

# Plant remains from the Polish Triassic. Present knowledge and future prospects

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**ABSTRACT.** The Triassic plant macrofossils of Poland are very poorly known. There are few Triassic rock exposures here, they contain very few plant specimens, there is little scientific interest in the subject, and the rare plant remains found in drill cores are of low stratigraphical significance. The Lower Triassic macroflora is surprisingly poorer taxonomically than coeval European floras, and only single specimens have been found. The flora of the Middle Triassic is even poorer as a result of the Muschelkalk sea transgression. Only the Upper Triassic floras contain many specimens and taxa. The Upper Triassic macrofloras from Polish territory are well known since the early 19<sup>th</sup> century. Pioneering descriptions of these floras were given by Goeppert and Raciborski. From the Polish Triassic, the seed fern *Lepidopteris ottonis* (index species for the Rhaetian stage) and *Neocalamites lehmannianus* (sphenopsid species typical of almost all European Upper Triassic and Lower Jurassic floras) were described for the first time ever. In the 20<sup>th</sup> century only single specimens were described from outcrops and drill cores. Barbacka revised *Lepidopteris ottonis* specimens from old collections and described some new material. Palynological research on Triassic strata in Poland intensified from the 1970s on. That work has produced spore-pollen and megaspore zonations for Triassic strata in Poland, but the correlation of the dispersed spores and pollen grains with their parent plants is low. The Polish Triassic flora is comprised of ferns, lycopsids, sphenopsids, cycads, bennettitaleans, ginkgoaleans and conifers. This flora is taxonomically poorer than equally old and geographically close European floras. All available data about Polish Triassic plants fossils are critically summarised in this paper for the first time. The biostratigraphical and lithostratigraphical correlations of Polish Triassic floras with other European Triassic floras are outlined. New macrofloral assemblages for the Lower and Middle Triassic and macrofloral assemblage zones for the Upper Triassic are proposed for Poland. Recent new finds of taxonomically rich, abundant and well-preserved floras accompanying vertebrate remains in Silesia provide an opportunity for comprehensive research on Polish Triassic floras. This should improve our perception of their taxonomy and allow them to be described in evolutionary and palaeoecological contexts.

**KEYWORDS:** fossil plants, biostratigraphy, *Lepidopteris* zone, Triassic, Krasiejów, Poland

## INTRODUCTION

The Triassic was one of the most important periods because it witnessed dynamic evolutionary changes and the formation of modern ecosystems for the first time in the history of life on Earth (Fraser 2006, Sues & Fraser 2010). It is also the period in which floras were restored after the most devastating extinction in Earth's history, at the Permian-Triassic boundary (Taylor et al. 2009). Floras that originated during this period would occur through almost the entire Mesozoic era and would be the source of food for herbivorous dinosaurs

(King 1996, Sues 2000). Yet the Triassic floras of the Northern Hemisphere are rare and poorly known (Meyen 1987). In this circumstance, each new site with plant macroremains and each new piece of information may fill a gap in our understanding of Triassic palaeoecology and evolution, locally and globally. The well-described localities of floras of this age are few (Kustatscher & van Konijnenburg-van Cittert 2005, 2008, Roghi et al. 2006, van Konijnenburg-van Cittert et al. 2006, Kustatscher et al. 2012) but the information they provide forms

our knowledge of the taxonomic composition of Triassic floras, particularly that of gymnosperms. Very intensive radiative processes occurred in this group at that time, leading to the appearance of new groups, possibly including the angiosperms (Anderson & Anderson 1997, 2003). The Triassic is an exceptionally interesting period as it saw the evolution of conifers (Miller 1977, Grauvogel-Stamm 1978, Rothwell et al. 2012). The oldest representatives of some modern families appeared in the Upper Triassic. The stages of transformation from primitive *Votziales* into evolutionarily advanced families of modern conifers in the Triassic are not yet fully documented (Miller 1977, Rothwell et al. 2012).

Problems of stratigraphy make it difficult to identify evolutionary events in the Triassic. Thick sequences of strata without good index fossils are difficult to correlate regionally and globally, hampering the task of distinguishing evolutionary processes and sequences of terrestrial organisms (Hunt & Lucas 1991, Lucas 1998, Rayfield et al. 2005, Lucas et al. 2007b, Kozur & Bachmann 2008). Plant micro- and macrofossils have proved useful in Triassic biostratigraphy, especially in palynological zonation (Dobruskina 1988, 1994, Fijałkowska-Mader 1999, Lucas 2006, 2007, Cirilli 2010, Kürschner & Herngreen 2010). Ash (1980, 1987) proposed a macrofossil plant biostratigraphy for the Upper Triassic Chinle Group in North America. Unfortunately not a single species is shared by the North American and European Upper Triassic floras, so an exact correlation is almost impossible.

Little is known about the Triassic floras of Poland (Lilpop & Kostyniuk 1957, Orłowska-Zwolińska & Senkowiczowa 1970, Reymanówna 1986). There are only a very few descriptions of macroremains (Goeppert 1844, 1846a, Raciborski 1890a), written mainly in the 19<sup>th</sup> century. They require a modern revision incorporating current nomenclature and meeting today's standards of description for fossil plants (Tab. 1). Palynological research on Triassic strata in Poland intensified beginning in the 1970s. It produced a useful palynological biostratigraphic scheme for the Polish Triassic, proposed by Orłowska-Zwolińska (1985). A comparable scheme based on plant macrofossils is proposed here (Tab. 2).

New prospects for research on Triassic floras in Poland were opened by discoveries of

localities with well-preserved floral remains in the 1990s and early 21<sup>st</sup> century. Krasiejów, Patoka and Lipie Śląskie-Lisowice are new fossil plant sites found during excavation of the bones of large land vertebrates. These localities have yielded numerous plant remains. Besides expanding our knowledge of Triassic floras in Poland, a full description of the macroflora from these localities will help reconstruct the palaeoenvironment of the animals at those sites. Equipped with knowledge of the flora that co-occurred with dinosaurs, we can more fully characterise those ecosystems, including the plant-animal interactions.

This paper gives an overview of the Triassic plant taxa of Poland, and summarises the data on diversity reported in historical documents.

