SPHENOPSID AND FERN REMAINS FROM THE UPPER TRIASSIC OF KRASIEJÓW (SW POLAND)

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Abstract: Hydrophilic elements, such as sphenopsids and ferns, are rare in the flora of the Krasiejów site and they are poorly preserved. One sphenopsid species, Neocalamites merianii, was recognised. It is preserved as impressions, flattened casts, moulds and isolated leaves. So far, only one small fern specimen, determined as Sphenopteris sp., has been found. These elements probably were transported to the site of deposition and did not grow where they were buried.

Key words: Fossil plants, Neocalamites, Sphenopteris, Germanic Basin.

Manuscript received 21 February 2019, accepted 11 August 2019

INTRODUCTION

Recent discoveries of Upper Triassic outcrops in Silesia (southwestern Poland) have yielded not only rich vertebrate material, but also new plant fossils (Dzik and Sulej, 2007; Pacyna, 2014). Plant macrofossils rarely are found in the Upper Triassic of Poland (Reymanówna, 1986; Pacyna, 2014; Pacyna et al., 2017; Kustatscher et al., 2018) and hence are poorly known; such discoveries open new opportunities for study of them. Krasiejów was the first Polish Triassic site with the bones of large land vertebrates described and it is still one of the most important (Sues and Fraser, 2010; Lucas, 2018). It is a window on ecosystem evolution at the beginning of the dominance of the dinosaurs. The discovery and description of Silesaurus give a new impetus for research on the origin of the dinosaurs and their diversification in the Triassic (Fraser and Sues, 2010; Langer et al., 2010; Agnolin and Rozadilla, 2018; Baron, 2019).

The fossil assemblage identified at the Krasiejów locality (Fig. 1) is abundant in specimens, is among the most taxonomically diverse ones in the Polish Triassic and is one of the richest in the European Triassic (Dzik and Sulej, 2007; Lucas et al., 2007, Sues and Fraser, 2010). The invertebrate fauna consists of conchostracans (Olempska, 2004), bivalves (Skawina, 2010, 2013; Skawina and Dzik, 2011), crustaceans and insects (Dzik and Sulej, 2007; Dzik, 2008; Qvarnström et al., 2019). The numerous vertebrates include fish (Dzik and Sulej, 2007; Antczak and Bodzioch, 2018a), temnospondyls (Sulej, 2002, 2007; Sulej and Ma-
rare sphenopsid and fern remains are present. They are poorly preserved, like most plant fossils from the Krasiejów locality, but they hold important data for studies of the palaeoecology, taphonomy and age of the assemblage. The implications of these new data are discussed in this paper. Numerous charophyte oogonia have been described from the lower bone-bearing horizon (Zatoń and Piechota, 2003; Zatoń et al., 2005). Palynomorphs are absent at this locality (Dzik and Sulej, 2007) and so palynological biostratigraphy cannot be applied.

GEOLOGICAL SETTING

In the late Triassic, the Upper Silesia region formed the southeastern part of the Germanic Basin. Uplands surrounding this area to the south and east provided siliciclastic material, which was deposited in fluvial, floodplain, and playa environments across the basin (Jewuła et al., 2019). One of the places where such sediments were commercially exploited is the now abandoned Krasiejów Quarry (Bilan, 1975). Geological setting of the Krasiejów site is well documented on the basis of sediments visible in the outcrop and shallow borehole (Szulc, 2005, fig. 2). The rock sequence at Krasiejów is dominated by variegated mudstones and siltstones. The sediments are reddish in colour, with grey planar or spotty intercalations. The dominant facies type are the alluvial deposits, formed on gently sloping sandflats to mudflats with small, ephemeral lacustrine basins (Szulc, 2005; Jewuła et al., 2019). About 6 metres below the top of the section, the lower bone-bearing horizon, ca. 1 m thick, occurs (Fig. 2). It contains well preserved, but mostly disarticulated skeletons of various aquatic, semi-aquatic and land vertebrates (Dzik and Sulej, 2007) and in only one part of the outcrop plant macrofossils, which are poorly preserved as iron-stained impressions.

