Review of Palaeobotany and Palynology 245 (2017) 28–54

Contents lists available at ScienceDirect

Review of Palaeobotany and Palynology

journal homepage: www.elsevier.com/locate/revpalbo

# A new conifer from the Upper Triassic of southern Poland linking the advanced voltzialean type of ovuliferous scale with *Brachyphyllum-Pagiophyllum*-like leaves

Grzegorz Pacyna [a,*], Maria Barbacka [b,c], Danuta Zdebska [a], Jadwiga Ziaja [b], Anna Fijałkowska-Mader [d], Károly Bóka [e], Tomasz Sulej [f]

[a] Jagiellonian University, Institute of Botany, Department of Taxonomy, Phytogeography and Palaeobotany, ul. Kopernika 27, PL-31-501 Kraków, Poland
[b] W. Szafer Institute of Botany, Polish Academy of Sciences, Lubicz 46, PL-31-512 Kraków, Poland
[c] Hungarian Natural History Museum, Department of Botany, H-1476, P.O. Box 222, Hungary
[d] Polish Geological Institute – National Research Institute, Holy Cross Branch, Zgoda 21, PL-25-953 Kielce, Poland
[e] Eötvös University, Biological Institute, Department of Plant Anatomy, Pázmány P. Stny 1/C, H-1117 Budapest, Hungary
[f] Institute of Paleobiology, Polish Academy of Sciences, ul. Twarda 51/55, PL-00-818 Warszawa, Poland

ARTICLE INFO

*Article history:*
Received 26 May 2016
Received in revised form 19 May 2017
Accepted 22 May 2017
Available online 11 June 2017

*Keywords:*
Triassic
Voltziales
*Brachyphyllum*
*Enzonalasporites*
Poland

ABSTRACT

The Triassic is an exceptionally interesting period from the point of view of conifer evolution. The oldest representatives of some modern families appear in the fossil record in the Upper Triassic and all recent conifer families probably originated during this time. The stages whereby the primitive Voltziales transformed into the evolutionarily advanced families of modern conifers in the Triassic are yet to be fully documented. A newly discovered Upper Triassic (Norian) locality in Patoka (SW Poland, Upper Silesia) with a unique fossil record offers us a rare opportunity to fill this gap. In this paper, we describe the very well preserved remains of a new conifer from this locality. We have been able to reconstruct the whole plant and propose a new taxon, *Patokaea silesiaca* gen. et sp. nov., on the basis of organic attachment and similar cuticular details on leaves, ovuliferous cones, seed scale-bract complexes, ovules and mature seeds as well as polliniferous cones containing pollen grains of the *Enzonalasporites* type in situ. This plant combines shoots bearing *Brachyphyllum-Pagiophyllum*-type leaves with a new type of seed scale-bract complex clearly derived from evolutionary advanced Voltziales and polliniferous cones somewhat similar to the Cheirolepidiaceae (*Classostrobus*) type. Based on this distinctive and hitherto unique combination of features, a new conifer family – Patokaeaceae – has been proposed. The ovuliferous cones of this conifer are lax and borne singly at the end of leafy twigs. Ovule-bearing scales are stalked and trilobate with two lateral oval lobes, each bearing one ovule, and one sterile reduced lobe between them, all in one plane. The bract is small and leaf-like. Polliniferous cones are simple with helically arranged microsporophylls. Five to seven pollen sacs are arranged around the microsporophyll stalk. Polliniferous cones are borne singly at the end of leafy twigs. This is also the first evidence of a relationship between *Enzonalasporites* pollen and the parent plant. The pollen occurs in the polliniferous cones, in the micropyle inside the ovule and in the micropylar region inside the seed of this new conifer. This plant expands our view of voltzialean conifer diversity at the roots of modern conifer families.



## 1. Introduction

The Triassic is especially interesting from the point of view of conifer evolution (Miller, 1977; Grauvogel-Stamm, 1978; Rothwell et al., 2012). Modern conifer families originated at this time, as shown by the fossil record and phylogenetic data (Quinn et al., 2002; Rothwell et al., 2012). Older, evolutionary less advanced conifers, traditionally referred to as Voltziales, reached their peak of diversity in the Triassic, in terms of both taxa number and their wide adaptation to different environments (e.g., Rothwell et al., 2000; Taylor et al., 2009). Ovuliferous scale-bract complexes in ovuliferous cones were very diversified among Triassic conifers, but one general evolutionary tendency is identified in most taxa – the flattening of seed scales and reduction of their lobes (Florin, 1938–1945, 1951; Schweitzer, 1963). At this same time, polliniferous cones were probably more diverse, varying from simple to compound cones, than at any other period in conifer history (Roselt, 1956; Schaarschmidt and Maubeuge, 1969; Grauvogel-Stamm, 1969, 1972,

* Corresponding author.
*E-mail addresses:* grzegorz.pacyna@uj.edu.pl (G. Pacyna), barbacka.maria@nhmus.hu (M. Barbacka), j.ziaja@botany.pl (J. Ziaja), anna.mader@pgi.gov (A. Fijałkowska-Mader), karolyboka@caesar.elte.hu (K. Bóka), sulej@twarda.pan.pl (T. Sulej).

http://dx.doi.org/10.1016/j.revpalbo.2017.05.015
0034-6667/

1978; Grauvogel-Stamm and Grauvogel, 1973; Grauvogel-Stamm and Schaarschmidt, 1979; Meyen, 1987; Grauvogel-Stamm and Galtier, 1998). The stages of transformation from the primitive Voltziales to evolutionary advanced families of modern conifers in the Triassic have been insufficiently documented to date (Miller, 1977, 1982, 1988; Rothwell et al., 2012). Such families as the Podocarpaceae have uncontested representatives in the Triassic, but the occurrence of members of other families, e.g. the Pinaceae, is still open to question (Delevoryas and Hope, 1973, 1987; Miller, 1976; Rothwell et al., 2012).

The Triassic conifers described thus far from Poland are poorly preserved and still imperfectly known (Goeppert, 1845, 1846; Kunisch, 1886; Raciborski, 1890; Reymanówna, 1986; Brzyski and Heflik, 1994; Dzik and Sulej, 2007; Pacyna et al., 2013; Pacyna, 2014). Some newly discovered localities provide an exceptional opportunity to supplement this scanty information. Krasiejów, Patoka, Poręba, Marciszów-Zawiercie, Woźniki, Lipie Śląskie-Lisowice (all in South Poland and Upper Silesia), contain yet to be described well-preserved floras rich in conifer taxa, with forms which can shed new light on conifer evolution during the Late Triassic (Brzyski and Heflik, 1994; Szulc et al., 2006; Dzik and Sulej, 2007; Dzik et al., 2008; Racki, 2010; Sulej et al., 2011, 2012; Sadlok and Wawrzyniak, 2013; Kubik et al., 2015; Philippe et al., 2015; Racki and Szulc, 2015). The material is from the Patoka locality, which is Norian in age, and contains a flora that is not diverse, but very well-preserved and dominated by conifers. It is worth noting that worldwide Norian plant fossils are extremely rare (Dobruskina, 1988, 1994; Mader, 1990; Petti et al., 2013). Nearby localities provide older (Carnian – Krasiejów) and younger (upper Norian?–Rhaetian – Lipie Śląskie-Lisowice) floras together with exceptional vertebrate assemblages containing dinosaurs and dicynodonts (Dzik, 2001, 2003; Dzik et al., 2008; Wawrzyniak, 2010; Sulej et al., 2011, 2012; Niedźwiedzki et al., 2012; Pacyna et al., 2013; Pacyna, 2013, 2014).

The purpose of this paper is to describe the very well preserved remains of a new conifer from Patoka (Fig. 1). The whole plant has been reconstructed on the basis of organic connections and cuticle details on leaves, ovuliferous cones, seed scale-bract complexes, ovules and developed seeds as well as polliniferous cones with pollen grains of the *Enzonalasporites* type in situ (Fig. 2). Such fully documented plants have been used successfully for developing phylogenetic hypotheses about fossil-conifer relationships (Rothwell et al., 2005).

## 2. Geological setting, materials, and methods

### 2.1. Geological setting

The specimens described in this study were collected in the northern, lowest part of the Patoka clay pit (northern part of Upper Silesia, Fig. 1). Fossil bearing strata belong to uppermost part of the marly mudstone-sandstone Patoka Member of the Grabowa Formation (Szulc and Racki, 2015; Racki and Szulc, 2015; Szulc et al., 2015a, 2015b). This formation is the main lithostratigraphic unit of the Upper Silesian Keuper and a lateral equivalent of the German Weser and Arnstadt formations within the Triassic Germanic Basin, which extends from France in the West across Germany to Poland in the East (Mader, 1997; Szulc et al., 2006; Szulc and Becker, 2007; Franz, 2009; Racki, 2010; Lucas, 2015). The first description of Upper Triassic strata in the Patoka region was provided by Römer (1870), but plant remains were observed for the first time by Znosko (1955) in a currently-flooded old clay pit. The plant fossils described here derive from greenish-yellowish, sometimes grey, layers of mudstone and siltstone with sandstone lenses and occur in few very thin layers containing mainly new, leafy conifer twigs. Small fern fragments and sporadic leaves of other gymnosperms have also been found. Numerous associated tree trunks preserved as coalified remains and charcoal fragments have already been described (Philippe et al., 2015).

Palynological data were used to determine the age of the Patoka Member as Norian, the local Polish *Corollina meyerana* Palynozone, Subzone b (Orłowska-Zwolińska, 1983, 1985; Fijałkowska-Mader et al., 2015), which is correlated with the Middle European *Granuloperculatipollis rudis* zone (Cirilli, 2010; Kürschner and Herngreen, 2010; Fijałkowska-Mader et al., 2015). The nearby Patoka 1 borehole probably failed to penetrate the fossil-bearing level exposed in the pit, but it has been well documented palynologically (Fijałkowska-Mader et al., 2015). Unfortunately, in the locality where the fossils have been found, clay pit works have strongly disturbed the section. Palynological analysis of samples containing macrofossils of the new conifer shows that the miospore assemblages are taxonomically impoverished in comparison with the *Corollina meyeriana* b Subzone and mainly consist of *Ovalipollis*, *Vallasporites* and *Corollina*. It is difficult to correlate these spectra with the subzones (within the *Corollina meyerana* Zone) distinguished by Orłowska-Zwolińska (1983, 1985) as she did not mention *Vallasporites*. According to Pacyna (2014), the flora from Patoka can be correlated with the German Stubensandstein-Burgsandstein Flora of Kelber (1998) and he referred it to the local *Brachyphyllum* Assemblage Zone.

### 2.2. Material

The plant remains are preserved as coalified compressions with well-preserved cuticles. Leafy shoots (up to 50 mm long) predominate in the material associated with ovuliferous scale-bract complexes, ovuliferous and polliniferous cones, ovules, mature seeds and dispersed pollen grains. All organs undoubtedly belong to the same plant species. Ovuliferous and polliniferous cones were found attached to leafy shoots. One seed was found attached to a seed-scale. Vegetative and reproductive structures have cuticles of the same type. The pollen grains found in the polliniferous cone are the same as those observed in the micropylar canal of the ovule, in the micropylar region inside the seed and dispersed in the source sediment.

The specimens are stored at the Institute of Botany, Jagiellonian University, under the palaeobotanical collection number KRA-PALEO 104.

### 2.3. Methods

The compressed remains were separated from the sediment by treatment with 40% hydrofluoric acid for one to several days, then washed with distilled water. Prepared remains are partly stored in water containing thymol and partly in the dry state in test tubes. Bulk samples were examined in water using a Leica stereomicroscope and individual specimens were selected for further study.

Some leaves, ovule and seeds were macerated in Schulze solution (Schulze, 1855) and then washed with 3% KOH after which permanent slides were prepared. These were examined using Nikon Eclipse E 600 and Axio Scope A1 Carl Zeiss light and fluorescent microscopes. Some specimens (separate seeds, polliniferous cone cuticles, polliniferous cone fragments with pollen sacs, pollen grains) were only treated with hydrofluoric acid (and some were macerated afterwards in Schulze solution) for SEM examination. They were sputter-coated with gold and observed with a Hitachi S-2360N scanning electron microscope at 22 kV accelerating voltage and secondary electron detection.

For the pollen wall ultrastructure investigation, pollen grains were soaked with propylene oxide, infiltrated and embedded in Durcupan resin. Ultrathin sections (70 nm) were cut with a Reichert-Jung Ultracut E ultramicrotome. Sections stained with uranyl acetate and lead citrate (Reynolds, 1963) were observed with a Hitachi 7100 transmission electron microscope at 75 kV accelerating voltage.

## 3. Results

### 3.1. Systematics

Division - Pinophytina
Class - Pinopsida
Order - Voltziales