## HISTORICAL SUMMARY OF RESEARCH ON TRIASSIC FLORAS IN POLAND

Goeppert (1836, 1841–1846, 1844, 1845, 1846a, b) was the first to describe the plant fossils of the Polish Triassic. His pioneering works on the Upper Triassic flora of Silesia gave descriptions of new taxa later regarded as index or very common taxa in many European Triassic floras. Goeppert's research was quite advanced for his time; for example, he described and illustrated anatomical details of the *Lepidopteris ottonis* cuticle (Goeppert 1846a). Such depth of approach was rare in early palaeobotany. Goeppert erroneously determined the age of the flora as Middle Jurassic, though some specimens he described (wood fragments) are indeed Middle Jurassic in age. Next, Roemer (1867, 1870), then the foremost expert on Silesian geology, corrected the age given by Goeppert to Upper Triassic (Rhaetian). Roemer compared the Silesian flora described by Goeppert with the German Keuper floras described by Schenk (1867). Roemer showed Goeppert's original specimens to Schenk, the top expert on floras of the Triassic-Jurassic boundary. Schenk studied Goeppert's specimens and described new specimens collected by Roemer, including some new taxa (Schenk 1867, Roemer 1867, 1870). Roemer also gave the first complete description of the Triassic geological setting in Silesia (Roemer 1862, 1863, 1867, 1870). Roemer (1870) discovered another Upper Triassic flora in Upper Silesia, preserved in crenogenic limestones known as

the Woźniki Limestone. Rich collections of fossil plants have been assembled from this limestone since then (Różycki 1930, Reymanówna 1986, Szulc et al. 2006, Szulc & Becker 2007) but not described. Kunisch (1886) and Michael (1895) described some plant remains from the Muschelkalk of Upper Silesia. In 1890, Raciborski described the Rhaetian flora from the Tatra Mountains at the Czerwone Żlebki locality (Raciborski 1890a, b, c).

Then research on Triassic plants in Poland came to a virtual halt. Some specimens discovered by geologists studying the geology of the Holy Cross Mountains at the beginning of the 20<sup>th</sup> century were noted in the literature (Czarnocki 1925, 1931, Samsonowicz 1929) but without descriptions or illustrations. After the Second World War, stratigraphical research by geologists produced new macroremains from drill cores and outcrops, only some of which have been described (Bocheński 1957, Piwocki 1970, Pawłowska 1979, Fuglewicz 1980b, Reymanówna 1986, Barbacka 1991, Brzyski & Heflik 1994, Barbacka & Wcisło-Luranc 2002, 2003, Ociepa et al. 2008, Barbacka et al. 2009). Barbacka revised the *Lepidopteris ottonis* specimens from old collections and described some new materials (Barbacka 1980, 1991, Reymanówna & Barbacka 1981).

Palynological research on Triassic strata in Poland accelerated starting from the 1970s (Pautsch 1958, 1971, 1973, Orłowska-Zwolińska 1967, 1971, 1976, 1977, 1983, 1984, 1985, 1986, 1988, Marcinkiewicz 1962, 1969, 1971, 1976, 1978, 1981, 1992a, b, c, Fuglewicz 1973, 1979a, b, 1980a, b, Dybova-Jachowicz & Laszko 1980, Fuglewicz & Śniezek 1980, Rdzanek 1982, Marcinkiewicz & Orłowska-Zwolińska 1985, 1994, Fuglewicz & Marcinkiewicz 1986, Fijałkowska 1989, 1990, 1992a, b, 1994a, b, 1995, Fijałkowska & Uchman 1993, Krupnik & Ziaja 2010, Pieńkowski et al. 2012, Fijałkowska-Mader 2013). From the outset these studies focused on biostratigraphy. Palynological research became especially useful in determining the age of nonmarine sediment sequences not bearing other index fossils. The investigations bore fruit in useful spore-pollen and megaspore zonations for Triassic strata in Poland (Marcinkiewicz 1971, 1978, 1992c, Fuglewicz 1980b, Orłowska-Zwolińska 1983, 1985, Fijałkowska-Mader 1999). The Permian-Triassic and Triassic-Jurassic boundaries have been well delineated based on

palynological data (Orłowska-Zwolińska 1967, Marcinkiewicz 1962, 1969, 1971, Fijałkowska 1990, 1992a, 1994a, 1995, Pieńkowski et al. 2012, Fijałkowska-Mader 2013). However, the correlation between the parent plants and the dispersed spores and pollen grains requires much more study.

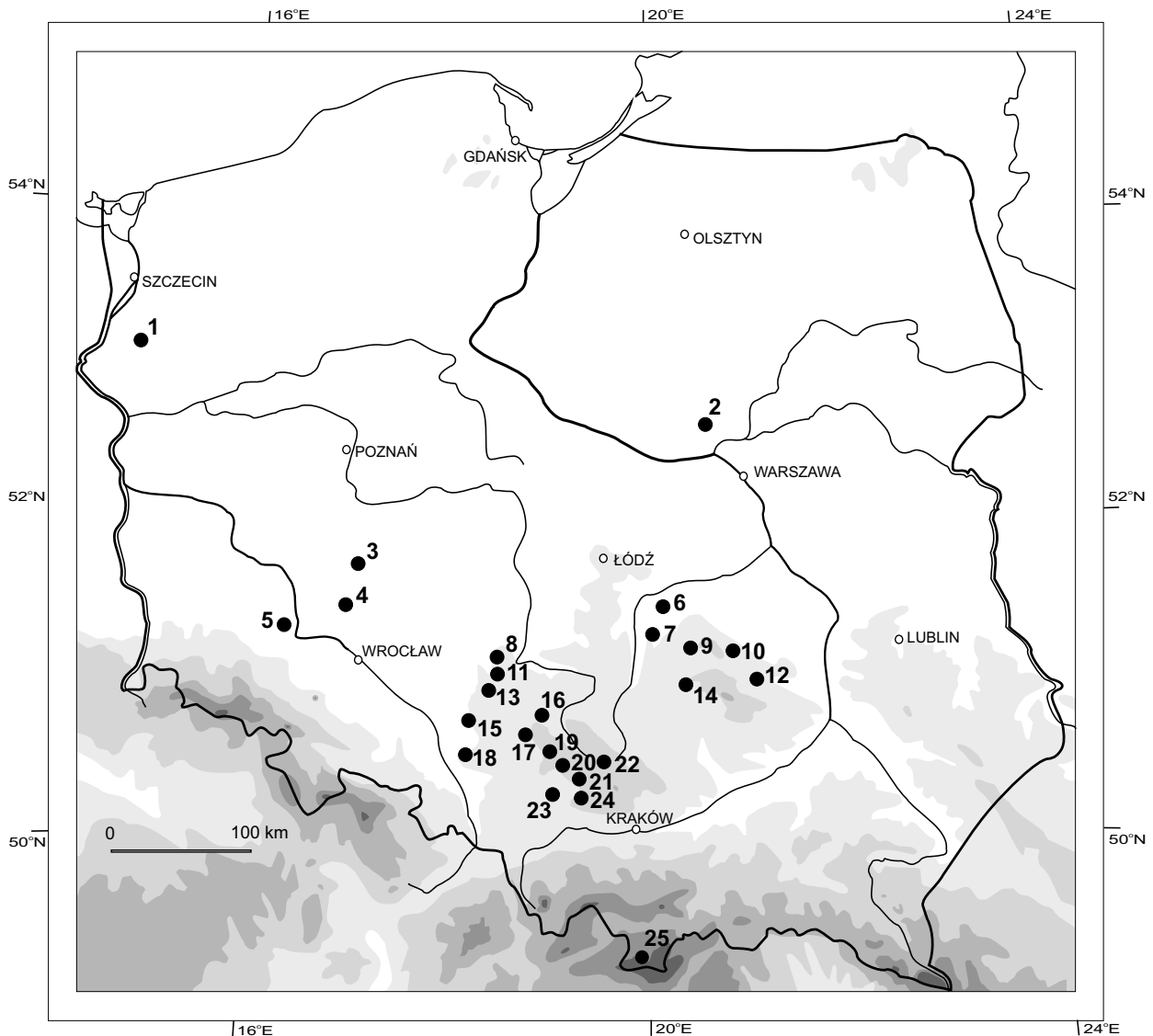
Recent finds of taxonomically rich, abundant and well-preserved floras accompanying vertebrate remains in Silesia have opened an opportunity for new research on Polish Triassic floras. The research on these localities is only just beginning (Dzik & Sulej 2007, Staneczko 2007, Dzik et al. 2008a, b, Wawrzyniak & Ziaja 2009, 2010, Wawrzyniak 2010a, b, c, Barbacka et al. 2012, Pacyna et al. 2013a, b).

## COMPOSITION AND EVOLUTION OF PLANT ASSEMBLAGES IN THE POLISH TRIASSIC, AND THEIR STRATIGRAPHICAL VALUE

### LOWER AND MIDDLE TRIASSIC (BUNTSANDSTEIN, MUSCHELKALK AND LOWER KEUPER)

Lower Triassic floras worldwide are rare and taxonomically impoverished as a result of the greatest extinction in Earth's history at the Permian-Triassic boundary (Looy et al. 1999, Grauvogel-Stamm & Ash 2005). This is also true for the Polish Triassic localities. The Permian-Triassic boundary has been documented palynologically from several Polish boreholes (Fijałkowska 1990, 1992a, 1994a, 1995, Fijałkowska-Mader 2013).

Plant macrofossils from the Polish Lower and Middle Triassic are exceptionally few in number of specimens and number of taxa (Tab. 1). Most recorded findings are from the Holy Cross Mountains (Czarnocki 1925, 1931, Samsonowicz 1929, Bocheński 1957, Lilpop & Kostyniuk 1957). Some are from Silesia (Kunisch 1886, Michael 1895b), the Tatra Mountains (Limanowski 1901), and boreholes from various regions of Poland (Fuglewicz 1980b). Only rare lycopsid, sphenopsid, conifer, and possibly seed fern remains have been identified so far (Tab. 1). Intensive new research on invertebrate and vertebrate tracks, which are very numerous and taxonomically diverse in the Holy Cross Mountains, has, surprisingly, provided only single new fossil plant specimens



**Fig. 1.** Macrofossil and selected microfossil plant localities from the Polish Triassic. 1 – Chabowo 2 borehole; 2 – Gradzanowo 1 and 3 boreholes; 3 – Gostyń 46 G borehole; 4 – Kołaczkowice near Rawicz; 5 – Otyń IG-1 borehole; 6 – Studzianna borehole; 7 – Radoszyce 3 borehole; 8 – Wieluń; 9 – Pałegi; 10 – Ratajów; 11 – Gorzów Śląski area (Łofkowitz, Sumpen); 12 – Majków area; 13 – Kluczbork area (Biadacz, Dobiercice, Gosław, Maciejów); 14 – Gacki 1, 3 and 4 boreholes; 15 – Krasiejów; 16 – Patoka; 17 – Lipie Śląskie-Lisowice; 18 – Krapkowice; 19 – Ligota near Woźniki; 20 – Woźniki; 21 – Myszków-Nowa Wieś; 22 – Kamienica Polska; 23 – Tarnowskie Góry; 24 – Poręba and Marciszów near Zawiercie; 25 – Czerwone Żlebki

(Karaszewski 1966, 1976, Gradziński et al. 1979, Fuglewicz et al. 1981, Senkowiczowa 1982, Mader & Rdzanek 1985, Fuglewicz et al. 1990, Gradziński & Uchman 1994, Machalski & Machalska 1994, Ptaszyński 1996, 2000a, b, Kuleta et al. 2001, 2005, 2006, Ptaszyński & Niedźwiedzki 2002, 2004, 2006, Niedźwiedzki et al. 2007, 2013, Niedźwiedzki & Ptaszyński 2007, Brusatte et al. 2011). In France, by contrast, well-preserved and taxonomically rich flora and fauna are known from coeval and similarly geologically structured Anisian strata – Grés a Voltzia (Grauvogel-Stamm 1978).

The palynological record of Lower Triassic plants in Poland is better than the record from macroremains (Fuglewicz 1973,

1979a, b, 1980a, b, Marcinkiewicz 1976, 1992c, Orłowska-Zwolińska 1977, 1984, 1985, 1988, Rdzanek 1982, Fijałkowska 1994b, Fijałkowska & Uchman 1993, Fuglewicz & Marcinkiewicz 1986). A biostratigraphical scheme was proposed based on palynology (Fuglewicz 1980b, Orłowska-Zwolińska 1985, Marcinkiewicz 1992c, Fijałkowska-Mader 1999) but the correlation of the dispersed spores and pollen grains with their parent plants is low. Lower Triassic vertebrate bone fossils are very rare in Poland (Borsuk-Białynicka et al. 1999, Borsuk-Białynicka & Evans 2009, Sulej & Niedźwiedzki 2013).

Buntsandstein-type facies (mostly terrestrial) were replaced by fully marine facies in

the Anisian as a result of the Muschelkalk sea transgression (Eck 1865, Marek & Pajchłowa 1997, Nawrocki & Szulc 2000, Szulc & Becker 2007, Kowal-Linka & Bodzioch 2012). Because of this, the flora of the Muschelkalk in Poland, as all over Europe, is even poorer than for the Lower Triassic. Palaeontological research on the Muschelkalk strata in Poland has a long history (Eck 1865), and rich marine vertebrate fauna have been described (Roemer 1870, Gürich 1884, Tarlo 1959, Lis & Wójcik 1960, Rieppel & Hagdorn 1997, Chrząstek & Niedźwiedzki 1998, Rieppel 2000, Bardziński et al. 2008, Chrząstek 2008). Macroscopic plant remains are almost entirely absent, however (Goeppert 1846b, Kunisch 1886, Michael 1895), and the palynological record is meager (Orłowska-Zwolińska 1977, 1985, 1986, 1988, Marcinkiewicz 1992a). Only calcified algae are well known from these strata (Raciborski 1892, 1927, Szulc & Becker 2007), some even rock-forming (Diplopora Beds). From the Muschelkalk sea regression in the Lower Keuper (Ladinian), rich swamp vegetation is known in Germany (Mader 1995), but in Poland only isolated horsetail remains have been described (Pawłowska 1979, Barbacka et al. 2009, Sulej et al. 2011b). Lilpop (in Raciborski 1927) noted the discovery of the Lettenkohle flora from Piekoszów in the Holy Cross Mountains. This flora consisted of cycadaleans and conifers and was never illustrated or even preliminarily described.

Recently an interesting new locality was found at the Pałęgi claypit in the Holy Cross Mountains (Kuleta et al. 2006, Żyła et al. 2013). There, Lower/Middle Triassic sediments (latest Olenekian–early Anisian, Upper Buntsandstein) crop out with numerous well-preserved remains of crustaceans and insects, and invertebrate and vertebrate tracks. Miospores from the fossiliferous level are abundant and typical of the *Voltziacaesporites heteromorpha* zone (Żyła et al. 2013). Macrofossil plant remains were also found there but they are not very well-preserved; some remains were recognised as horsetail stems (Kuleta et al. 2006, Żyła et al. 2013) and others were indeterminable. In the collection from this locality held in the W. Szafer Institute of Botany, Polish Academy of Sciences, none of the plant remains could be determined even approximately (pers. observ.). This fossil assemblage is similar in age to the famous Grés à Voltzia.

#### UPPER TRIASSIC (MIDDLE AND UPPER KEUPER)

The Upper Triassic stratigraphy of Poland is confused, as it uses local stratigraphic divisions poorly correlated with the Germanic Basin stratigraphy accepted in Europe (Znosko 1955, Szyperko-Śliwczyńska 1960, Dadlez & Kopik 1963, Senkowiczowa 1966, 1970, Marcinkiewicz 1969, 1971, 1978, Grodzicka-Szymanko 1971, Grodzicka-Szymanko & Orłowska-Zwolińska 1972, Kotlicki 1974, Gajewska 1978, Czapowski & Romanek 1986, Pieńkowski 1988, Marek & Pajchłowa 1997). The first descriptions of Upper Triassic strata in Poland, given by Romer (1862, 1863, 1867, 1870), were based on the German geological tradition and correspond to the rest of the Germanic Basin. Unfortunately, Samsonowicz (1924, 1929) then proposed a local stratigraphical division for the Polish Upper Triassic, a division somewhat similar to that used in France. Polish geologists used stratigraphical nomenclature typical of the German part of the Germanic Basin but differing in meaning from that used in Germany: for example, Rhaetian sensu polonico (Znosko 1955, Mader 1997, Marek & Pajchłowa 1997, Kozur & Bachmann 2008, Franz 2009). This is the source of so much confusion in the geological literature, especially that created by foreign authors unfamiliar with the Polish local tradition. It is clear that the Polish Triassic sedimentary basin is part of the Germanic Basin (Mader 1997, Franz 2009), but because it is a marginal part of this basin, and because of local variability in the facies typical of the Germanic Basin, the stratigraphical correlations are difficult (Racki 2010). This is the Polish share in the global problems of Triassic stratigraphy as discussed above (Szulc et al. 2006, Szulc & Becker 2007).

The Upper Triassic macro- and microflora from Poland are well known but many descriptions are outdated (Goeppert 1836, 1841–1846, 1844, 1845, 1846a, b, Raciborski 1890a, b, c, Orłowska-Zwolińska & Senkowiczowa 1970, Reymanówna 1986) and new discoveries have yet to be described (Dzik & Sulej 2007, Dzik et al. 2008a, b, Niedźwiedzki & Sulej 2008, Ociepa et al. 2008, Wawrzyniak & Ziaja 2009, 2010, Wawrzyniak 2010a, b). A comparison of the available data with floras described thus far from Germany (Linck 1950, Kräusel 1952, Mägdefrau 1953, 1956, 1963, Kelber & Hansch 1996, Axsmith & Taylor 1997, Kelber & van Konijnenburg-van Cittert 1997, Kelber 1998,

2005, Arndt 2002, Kelber & Nitsch 2005) can yield useful stratigraphical conclusions. I propose such a correlation, for the first time in the Polish palaeontological literature, in Table 2. Many data on Polish Upper Triassic palynology have been gathered (Pautsch 1958, 1971, 1973, Orłowska-Zwolińska 1967, 1971, 1976, 1983, 1984, 1985, 1986, 1988, Marcinkiewicz 1969, 1971, 1978, 1981, 1992b, Fuglewicz 1980a, Fuglewicz & Śniezek 1980, Marcinkiewicz & Orłowska-Zwolińska 1985, 1994, Fuglewicz & Marcinkiewicz 1986, Fijałkowska 1989, 1992b, Pieńkowski et al. 2012). Well-grounded biostratigraphical schemes have been proposed (Marcinkiewicz 1971, 1978, Orłowska-Zwolińska 1983, 1985, Fijałkowska-Mader 1999). The Triassic-Jurassic boundary has been identified based on palynological data (Orłowska-Zwolińska 1967, Marcinkiewicz 1969, 1971, Pieńkowski et al. 2012, Pacyna 2013).

### The Carnian flora

#### – *Voltzia* floral assemblage zone

One of the most significant discoveries in Polish palaeontology was the Krasiejów locality, found in the 1990s (Dzik et al. 2000, Dzik 2001, 2003a, b, Sulej 2003, 2004). This is the most important Triassic Polish vertebrate locality, of international repute (Sues & Fraser 2010, Jagt-Yazykova et al. 2012). For our understanding of the evolution of Triassic ecosystems the Krasiejów locality is among the world's key sites, as seen in publications about its fauna (Dzik 2001, 2003a, b, 2008, Sulej 2002, 2005, 2007, 2010, Dzik & Sulej 2004, 2007, Lucas et al. 2007a, Fostowicz-Frelik & Sulej 2010, Mazurek & Słowiak 2009, Olempska 2004, 2011, Piechowski & Dzik 2010, Skawina & Dzik 2011). Taxonomically, the fossil assemblage of this locality is the richest in the Polish Triassic and one of the richest in the European Triassic (Sulej 2003, 2004, Dzik & Sulej 2004, 2007, Lucas et al. 2007a, Sues & Fraser 2010). The precise age, stratigraphy and taphonomy of this locality are the subject of debate but plausible solutions to these issues have been offered (Kotlicki & Kubicz 1974, Bilan 1975, Kłapciński 1993, Dzik et al. 2000, Dzik 2001, Szulc 2005, Szulc & Becker 2007, Gruszka & Zieliński 2008, Bodzioch & Kowal-Linka 2012). Its rich invertebrate fauna consists of conchostracans (Olempska 2004, 2011, Kozur & Weems 2010), bivalves (Skawina 2010, 2013, Skawina & Dzik 2011), crustaceans and

insects (Dzik & Sulej 2007, Dzik 2008). The site's superbly preserved vertebrates include fish (Dzik & Sulej 2007), temnospondyls (Sulej 2002, 2007, Sulej & Majer 2005, Barycka 2007, Konietzko-Meier & Wawro 2007, Konietzko-Meier & Klein 2013, Konietzko-Meier & Sander 2013, Konietzko-Meier et al. 2013), a phytosaur (Butler et al. 2014), a rauisuchian (Sulej 2005, Brusatte et al. 2009), an aetosaur (Sulej 2010, Desojo et al. 2013) and a dinosauromorph (Dzik 2003a, Dzik & Sulej 2004, Mazurek & Słowiak 2009, Fostowicz-Frelik & Sulej 2010, Piechowski & Dzik 2010).

Numerous charophyte oogonia have been described (Zatoń & Piechota 2003, Zatoń et al. 2005) but unfortunately this locality contains no palynological record. This prevents the use of palynological biostratigraphy here. The macroflora of this site has not yet been described in detail. Preliminary information has been given (Dzik 2003b, Dzik & Sulej 2004, 2007) and a detailed report is in preparation (Pacyna & Zdebska in prep.). The macroflora assemblage from Krasiejów consists predominantly of conifers (*Pseudohirmerella* sp., *Glyptolepis keuperiana*, *Voltzia* spp., *Pachylepis quinques*, *Desmiophyllum* spp., new taxa), and rare ferns (*Sphenopteris schoenleiniana*) and bennettitaleans (*Pterophyllum* sp.). This taxonomically poor flora is not well-preserved (cuticular details not recognisable). Xeromorphic features of the plants indicate rather dry climatic conditions. The most taxonomically similar flora was described by Mägdefrau (1953, 1956, 1963) from the Coburger Sandstein (= *Semionotus* Sandstein) at Haßfurt am Main. It could be useful in determining the age of the Krasiejów fossil assemblage. The Coburger Sandstein corresponds to the Kieselsandstein and Blasen-sandstein (Mader 1990), now referred to as the Hassberge Formation (Kozur & Weems 2010), whose age is estimated as Late Carnian (Middle Tuvanian). Thus, Late Carnian age is proposed here for the Krasiejów fossil assemblage. A full description of the Krasiejów macroflora will improve our knowledge of the Triassic floras of Poland and the palaeoenvironment of the animals at this site.

The fossil assemblage from the Woźniki claypit may be similar in age to the Krasiejów assemblage. Norian Woźniki Limestone has been identified without doubt above the fossiliferous level (Sulej et al. 2011a). Besides invertebrate and vertebrate remains, characean

gyrogonites and conifer shoots similar to those discovered in Krasiejów have also been found (Sulej et al. 2011a, T. Sulej pers. comm. 2011).

### **The Norian flora – *Brachyphyllum* floral assemblage zone**

There are some Upper Triassic localities in Silesia with taxonomically very poor floras whose most characteristic feature is the occurrence of *Brachyphyllum*-like shoots. These floras are distinguished here as Norian (=Lower Rhaetian sensu polonico) in age, based on palynological and geological data (Szulc et al. 2006, Szulc & Becker 2007). Floras of the Norian stage are seldom preserved and are extremely rare all over the world. The taxonomic composition of the younger (Rhaetian) and older (Carnian) floras indicate that rapid evolutionary changes took place just then, especially within the conifers. Modern conifer families probably originated during this time.

The first such flora was identified by Roemer (1870) in crenogenic limestones in the northern part of Upper Silesia (Ligota, Myszków, Poręba), called the Woźniki Limestone. Rich collections of fossil plants have since been assembled from it (Różycki 1930, Reymanówna 1986) but unfortunately not described. The plants are preserved as voids or casts in the limestone (Szulc et al. 2006, Szulc & Becker 2007). Besides the most numerous *Brachyphyllum* shoots along with seed scales and male cones probably belonging to the same plant, rare fern and bennettitalean leaves and sphenopsid shoots have been found in this flora (Tab. 3). During his examination of the Roemer collection, Raciborski found some liverwort remains which he described as the new species *Palaeohepatica roemeri* (Raciborski 1892, 1893, Wcisło-Luranc 1984) but this species was never illustrated and requires revision.

Patoka is an Upper Silesian locality newly discovered by T. Sulej and G. Niedźwiedzki, with a rather homogeneous but very interesting flora of the same type as in the Woźniki Limestone (Barbacka et al. 2012). The assemblage from Patoka is also dominated by branches of *Brachyphyllum*, but unlike the Woźniki Limestone the flora from Patoka is very well-preserved, with anatomical details. Besides *Brachyphyllum* branches and leaves, *Pachylepis* seed scales whose cuticle matches some of the *Brachyphyllum* leaves were found.

There is also another new type of ovulate scale with two oval lobes – probably the place of ovule attachment – and one reduced lobe between them, in one plane. The scales also show cuticular structure similar to the mass of *Brachyphyllum* leaves in the same rock slabs. Together with the branches and scales was one ovule whose shape and size suggest that it might be associated with the scales. The ovule is oval and has an exposed micropylar beak. Pollen grains were found inside the ovule. The same type of pollen grain has been found in well-preserved male cones. The *Brachyphyllum*-type conifers are accompanied by fragments of cf. *Czekanowskia* leaves, isolated seeds of unknown affiliation, and gymnosperm wood. Adaptations to dry climate are obvious in the cuticle structure of all the plants from the Patoka locality (compare Preto et al. 2010).

Yet another locality, Poręba, was recently discovered; it may represent the same floral assemblage (Sulej et al. 2012). A very interesting assemblage of turtles, aetosaurs, and coelophysoid dinosaurs was found at this locality. In the flora, *Brachyphyllum* shoots and conifer trunks, ginkgoalean (?) leaves and sporomorphs were identified (Sulej et al. 2012). The Marciszów-Zawiercie locality could also be Norian in age; besides, the remains of freshwater bivalves, vertebrate (dicynodontid) bones, and tracks assignable to archosaurs and dicynodonts, only palynomorphs and equisetalean remains are known to derive from that site (Szulc et al. 2006, Budziszewska-Karwowska et al. 2010, Racki 2010, Skawina & Dzik 2011, Sadlok & Wawrzyniak 2013). Also Norian in age are rocks exposed in a claypit in Wyszyna Machorowska near Radoszyce in the north-western part of the Holy Cross Mountains. At that site, apart from a vertebrate burrow system some plant remains were recognised (Tałanda et al. 2011).

### **The Rhaetian flora – *Lepidopteris ottonis* floral assemblage zone**

It was from the Upper Silesian Kluczbork area (Biadacz, Dobiercice, Gosław, Maciejów) that Goeppert (1836, 1841–1846, 1844, 1845, 1846a) described the first Polish Triassic macroflora. It was also the first Rhaetian flora described in Europe. Then Schenk (1867) and Roemer (1867, 1870) published new data for this flora, based mostly on new specimens. Plant remains were preserved in sideritic

nodules along with fish (Michael 1893, 1894, 1895a, Gallinek 1894). Goeppert's papers (1836, 1846a) described for the first time the seed fern *Lepidopteris ottonis* (the index species for the Rhaetic stage) and *Neocalamites lehmannianus*, a sphenopsid species typical of almost all European Upper Triassic and Lower Jurassic floras. This flora is not very diversified; besides the taxa listed earlier, fern and bennettitalean or cycad leaves have been described (Tab. 3). The flora requires reworking in the context of current taxonomy, nomenclature rules, and standards of description. As is already clear from Schenk's (1867) revision, some species described by Goeppert are junior synonyms of previously described species, some new species were described from small, badly preserved remains, and species in some genera are oversplit (e.g. *Pterophyllum*). Needed is a comparison of the revised taxa from this flora with taxa from the new Silesian Rhaetic floral localities. Gothan (1909a) and Barbacka (Barbacka 1980, 1991, Reymanówna & Barbacka 1981) revised the *Lepidopteris ottonis* specimens from the Goeppert and Roemer collections and described some new material. In the old collection, Barbacka (1991) recognised a *Peltaspermum rotula* cupulate disc and several isolated seeds that belong to *Lepidopteris ottonis*.

The Lipie Śląskie-Lisowice locality was discovered at the beginning of the 21<sup>st</sup> century in an active claypit (Dzik et al. 2008a, b, Niedźwiedzki & Sulej 2008). Remains of theropods and dicynodonts were found together there, an interesting finding from biogeographical and evolutionary points of view (Dzik et al. 2008a, b, Niedźwiedzki & Sulej 2008, Niedźwiedzki et al. 2011, 2012). Fossils of other archosaurs, temnospondyls, fish, a mammal-like tooth, conchostracans and bivalves, and invertebrate and vertebrate tracks were also identified (Dzik et al. 2008a, b, Gorzelak et al. 2010, Świło 2010, Skawina & Dzik 2011, Świło et al. 2014). Plant remains from the Lipie Śląskie-Lisowice claypit were first noted in the early 1980s (Fuglewicz & Śniezek 1980, Marcinkiewicz 1981) but only megaspores were preliminarily described. Current research on this locality has yielded many different well-preserved plant macroremains (Dzik et al. 2008a, b). Staneczko's finding of cf. *Lepidopteris ottonis* isolated cuticles (Staneczko 2007, Ociepa et al. 2008) and also palynological data (Dzik et al. 2008a, b) confirm the Rhaetic age

of this fossil assemblage. Cycad leaves and cones, ginkgoalean leaves, conifer wood, twigs, seed scales, male cones, and seeds have also been preliminarily described (Dzik et al. 2008a, b, Marynowski & Simoneit 2009, Wawrzyniak & Ziaja 2009, 2010, Wawrzyniak 2010a, b, c, d, e, 2011, Jarzynka & Wawrzyniak 2012). The macroflora from Lipie Śląskie-Lisowice is surprisingly advanced, with many taxa, mainly of cycads and conifers similar to younger Jurassic taxa (Harris 1932, 1935, 1937), but there are also some taxa, especially of conifers, with obvious evolutionary roots in older Triassic Silesian floras, especially at Krasiejów and Patoka. These facts and the richness of the well-preserved taxa place this flora among the most interesting Rhaetic floras of Europe (compare Harris 1926, Kelber & Hansch 1996, Kelber & van Konijnenburg-van Cittert 1997, Kelber 1998).

In the Tatra Mountains the Upper Triassic strata are developed in Keuper facies typical of the Germanic Basin. In Czerwone Żlebki (West Tatras, Czerwone Wierchy Massif), Raciborski (1890a, b, c) discovered and then described an interesting Rhaetic flora. The plant remains are not well-preserved and the cuticular details are not suitable for preparation. The occurrence of the endemic horsetail species *Equisetum chalubinskii* is this flora's most characteristic feature. Other horsetails, ferns and conifers are rare in this flora (Tab. 1). Later researchers (Reymanówna 1984, 1986, Michalík et al. 1976, 1988) attempted to find new plant remains at this locality but without success. In the M. Reymanówna collection (W. Szafer Institute of Botany, Polish Academy of Sciences) from Czerwone Żlebki there are no determinable plant remains. Nor has the flora of Czerwone Żlebki been revised since its original description. Geologists and palaeobotanists have long awaited a modern revision of this flora (Reymanówna 1984, Niedźwiedzki 2011, Lintnerová et al. 2013). Such a revision would improve our grasp of Tatra Upper Triassic palaeoecology, a key element of the complex geological history of the Tatra Mountains and the palaeogeographic connections between the Germanic Basin and the Alpine Tethys Ocean. Those relationships can be determined from the similarities or differences in the taxonomic composition of the flora. Important dinosaur ichnotaxa were discovered at this site and described recently (Niedźwiedzki 2005, 2008,



2011, Niedźwiedzki & Sulej 2007). That discovery gives a further reason for studying the flora of that place.

Some other plant macroremains have been found in the Upper Triassic strata of other Tatra localities but as a rule they are badly preserved (Raciborski 1892, Limanowski 1901, Uchman pers. comm. 2012) and have never been properly described or illustrated.

There are other plant fossil localities originally proposed as Rhaetian in age but these claims remain unconfirmed. Roemer (1866) identified a *Lepidopteris ottonis* specimen in Mierzęcina (Miedzeczo in Roemer's paper) near Kielce but as Barbacka (Reymanówna & Barbacka 1981, Barbacka 1991) showed this specimen belongs to an unidentified fern. Lilpop (in Raciborski 1927) noted the discovery of a new Keuper or Rhaetian flora in iron ore mines in Biała Góra near Blizyn (Holy Cross Mountains). This flora, however, was never illustrated or even preliminarily described. The above mentioned plant remains probably derive from Lower Jurassic strata widely outcropping in this area (Pieńkowski 2004, Pacyna 2013), but not from Keuper or Rhaetian strata, as Roemer (1866) and Lilpop (Lilpop in Raciborski 1927) originally proposed.

A macrofloristic zonation of the strata of the Triassic-Jurassic boundary in Europe was proposed by Nathorst (1910) and developed by Harris (1931, 1937). As currently understood, the occurrence of *Lepidopteris ottonis* marks the Rhaetian stage in nonmarine strata of the European Triassic. The known stratigraphic range of *Lepidopteris ottonis* coincides with the *Riccisporites tuberculatus* palynological zone. It is standard practice in Polish geology and palaeontology to refer the source strata to the Rhaetian when *Lepidopteris ottonis* remains are found in drill cores (Piwocki 1970, Barbacka 1980, 1991, Reymanówna & Barbacka 1981, Staneczko 2007, Ociepa et al. 2008). During palynological examination of strata from the *Corollina meyerana* zone (Norian), Marcinkiewicz and Orłowska-Zwolińska (1985, 1994) noted cuticle fragments which they determined to be cf. *Lepidopteris ottonis*. On this basis they suggested that the range of the *Lepidopteris ottonis* zone might overlap the *Corollina meyerana* and *Riccisporites tuberculatus* palynological zones, thus the Norian and Rhaetian. They had only small cuticle fragments, however; Norian macroremains of *Lepidopteris ottonis* have not

thus far been discovered anywhere. The genus *Lepidopteris* Schimper 1869 is known in the Germanic Basin from the beginning of the Upper Triassic (Schimper 1869, Gothan 1909a, b, c, Antevs 1914). *Lepidopteris stuttgardiensis* (Jäger 1827) Schimper 1869 and *Lepidopteris brevipinnata* Mägdefrau 1953 have been described from the Schilfsandstein strata – Lower-Middle Carnian (Jäger 1827, Schimper 1869, Gothan 1909b, Mägdefrau 1953). The cuticle structure of these species is not known. *Lepidopteris ottonis* is known from Rhaetian strata but no species of *Lepidopteris* has been described from the Norian. Because the cuticular differences among *Lepidopteris* species from the Upper Triassic of Europe cannot be compared at present, the question of extending the *Lepidopteris ottonis* zone to the Norian on the basis of isolated cuticle fragments cannot be settled. The Norian specimens of *Lepidopteris* may belong to a species undescribed as yet. The inter- and intraspecific variation of the cuticle in *Lepidopteris* is very poorly known. Some authors have suggested that *Lepidopteris stuttgariensis* and *L. ottonis* belong to the same species (Kelber & van Konijnenburg-van Cittert 1997, Kiritchkova 2006, 2008) but this has not been shown with certainty. The type specimen of *Lepidopteris ottonis*, described by Goepfert (1836) from Wieluń, has not been found in Polish collections (Barbacka 1980, 1991, Reymanówna & Barbacka 1981) and its whereabouts are not known, so the typification proposed by Kiritchkova (2006, 2008) is unwarranted.

## COMMENTS TO TABLES

Poland was partitioned by foreign powers three times in the second half of the 18<sup>th</sup> century, ultimately ending Poland's existence as an independent country for more than a century. Poland was split between Prussia, the Austro-Hungarian Empire and Russia. Mostly German-speaking scientists were working in Silesia during that time, and the official place names were in German. Below is a list of those localities in Silesia; their current names are paired with their pre-1945 German names. It was not possible to establish the current Polish names of some localities, especially when the papers used vernacular German names of localities in the Russian partition (e.g. in Goepfert 1846a). Table 1 includes comments on the

nomenclatural status of taxa and the status of specimens described from Poland. Synonyms are also given. The original published names of boreholes, horizons and age determinations are given in Table 1; Table 2 correlates the strata. References for the main localities are listed in Table 4.

Explanation of symbols and abbreviations in Table 1

\* – papers containing an illustration of a given taxon

^ – papers in which a given taxon was described as new to science based on specimens from Polish territory

MAIN LOCALITIES OF TRIASSIC GEOLOGICAL  
OUTCROPS WITH FOSSIL PLANTS PRESERVED  
IN UPPER SILESIA BEFORE 1945 (LOCALITY  
NAMES AFTER ROSPOND 1951)

**Polish – German**

Biadacz – Ludwigsdorf  
Bogdańczowice – Wüttendorf  
Byczyna – Pitschen  
Dobiercice – Wilmsdorf  
Gorzów Śląski – Landsberg  
Gosław – Goslau  
Helenowo – Hellewald  
Kluczbork – Kreuzburg, Kreu(t)zburg  
Krapkowice – Krappitz  
Kujanowice – Ober Kunzendorf  
Ligota – Ellguth  
Lubliniec – Lublinitz  
Maciejów – Matzdorf  
Nowa Wieś Oleska – Neudorf

Panoszów (=Ponoszów) – Ponoschau (=Ponoschau, Hegersfelde)  
Patoka – Klinkerwerk (=Patoka, Kreis Lublinitz)  
Sternalice – Sternalitz (=Ammern)  
Szubin – Schubin  
Tarnowskie Góry – Tarnowitz  
Woźniki – Woischnik  
Zakrzów – Sacrau  
Zborowskie – Zborowsky

**German – Polish**

Ellguth – Ligota  
Goslau – Gosław  
Hellewald – Helenowo  
Landsberg – Gorzów Śląski  
Lublinitz – Lubliniec  
Ludwigsdorf – Biadacz  
Klinkerwerk (=Patoka, Kreis Lublinitz) – Patoka  
Krappitz – Krapkowice  
Kreuzburg, Kreu(t)zburg – Kluczbork  
Matzdorf – Maciejów  
Neudorf – Nowa Wieś Oleska  
Ober Kunzendorf – Kujanowice  
Pitschen – Byczyna  
Ponoschau (=Ponoschau, Hegersfelde) – Panoszów, Ponoszów  
Sacrau – Zakrzów  
Schubin – Szubin  
Sternalitz (=Ammern) – Sternalice  
Tarnowitz – Tarnowskie Góry  
Wilmsdorf – Dobiercice  
Woischnik – Woźniki  
Wüttendorf – Bogdańczowice  
Zborowsky – Zborowskie

**Table 1.** Triassic plant macroremains described so far from Poland

Taxon as originally described, selected nomenclatural synonyms	Botanical affinity, taxon validity, taxonomical synonyms	Location	Horizon, age	References, comments
<b><i>Alethopteris insignis</i></b> (Lindley & Hutton 1833–1835) Goeppert 1836 (= <i>Pecopteris insignis</i> Lindley & Hutton 1833–1835, basonym)	Pterophytina, according to Harris (1961) <i>Pecopteris insignis</i> is synonym of <i>Cladophlebis denticulata</i> (Brongniart 1834) Schimper 1874; Goeppert's (1846a) specimen is small and hardly determinable	Dobiercice (Upper Silesia)	Wilmsdorfer Schichten; Upper Triassic, Rhaetian	Goeppert 1846a*, Schenk 1867, Roemer 1867
<b><i>Araucarioxylon</i></b> Kraus 1870 <b><i>Araucarioxylon</i></b> sp.	Coniferales	Poręba near Zawiercie (Upper Silesia)	Upper Triassic – Lower Jurassic, Rhaetico – Liassic	Brzyski & Heflik 1994*

Table 1. Continued

Taxon as originally described, selected nomenclatural synonyms	Botanical affinity, taxon validity, taxonomical synonyms	Location	Horizon, age	References, comments
<b>Brachyphyllum</b> Brongniart 1828 <b>Brachyphyllum</b> sp.	Coniferales	Patoka (Upper Silesia)	Jarkowo/Zbąszynek Beds; Upper Triassic, Norian	Barbacka et al. 2012
		Lipie Śląskie-Lisowice (Upper Silesia)	Wielichowo Beds; Upper Triassic, Rhaetian	Dzik et al. 2008a, b (as <i>Hirmeriella</i> twigs), Wawrzyniak & Ziąja 2010, Jarzynka & Wawrzyniak 2012
<b>Calamites</b> Brongniart 1828 <b>Calamites</b> sp.	Equisetales	Ratajów (north part of Holy Cross Mts.)	Upper Buntsandstein, Röt; Lower Triassic	Samsonowicz 1929 (record without description or illustration)
<b>Cladophlebis roeserti</b> (Presl in Sternberg 1838) Saporta 1872 (= <i>Asplenites roesertii</i> (Presl in Sternberg 1838) Schenk 1867)	Pterophytina, valid species	Dobiercice (Upper Silesia)	Wilmsdorfer Schichten; Upper Triassic, Rhaetian	Roemer 1867, 1870, Schenk 1867
		Czerwone Żlebki (Tatra Mountains)	Tomanová Formation; Upper Triassic, Rhaetian	Raciborski 1890a*, b, c, Reymanówna 1986
<b>Cladophlebis roeserti</b> forma <b>parvifolia</b> Raciborski 1890	Pterophytina, specimens need revision	Czerwone Żlebki (Tatra Mountains)	Tomanová Formation; Upper Triassic, Rhaetian	Raciborski 1890a* <sup>^</sup> , b, c
<b>Calamites lehmannianus</b> Goepfert 1846a (= <i>Neocalamites hoerensis</i> (Schimper 1869) Halle 1908 <i>sensu</i> Halle 1908) (= <i>Schizoneura hoerensis</i> (Hisinger 1840) Schimper 1869)	Equisetales, valid taxon, valid name – <b>Neocalamites lehmannianus</b> (Goepfert 1846a) Weber 1968	Dobiercice (Upper Silesia)	Wilmsdorfer Schichten; Upper Triassic, Rhaetian	Goepfert 1845, 1846a <sup>^</sup> *, Schenk 1867, Roemer 1867 (as <i>Equisetites arenaceus</i> (?)), 1870*, (older synonym of <i>Neocalamites hoerensis</i> (Schimper 1869) Halle 1908 <i>sensu</i> Halle 1908 according to Weber 1968)
<b>Camptopteris jurasica</b> Goepfert 1846a (= <i>Aspidium jurassicum</i> (Goepfert 1846a) Ettingshausen 1865)	Pterophytina, Dipteridaceae, synonym of <b>Clathropteris meniscoides</b> (Brongniart 1824) Brongniart 1828	Maciejów (Upper Silesia)	Wilmsdorfer Schichten; Upper Triassic, Rhaetian	Goepfert 1846a <sup>^</sup> , 1841–1846*, Roemer 1867, Schenk 1867 (most probably synonymous with <i>Clathropteris platyphylla</i> = <i>C. meniscoides</i> )
<b>Carpolithes cardiocarpoides</b> Goepfert 1846a	Gymnosperm seed	Dobiercice (Upper Silesia)	Wilmsdorfer Schichten; Upper Triassic, Rhaetian	Goepfert 1846a <sup>^</sup> *
<b>Clathropteris muensteriana</b> (Presl in Sternberg 1838) Schenk 1867 (= <i>Camptopteris münsteriana</i> Presl in Sternberg 1838)	Pterophytina, Dipteridaceae, synonym of <b>Clathropteris meniscoides</b> (Brongniart 1824) Brongniart 1828	Dobiercice, Maciejów (Upper Silesia)	Wilmsdorfer Schichten; Upper Triassic, Rhaetian	Schenk 1867, Orłowska-Zwolińska & Senkowiczowa (1970) erroneously listed <i>Clathropteris münsteri</i> (sic) based on Lilpop & Kostyniuk (1957); using this species name they ascribed it to Goepfert (1845, 1846a), which is incorrect
		Ligota near Woźniki (Upper Silesia)	Woźniki Limestone; Upper Triassic, Norian	Roemer 1870* (as <i>Clathropteris Münsteriana</i> )
<b>Clathropteris platyphylla</b> Goepfert 1846	Pterophytina, Dipteridaceae, synonym of <b>Clathropteris meniscoides</b> (Brongniart 1824) Brongniart 1828 (Harris 1931)	Czerwone Żlebki (Tatra Mountains)	Tomanová Formation; Upper Triassic, Rhaetian	Raciborski 1890a*, b, c, Harris 1931, Reymanówna 1986

Table 1. