have been described in a number of studies, providing, for example, new insights into the origin of dinosaurs, there are few studies focusing on the bones. Here, we describe new amphibian and reptile material from the Buntsandstein fluvial sandstones of early Olenekian age exposed at Stryczowice on the north-eastern margin of the Holy Cross Mountains. These finds include fragmentary cranial specimens referred to as Trematosauridae gen. et sp. indet. and Procolophonidae gen. et sp. indet. Faunal differences between Stryczowice and the best-known Polish Olenekian vertebrate-bearing site of Czatkowice 1 near Kraków support heterogeneity in the Early Triassic vertebrate distribution across Pangea.

Key words: Temnospondyli, Parareptilia, tooth, parasphenoid, maxilla, Olenekian, Triassic, Poland.

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Introduction

Continental Lower Triassic (Middle Buntsandstein in lithostratigraphic scheme) siliciclastic deposits of Olenekian age are exposed along the margins of the Holy Cross Mountains, Poland (Senkowiczowa and Ślączka 1962; Senkowiczowa 1970; Mader and Barczuk 1985; Mader and Rdzanek 1985; Ptaszyński and Niedźwiedzki 2006; Brusatte et al. 2011). Locally, these strata yield abundant vertebrate footprints and bones.

The vertebrate footprints from the Middle Buntsandstein succession have been described in a number of studies (e.g., Fuglewicz et al. 1990; Ptaszyński 2000; Niedźwiedzki and Ptaszyński 2007; Klein and Niedźwiedzki 2012), some providing new insights into the origin of dinosaurs (Brusatte et al. 2011; Niedźwiedzki et al. 2013).

In contrast, there are few studies on vertebrate skeletal material from these deposits (Sulej and Niedźwiedzki 2009, 2013; Skrzycki et al. 2018), although the vertebrate remains, largely assigned to Temnospondyli, are common at some levels of the Buntsandstein succession (the „Labyrinthodontidae Beds" of Senkowiczowa and Ślączka 1962).

Here we describe new vertebrate material recovered from the fluvial Middle Buntsandstein sandstones (the "Labyrinthodontidae Beds") exposed at Stryczowice, in the north-eastern margin of the Holy Cross Mts., Poland (Fig. 1). This is the same locality that yielded abundant arthropod trackways, possibly of notostracan origin (Machalski and Machalska 1994). The material studied is fragmentary and includes a labyrinthodont tooth, a skull fragment of a trematosaurid amphibian (identified as Trematosauridae gen. et sp. indet.) and a jaw fragment of a prolocophonid reptile (identified as Procolophonidae gen. et sp. indet.). These new records add to our knowledge of regional Early Triassic vertebrate faunas and communities, which are poorly understood in the Germanic Basin due to the sparse skeletal record (Sues et al. 2022).

A diverse fauna of small vertebrates has been found on the edge of this basin in a bone breccia of early late Olenekian age that infilled paleokarst structures developed in Carboniferous limestones at the locality of Czatkowice 1 near Kraków, southern Poland (Paszkowski 2009; Borsuk-Białynicka 2018; Borsuk-Białynicka et al. 2003; Cook and Trueman 2009; Evans and Borsuk-Białynicka 1998). The Czatkowice 1 bone

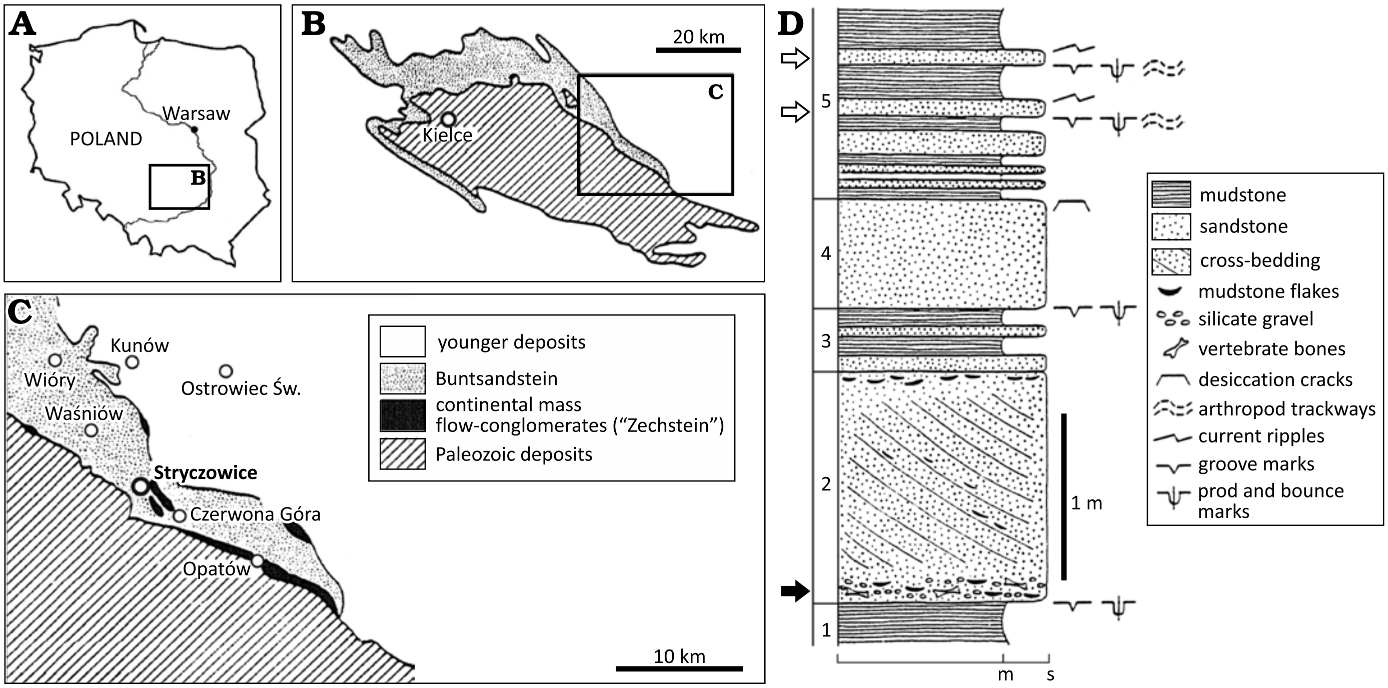

Fig. 1. The geological setting of the vertebrate-bearing locality at Stryczowice. **A**. Location of the Holy Cross Mountains in Poland. **B**. Simplified geological map of the Holy Cross Mountains with Paleozoic core and range of the Bundsandstein exposures. **C**. Location of the Stryczowice locality on the geological map of the north-eastern margin of the Holy Cross Mountains with Paleozoic deposits, continental mass flow-conglomerates traditionally referred to as the “Zechstein”, Buntsandstein, and younger deposits. **D**. Log of the Stryczowice quarry with location of the bone-bearing basal conglomerate marked by a black arrow, and location of the levels with arthropod trackways marked by white arrows; numbers 1–5 mark units discussed in text. Figure adopted from Machalski and Machalska 1994: fig. 1.

breccia originated in an upland environment, which significantly contrasted with the lowland floodplain setting of the Stryczowice section described here. Therefore, the present study creates an opportunity to compare the distibution of amphibians and reptiles in not far distant but different Olenekian environments of the Germanic Basin.

Institutional abbreviations.—MSB (Museum Schloss Bernburg, Germany; PIN, Paleontological Institute, Russian Academy of Sciences, Moscow, Russia; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Geological setting

A small inactive quarry is located on a hill south of Stryczowice, a village south-west of the town of Ostrowiec Świętokrzyski at the north-eastern margin of the Holy Cross Mountains (Fig. 1; outcrop 32 in Mader and Barczuk 1985: fig. 5). The outcrop section, which is heavily overgrown and largely inaccessible today, is composed of intercalated sandstone and mudstone beds, with a distinct decrease in the thickness of the sandstones upward in the section (Fig. 1D).

Stratigraphically, the quarry section at Stryczowice was assigned by Machalski and Machalska (1994) to the “Labirynthodontidae Beds” of the Middle Buntsandstein. According to Brusatte et al. (2011), the conchostracans and palynomorphs indicate an early Olenekian age for the Stryczowice succession. In terms of sedimentology, the section at Stryczowice was studied in detail by Machalski and Machalska (1994), who interpreted it as a typical cyclothem of a weakly braided river system, which characterised the depositional environment of this part of the Buntsandstein succession (Mader and Rdzanek 1985; Fuglewicz et al. 1990). The massive cross-bedded sandstone bed with the basal conglomerate containing vertebrate remains, quartz gravel and mudstone intraclasts (Fig. 1D: unit 2) was interpreted by these authors as the main channel deposit. According to Machalski and Machalska (1994), the intercalating mudstones and sandstones in the upper part of the section (Fig. 1D: units 3–5) were deposited in a floodplain environment. The mudstones were deposited in stagnant water (i.e., ponds and/or lakes), whereas the intercalated sands accumulated as crevasse-splay deposits during periodic floods.

The osteological material described here was recovered by MM during the mid 1980s from the conglomerate at the bottom of the massive sandstone bed in the lower portion of the section (Fig. 1D: unit 2, the conglomerate is marked by a black arrow). In addition to the specimens described in the present study, the presence of distinctive cross sections of the “labyrinthodont” teeth was noted during exploitation of the conglomeratic level. All the fossils studied are represented by isolated fragmentary skeletal elements, pointing, along with their occurence in a basal conglomerate, to the allochthonous nature of the fossil assemblage. This admix-

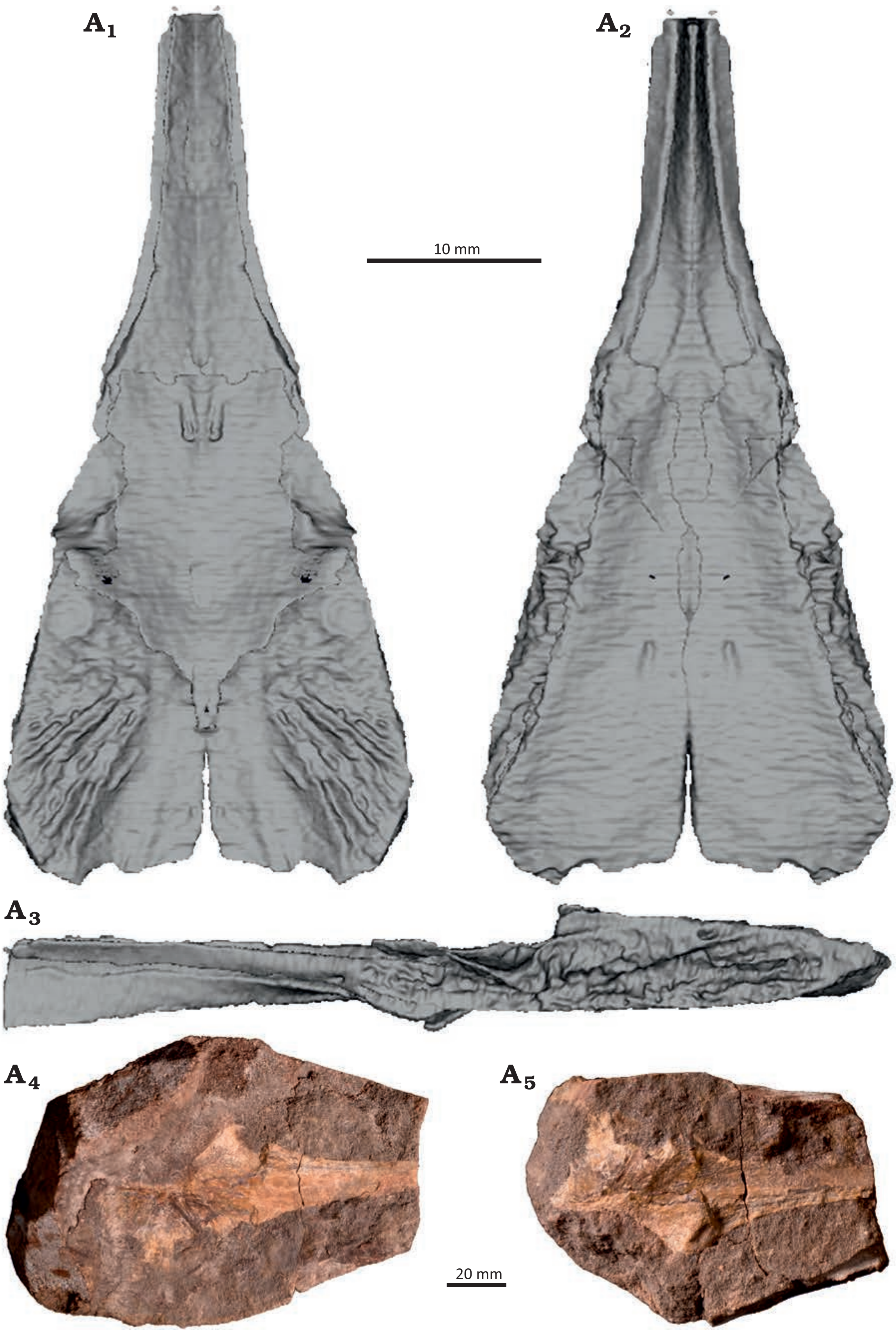

Fig. 2. Parasphenoid of Trematosauridae gen. et sp. indet. from Lower Triassic of Stryczowice, Holy Cross Mountains, Poland. ZPAL V. 78/3, reconstruction in dorsal (A_1), ventral (A_2), and lateral (A_3) views, original specimen, part and counterpart (A4, A5). The restoration was based on the CT scan by supplementing the missing fragment with a mirror image of the preserved part (Fig. 3B).

ture of fossils was probably formed as the result of lateral migration of a river channel leading to exhumation, reworking and redeposition of remains originally buried in the floodplain deposits. The allochthonous and mixed character of the Stryczowice taphocoenosis is also supported by the fact that trematosaurids were largely fully-aquatic predators (Schoch and Millner 2000), whereas procolophonids are regarded as exclusively terrestrial animals (de Braga 2003; Cisneros 2008; Botha-Brink and Smith 2012).

The bone material from the Stryczowice quarry has not been described so far. As far as trace fossils are concerned, only arthropod (presumably notostracan) walking trackways assigned to the ichnospecies "*Diplichnites*" *triassicus* have been reported to date from the Stryczowice quarry (Machalski and Machalska 1994). They were recorded on the soles of two crevasse-splay sandstone beds (Fig. 1D: white arrows). No vertebrate footprints were recorded from the Stryczowice quarry by Machalski and Machalska (1994). However, the vertebrate footprints reported from Stryczowice by Brusatte et al. (2011) probably come from a location close to the quarry succession (see Brusatte et al. 2011: electronic supplementary material).

The material described here is housed at the Institute of Paleobiology, Polish Academy of Sciences (abbreviated ZPAL V. 78).

Systematic palaeontology

Class Amphibia Gray, 1825

Order Temnospondyli Zittel, 1888

Family Trematosauridae Watson, 1919

Trematosauridae gen. et sp. indet.

Figs. 2, 3B.

Material.—ZPAL V. 78/3, parasphenoid from lower Olenekian (Lower Triassic) of Stryczowice, north-eastern margin of the Holy Cross Mountains, Poland.

Description.—An almost complete parasphenoid ZPAL V. 78/3 is preserved in a conglomerate slab in two pieces (part and counterpart) with the bone visible in cross-section (Fig. 2). The anterior part of cultriform process and the left part of the parasphenoid plate are broken (Fig. 3B$_1$).

A large area for the exoccipital is visible on the posterolateral corner of the dorsal side. It has a similar shape, size and texture to those of *Inflectosaurus amplus* Shishkin, 1960 (PIN 953/100; Shishkin 1968; Novikov 2007). The posterior part is divided on three belts by distinct ridges. The opening for the intracranial branch of the internal carotid is located more anteriorly than in *Trematosaurus brauni* Burmeister, 1849 (Schoch 2019) and *Inflectosaurus amplus* (Shishkin 1968; PIN 953/100). The posterior aspect of the pterygoid area is not visible in dorsal view, unlike in *Inflectosaurus amplus* (Shishkin 1968; PIN 953/100). The entrance foramen for the palatine nerve, which is also the exit for the posterior branch of the palatine artery, is well visible only in *Inflectosaurus amplus* (PIN 953/100). This foramen is much larger in *Trematosaurus galae* Novikov, 2010 (Novikov 2010: fig. 1d) and has a large ornamented area, which is absent in the new Polish specimen.

The long, irregular area for suture with the pterygoid is well visible on the ventral side of the parasphenoid plate. Its ventral edge is bent inwards (Fig. 3) as in *Trematosaurus brauni* (Schoch 2019). The posterior edge of the parasphenoid plate is slightly bent inwards, similar to *Inflectosaurus amplus* (Novikov 2007). A small opening is visible in the central area of the parasphenoid plate, which was not reported in any trematosaurid so far.

The cultriform process is T-shaped in cross-section with shallow grooves on both sides. Its ventral and lateral edges

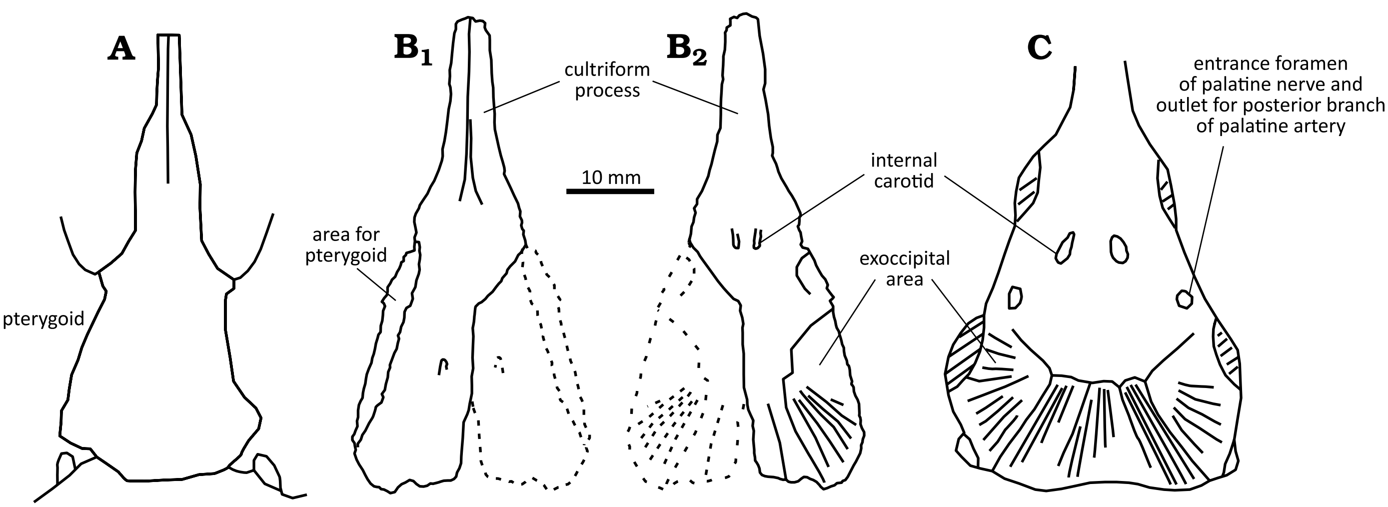

Fig. 3. Comparison of the parasphenoid of Trematosauridae gen. et sp. indet. with specimens from Germany and Russia. **A**. *Trematosaurus brauni* Burmeister, 1849, Merkel's Quarry, Germany, ?late Olenekian, MSB G 366 in ventral view (modified from Schoch 2019: fig. 7B). **B**. Trematosauridae gen. et sp. indet., Stryczowice, Holy Cross Mountains, Poland, early Olenekian{?}, ZPAL V. 78/3 in ventral (B$_1$) and dorsal (B$_1$) views. **C**. *Inflectosaurus amplus* Shishkin, 1960, Bolshoe Bogdo locality, late Olenekian, PIN 953/100 in dorsal view (modified from Shishkin 1968: fig. 2c).

are sharp. This morphology is very similar to that observed in *Trematosaurus brauni* (Schoch 2019) and unlike *Angusaurus* Getmanov, 1989, which has a very narrow cultriform process (Fernández-Coll et al. 2019). The posterior aspect of the lateral edge of the cultriform process is slightly convexly curved compared to the same feature in *Trematosaurus brauni* and *Inflectosaurus amplus*, which is strongly curved.

Remarks.—The Germanic Basin trematosaurids were originally described based on material from two localities: Merkel's Quarry and Kappel in the Black Forest, Germany (Schoch and Werneburg 1998; Schoch and Milner 2000). Up until 2009, the geographically closest sites to the Holy Cross Mountains that yielded termatosaurid material were in Eastern Europe (Shishkin 1968; Novikov 2007, 2010). Sulej and Niedźwiedzki (2009) then reported the first trematosaurid from Poland from the Wióry locality, dated as Olenekian (Early Triassic). Later, Sulej and Niedźwiedzki (2013) described the capitosauroid *Parotosuchus ptaszynski* Sulej & Niedźwiedzki, 2013, from the same locality, based on fragments of a cranium and mandible. Globally, trematosaurids are also known from Middle and Late Triassic-aged deposits from Madagascar (Lehman 1966, 1979) and South Africa (Watson 1919; Welles 1993; Shishkin and Welman 1994).

Temnospondyli indet.

Fig. 4A.

Material.—ZPAL V. 78/2, tooth with broken tip from lower Olenekian (Lower Triassic) of Stryczowice, north-eastern margin of the Holy Cross Mountains, Poland.

Description.—Only the base of the crown of a tooth (ZPAL V. 78/2) was preserved in the conglomerate (Fig. 4A). In their comprehensive comparison of amphibian and reptile teeth from the Middle Triassic, Schoch et al. (2018) showed that temnospondyl teeth were the same for the entire Lower Triassic material. Based on the fact that deep grooves are limited to the basal aspect of the tooth crown and are aligned parallel to the apicobasal axis of the tooth crown, the features present in ZPAL V. 78/2 are most consistent with this tooth being assigned to a temnospondyl. The lack of the tip of the tooth complicates any taxonomical ascription below the subordinal level.

Class Reptilia Laurenti, 1768

Order Procolophonomorpha Romer, 1964

Family Procolophonidae Lydekker in Nicholson and Lydekker, 1889

Procolophonidae gen. et sp. indet.

Fig. 4B.

Material.—ZPAL V. 78/1, maxilla with broken posterior part from lower Olenekian (Lower Triassic) of Stryczowice, north-eastern margin of the Holy Cross Mountains, Poland.

Description.—Maxilla (ZPAL V. 78/1) is broken into two parts embedded in rock matrix, one preserving most of the bone and three teeth, whereas the other has three teeth and the posterior piece of the same bone (Fig. 4B). The lateral surface of the bone is poorly preserved and provides little anatomical information. The lateral surface is flat with no visible postnarial maxillary depression. The maxillary foramen opens anteroventrally near the ventral margin of the bone and near the facet for the premaxilla. The facet is well preserved and oriented anteromedially, although it is still partially covered by sediment. This anterior margin of the bone is blunt and dorsoventrally tall. There is no emargination for the naris. The bone is anteroposteriorly straight and labiolingually broad in ventral view. The posterior aspect of the maxilla is broken and incomplete.

The teeth are visible only in lateral view and in cross-section, which limits their description to some extent. The preserved portion of the maxilla bears ten tooth positions, but only six teeth remain in place (4th to 8th, and 10th maxillary teeth). All teeth are subtriangular in lateral view with broad bases (Fig. 4). Their tips are rather blunt, but it is not visible due to rock matrix if they have one or two cusps. The teeth gradually increase in size posteriorly up to seventh tooth, but the differences are modest. The enamel has a rather featureless surface, with no visible grooves or other structures. The first tooth was virtually circular in cross-section (orthogonal diameters of 0.88 mm vs 0.89 mm). The following teeth gradually increase in labiolingual breath, which becomes much larger than their mesiodistal length. The sixth tooth is the posteriormost one for which the measurement is possible. It is 1.63 mm wide labiolingually and 1.16 mm long mesiodistally. After the seventh tooth they seem to slightly decrease in size but the rock matrix precludes exact measurements.

Remarks.—Up to four different procolophonids were described from roughly coeval (Olenekian) paleokarst bone breccia recovered from the Czatkowice 1 site (Borsuk-Białynicka and Lubka 2009). Procolophonids found there have much lower maxillary tooth counts (5–6 and 7), and the teeth are more heterodont in size compared to those from Stryczowice. *Procolina teresae* Borsuk-Białynicka & Lubka, 2009, has a much more pronounced anterior slope of the maxilla and its teeth are less triangular. The latter is also true for Procolophonidae gen. indet. II and III from Czatkowice 1. Procolophonidae gen. indet. I from Czatkowice 1 has subcircular teeth in cross-section throughout the entire maxilla, whereas the Stryczowice specimen has transversely expanded the posterior teeth. Therefore we can exclude assignment of the new material to any of the taxa from Czatkowice 1.

Numerous other procolophonids were described from the Buntsandstein of Germany (Huene 1912; Säilä 2008; Sues and Reisz 2008). The Stryczowice material cannot be assigned to *Sclerosaurus armatus* Meyer in Fischer, 1857, because the latter has a lower tooth count (7) and its teeth have long-axes oriented mesiolingually (Sues and Reisz 2008) rather than lingually. The comparison to *Anomoidon liliensterni* Huene, 1939, is fairly limited due to its poorly preserved maxillae (Säilä 2008), but the teeth seem to be much more heterodont in terms of size compared to the Stryczowice material.

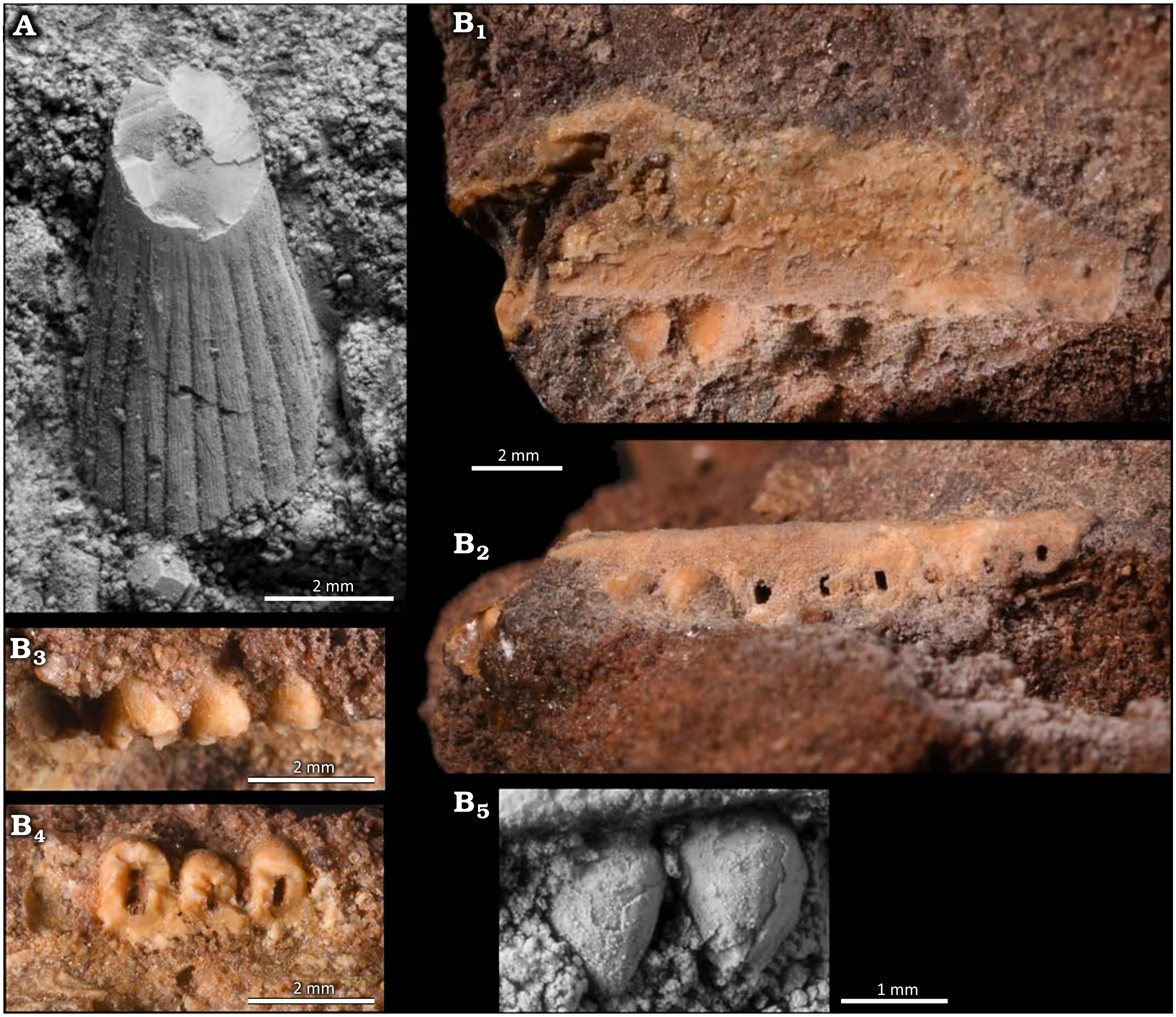

Fig. 4. Temnospondyli indet. (A) and Procolophonidae gen. et sp. indet (B) from Lower Triassic of Stryczowice, Holy Cross Mountains, Poland. **A**. ZPAL V. 78/2, tooth. **B**. ZPAL V. 78/1, maxilla in lateral (B_1) and ventral (B_2) views; teeth in lateral view (B_3, B_5); cross-section of maxillary teeth in dorsal view (B_4).

Koiloskiosaurus coburgensis Huene, 1912, has a similar tooth count (9 or 10) in the maxilla and its teeth are expanded transversely (Huene 1912) as in the Stryczowice material.

Procolophonids are also very diverse in the Lower Triassic of Russia (Ivakhnenko 1979; Ivakhnenko and Kurochkin 2008; Spencer and Benton 2000). The specimen from Stryczowice differs from specimens assigned to species of *Tichvinskia*, *Orenburgia*, and *Kapes* in having a higher tooth count (Ivakhnenko 1973, 1975, 1983; Spencer and Benton 2000). *Phaanthosaurus* (= *Contritosaurus*) has 10 rather uniform teeth in its maxilla but also possesses a large fossa surrounding the external naris (Ivakhnenko 1974, 1979; Spencer and Benton 2000). The latter feature seems to be absent in the Stryczowice specimen.

To sum up, the Stryczowice material can be distinguished from all species mentioned above except maybe *Koiloskiosaurus coburgensis* Huene, 1912, described from the Buntsandstein of Germany. However, more detailed comparisons between the two are difficult as the material of *Koiloskiosaurus coburgensis* requires redescription (Sues and Reisz 2008) and we did not study these specimens personally. Therefore, their possible conspecificity requires further study.

Concluding remarks

The vertebrate fauna described from Czatkowice 1 is of similar age (Olenekian, Early Triassic) to the material recovered from the Stryczowice section. The Czatkowice 1 locality is located just about 100 km southwest of Stryczowice. The absence of trematosaurids in Czatkowice 1 was already discussed by Shishkin and Sulej (2009). They stated that at Czatkowice 1 the accumulation of bones in the palaeocaves developed in the upland area and was more conducive to gathering terrestrial vertebrates than water-dependent amphibians (see Cook and Trueman 2009 for a detailed taphonomical study of the Czatkowice 1 assemblages). However, we observe that procolophonid faunas also differ between Czatkowice 1 and other Germanic Basin sites, including the Stryczowice site. These animals were terrestrial, so the taphonomic reasoning presented above cannot be applied to them. Although the new material is fragmentary, our preliminary observations suggest that the distribution of these two groups was strongly dependent on local palaeoecological, rather than only taphonomic, conditions. Indeed, the presence of a trematosaurid and a prolocophonid similar to species of *Koiloskiosaurus* link Stryczowice to the far more distant localities in Germany than to the Czatkowice 1 site. This is consistent with studies from better sampled areas that found that the distribution of Early Triassic vertebrates was heterogeneous across Pangea (Shishkin et al. 2006; Sidor et al. 2013).

This study adds a new record of procolophonids, a group of highly successful Permo-Triassic reptiles (Cisneros 2008). Up to four distinct taxa are known from the Czatkowice 1 locality and they differ from the three taxa from the Buntsandstein and from more eastern basins (Borsuk-Białynicka and Lubka 2009; Huene 1912; Säilä 2008; Sues and Reisz 2008; Ivakhnenko 1979; Ivakhnenko and Kurochkin 2008; Spencer and Benton 2000). It shows their relatively high diversity in that part of Pangea just a few million years after the end of the Permian.

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