The age of the Krasiejów assemblage was proposed originally by Dzik (2001) and Dzik and Sulej (2007) as late Carnian, on the basis of tetrapod biochronology and the correlation of strata. According to them, the Krasiejów strata correlate with the Drawno Beds of the Polish Lowland and the Lehrberg Schichten (now the Steigerwald Formation) in Germany. This age proposal was confirmed later by Lucas (Lucas et al., 2007; Lucas, 2015, 2018), also on the basis of tetrapod biochronology, and by Pacyna (2014) on the basis of correlation of the macrofossil plant assemblages with the German part of the Germanic Basin. This age determination was questioned by Szulc and collaborators (Szulc, 2005; Szulc et al., 2015a, b; Jewuła et al., 2019), on the basis of integrated stratigraphy, facies analysis and event geology. They proposed a Norian age for the assemblage and referred it to the basal part of the Patoka Member of the formation that they defined as the Grabowa Formation. The Grabowa Variegated Mudstone-Carbonate Formation (Szulc et al., 2015a) is a thick succession of variegated mudstone to claystone deposits, reaching up to ca. 400 m with a carbonate admixture and with calcareous breccias in the upper part. This formation is a lateral equivalent of German Wesser and Arnstadt formations (Szulc et al., 2015a; Jewuła et al., 2019). The Patoka Marly Mudstone-Sandstone Member is the thickest member of this formation (up to ca. 300 m), composed of variegated, mostly red to brownish, marly, massive mudstones, with numerous horizons of limestone-claystone conglomerates.

An absolute age, based on detrital zircon analysis, could settle the question of age for the Upper Silesian bone-beds (Kowal-Linka et al., 2019). However, the ages of the stage boundaries in the Upper Triassic are still a matter of debate. Also, owing to problems in correlating the non-marine Upper Triassic strata, an age determination for the Krasiejów assemblage awaits further research.

MATERIAL AND METHODS

The plant fossils described here were collected during field work at the Krasiejów locality, which was organized and conducted by J. Dzik and T. Sulej (Institute of Paleobiology, Polish Academy of Sciences) during the 2000–2002 field seasons. The specimens the author and D. Zdebska excavated are stored in the Institute of Botany of the Jagiellonian University (Fossil Plants Collection of Herbarium Universitatis Jagellonicae Cracoviensis, collection number KRA-PALEO 102). Specimens found by other members of the excavation team are stored in the Institute of Paleobiology (Collection ZPAL Ab III) and were available for study. The specimens were collected under an excavation permit granted to the Institute of Paleobiology, Polish Academy of Sciences, before the Krasiejów locality was placed under special protection as a Trias Geological Documentary Site (Wojewoda Opolski, 2003). Plant fossils were found in only one place within the lower fossil-bearing horizon (Figs 1, 2). They formed a dense accumulation in an area covering about 3 m². Beside plant debris, only the well-preserved remains of the crustacean *Opolanka decorosa* Dzik are encountered in this accumulation. The plant remains are fragmented, consisting of conifer and sphenopsid shoot fragments, up to about 10 cm long, very rarely longer, completely mixed and showing no discernible direction of transport. Even more poorly preserved and rare plant remains were dispersed in a radius of 2–3 m around the main concentration; bivalve fossils and some vertebrate remains were also present there, especially isolated vertebrae of *Metoposaurus krasiejowensis* Sulej. The plant fossils are preserved mainly as iron-stained impressions, completely devoid of any organic remains. Larger sphenopsid shoot fragments are preserved as somewhat flattened casts.

The plant remains were carefully dissected using needles, examined under a Technival 2 stereo microscoope and photographed with a Nikon NIKKOR AF-s DX Micro NIKKOR 85 mm f/3.5G ED VR Camera.

SYSTEMATIC PALAEONTOLOGY

The suprageneric classification follows Cronquist et al. (1966), Kenrick and Crane (1997), Taylor et al. (2009) and PPG I (2016). For the nomenclatural treatment, the International Code of Nomenclature for Algae, Fungi and Plants (Shenzhen Code, 2017) and the International Code of Phylogenetic Nomenclature (Cantino et al., 2007) were used.
Class EQUISETOPSIDA Agardh, 1825

Order EQUISETALES de Candolle ex von Berchtold & Presl, 1820

Family incertae sedis

Genus Neocalamites Halle, 1908 emend. Bomfleur et al., 2013

Type species: Neocalamites lehmannianus (Goeppert, 1846) Weber, 1968; Upper Silesia, Dobiercice; Upper Triassic.

Neocalamites merianii (Brongniart, 1828) Halle, 1908


Description: Shoot fragments preserved fragmentarily as flattened casts and moulds, 5 mm to at least 26 mm wide, distinctly ribbed longitudinally (Fig. 3A–F). Ribs 0.75–4 mm wide depending on shoot width. On broadest shoots, protruding bands 0.5–0.8 mm wide lying between ribs (these are vestiges of vascular bundles exposed on the external shoot ribs from beneath; Fig. 3A). Nodes only rarely preserved, poorly visible (Fig. 3B). No visible traces of leaf scars, leaf sheath or branch scars in nodes. Nodes not expanded. Two nodes not visible on any shoot fragments, so internode length not measurable. Longest preserved shoot fragment without node 95 mm long, 20 mm wide (hence, internode length could be at least that long). Leaves found only as isolated, fragmented specimens, without bases or apices preserved, 10–27 mm long, neither narrowing or expanding along leaf length (Fig 3G–I). No traces indicating fusing of leaves in a sheath. Leaf vascular bundle remnants are not traceable on a leaf surface.

Remarks: The genus Neocalamites was proposed by Halle (1908) to accommodate several early Mesozoic equisetophyte species that previously had been erroneously assigned to Schizoneura. The genus Schizoneura is characterised by leaf sheaths that split into several strap-shaped leaf-sheath segments in mature stems. In contrast, Neocalamites has long, linear, narrow, single-veined leaves.
whose bases may be separate, overlapping or even connate. Modern ideas about these genera were extensively discussed by Bomfleur et al. (2013), who also proposed a very precise, emended diagnosis for Neocalamites, which is followed here.

Neocalamites merianii (Brongniart) Halle was described first by Brongniart (1828) as Equisetum merianii, on the basis of material from the Carnian of the Neuwelt locality in Switzerland. Kräusel (1958, 1959) described and illustrated numerous well-preserved specimens. Pott et al. (2008, 2018) gave a detailed description of the species, based on rich material from Lunz (Austria). The material described here corresponds well with the specimens reported by Kräusel (1958, 1959), Kelber and Hansch (1995), Pott et al. (2008, 2018), Barbacka et al. (2014) and Kelber (2015). In N. merianii, unlike in extant sphenopsid species, the number of vascular bundles is not equal to the number of ribs visible on the shoot surface (Kustatscher and Van Konijnenburg-Van Cittert, 2008; Barbacka et al., 2014). The shoot surface was covered with wide ribs, and about ten vascular bundles were beneath each rib. The vascular bundles are visibly exposed on the external shoot ribs from below. Among the Neocalamites species, external shoot surfaces in connection with vascular bundles are preserved especially frequently in N. merianii (Kelber and Hansch, 1995; Kelber, 2015). Probably the cortical tissue decayed quickly, but the more resistant vascular bundles persisted longer and appeared on its surface. This interesting mode of preservation of fossil sphenopsids as exemplified by this species was described and well-illustrated by Kräusel (1958, 1959), Kelber and Hansch (1995; fig. 105), Kustatscher and Van Konijnenburg-Van Cittert (2008), Pott et al. (2008, 2018) and Kelber (2015), and for other Neocalamites species by Jarzynka and Pacyna (2015).

Reproductive structures of Neocalamites are not often found (Bomfleur et al., 2013). Specimens in organic connection to their stems are rare. Most of the specimens discovered only occur with sterile shoots. However, on the basis of well preserved and properly documented specimens, it is assumed that Neocalamites produced compact strobili consisting of successive whorls of peltate sporangiophores, each sporangiophore bearing six or more sporangia (Kon’no, 1962; Brea and Artabe, 1999; Escapa and Cúneo, 2006; Pott et al., 2008, 2018; Zan et al., 2012).

Because of problems in recognising reproductive structures and evidence that Neocalamites-type stems had secondary growth (Kelber and Hansch, 1995), the systematic position of this genus is unclear. Neocalamites stems probably could grow several metres high (Holt, 1947); such huge plants are unknown in the modern Equisetum lineage. Secondary growth and free leaves, similar to those in calamitaleans, could indicate that this form is a vestige of that group. Recently, Elgorriaga et al. (2018) provided the first comprehensive phylogenetic analysis of Equisetales, with
special emphasis on the origin of the genus *Equisetum*. They recovered Equisetaceae plus Neocalamites as a sister to the Calamitaceae, plus a clade of Anaran and Gondwanan sphenophytes, with the four groups forming a clade that is sister to the Archaceocalamitaceae. According to them, Neocalamites is a sister to the Equisetaceae, but they concluded that Neocalamites appears to have a mosaic of equisetalean features not present in any other clade, supporting the idea that it was part of a distinct natural group. Probably this group forms an evolutionary bridge between the Archaceocalamitaceae and the Equisetaceae.

**Distribution:** Neocalamites merianii is common in the Triassic (especially Ladinian–Carnian, mainly southern Germany and the Neuwelt, Switzerland and Lunz, Austria localities) and less common in Early Jurassic floras of Europe (Kräusel, 1958, 1959; Kelber and Hansch, 1995; Pott et al., 2008). In Poland, it was noted previously only once, from the upper Ladinian and Hettangian strata of the Holy Cross Mountains region (Barbecka et al., 2014).

**Class** POLYPODIOPSIDA Cronquist et al., 1966

**Order and family** incertae sedis

Genus *Sphenopteris* (Brongniart, 1822) Sternberg, 1825

**Type species:** *Sphenopteris elegans* (Brongniart, 1822) Sternberg, 1825

**Stemberg, 1825; Lower Silesia, Wałbrzych; Carboniferous, Namurian A.**

*Sphenopteris* sp.

Fig. 3J

**Material:** KRA–PALEO 102/3 – small leaf fragment.

**Description:** Penultimate and ultimate fragments of compound leaf (Fig. 3J). Penultimate fragment 4 mm long, 2.5 mm wide, dividing into five ultimate pinnules alternately arranged. Ultimate pinnules 2 mm long, 1 mm wide, probably ovate in shape, constricted toward axis. Lamina poorly preserved, mainly dichotomizing veins visible, dividing three times within lamina. Ultimate pinnule margins not preserved. Pinnules arise from main penultimate segment axis at acute angles (about 5°).

**Remarks:** This specimen probably is a second-order pinna, dividing into pinnules of the third order or pinnula dividing into segments. The present author could not determine the extent to which the neighbouring pinnules were fused together, if at all, owing to the poor preservation of the specimen. The shape and type of venation are compatible with the genus *Sphenopteris*.

The author has at his disposal only one small, sterile leaf fragment, therefore its closer affinity within any group of ferns could not be resolved. The morphological genus name *Sphenopteris* was used strictly for its determination. This genus is characterized by pinnules usually decurrent, constricted at the base, oval in outline and almost entire margined, lobed or variously toothed. The midvein is straight and produces forking secondary veins that depart at a steep angle and extend toward the margin. Genus *Sphenopteris*

was used for fern foliage from the Palaeozoic and Mesozoic eras and its affinity could not be settled with certainty (Taylor et al., 2009). The specimen from Krasiejów has pinnule shape and venation typical for that genus.

Species determination for such small plant fragment is always difficult or impossible. The most similar species is *Sphenopteris schoenleiniana* (Brongniart, 1835; Presl in Sternberg, 1838) known from the upper Anisian (Van Konijnenburg-Van Cittert et al., 2006), Ladinian (Mader, 1990; Kustatscher and Van Konijnenburg-Van Cittert, 2011) and Carnian (Kelber and Hansch, 1995). Pinnate shape and venation are similar, but the dimensions are smaller in the Krasiejów specimen (Schenk, 1864; Schoenlein and Schenk, 1865; Kelber and Hansch, 1995; Van Konijnenburg-Van Cittert et al., 2006; Kustatscher and Van Konijnenburg-Van Cittert, 2011). Another similar species is *Coniopteris lunzensis* (Carnian, Lunz, Austria; Pott et al., 2018), which has similar pinna shape and venation in the central part of the primary pinna. However, the apical portion of a pinna in this species has linear pinnules with pointed apices arranged at very acute angles. The pinna dimensions are also larger in this species. Species *Todites limnaeifolius* (also Carnian, Lunz, Austria; Pott et al., 2018) has similar pinna shape, but typical neuropterid venation in contrast to sphenopterid in Krasiejów specimen. There are other somewhat similar but weakly known species referred to genus *Sphenopteris* from the Triassic of Europe, e.g. *Sphenopteris myriophyllum* Brongniart, 1828, *Sphenopteris oppositifolia* Presl in Sternberg, 1838, *Sphenopteris clavata* Presl in Sternberg 1838, *Sphenopteris kirchneri* Goeppert, 1841, *Sphenopteris braunii* Goeppert, 1841, *Sphenopteris patentissima* Goeppert, 1841 and *Sphenopteris birsina* Heer, 1877 (Sternberg, 1820–1838; Brongniart, 1828–1837; Goeppert, 1841; Heer, 1877). They were discussed throughly by Kustatscher and Van Konijnenburg-Van Cittert (2011) in comparison with *Sphenopteris schoenleiniana*. These species established in the 19th century as a rule were briefly described, poorly illustrated by means of drawings, and have not been revised after the original description. It is not possible to compare such a small specimen as that from Krasiejów with other species in any detail because of the small number of features visible. The specimen from Krasiejów could be referred to almost all of them with equal probability.

**DISCUSSION**

In the Krasiejów flora, hygrophilous elements, such as cryptogamous plants, are infrequent and are poorly preserved. Ferns are extremely rare – only one specimen was found. Sphenophytes are not numerous, and disarticulated leaves are found separately. This may mean that these elements were transported to the deposition site and did not grow where they were buried. Transportation did not favour the preservation of fragile plant organs such as fern leaves and caused disarticulation (sphenopsid leaves separated from shoots). The transport may have been long-distance or high-energy.

Climatic conditions may have made ferns rare in the sedimentary basin. Sphenophytes and ferns are dependent
on molecular water and thus connected with water bodies, even seasonal ones; they can grow around large or small ones or along rivers, permanent or seasonal. Sphenophytes and ferns are rarer than gymnosperms in the flora, especially rarer than the conifers, among which easily transportable and durable seeds predominate. The taphonomy of the sphenophytes and ferns from Krasiejów is in good agreement with the environmental models for this locality proposed by Bodzioch and Kowal-Linka (2012) and Jewuła et al. (2019).

The plants described here are poor indicators of age. _Neocalamites merianii_ is known from the Middle Triassic to Lower Jurassic (Kräusel, 1958), but is best known from and most characteristic for the Ladinian (e.g., Thale flora; Kustatscher and Van Konijnenburg-Van Cittert, 2008) and especially the Carnian floras (Lunz, Austria; and Neuwelt, Switzerland; Kräusel, 1959; Kelber, 1998, 2005; Pott et al., 2008, 2018; Franz et al., 2019). This may indicate a Carnian age for the Krasiejów assemblage (see also Pacyna, 2014 and Kustatscher et al., 2018 for other arguments for Carnian age of Krasiejów plants). If the rocks exposed in the Krasiejów outcrop are indeed Norian in age, as postulated by Szulc and collaborators (Szulc, 2005; Szulc et al., 2015a, b; Jewuła et al., 2019), redeposition of the fossils could have been a factor here. Redeposition of plant microfossils (spores and pollen) is a well-known phenomenon in palaeobotany (Taylor et al., 2009). However, palynomorphs are absent at the Krasiejów locality. Petrified, silicified or calcified plant macrofossils, especially of woody stems could be redeposited (Florjan and Worobiec, 2016). However, redeposited plant compressions or impressions have not been described so far. The plant remains from Krasiejów are preserved as impressions. Plant organs (shoots, leaves, seeds) were transported before burial, but they were not redeposited as individual elements. They are too fragile to have been redeposited and preserved in a taxonomically identifiable form. Redeposition, if this was the case, must have been on a large scale, e.g. caused by intense syndepositional tectonics involving the transportation of a huge volume of rock containing plant matter.

**Acknowledgments**

I sincerely thank J. Dzik and T. Sulej (Institute of Paleobiology, Polish Academy of Sciences, Warsaw) for allowing me to collect plant specimens at the Krasiejów locality and for giving me access to their collection of fossil plants from Krasiejów for this research. I thank D. Zdebska (Institute of Botany, Jagiellonian University, Cracow) for discussions and help with problems during the preparation of this article. I thank journal referees Mihai Popa (Faculty of Geology and Geophysics, University of Bucharest, Bucharest), Christian Pott (LWL-Museum für Naturkunde, Münster) and Joachim Szulc (Institute of Geological Sciences, Jagiellonian University, Cracow) for their helpful comments and suggestions. M. Jacobs and F. Simpson (School of the Environment, University of Windsor, Windsor) skilfully corrected the language. M. Szewczyk took photos of some specimens, A. Sojka prepared the figures. The project was financed by funds from the Polish National Science Centre (Grant No. DEC-2017/01/X/ST10/01867).

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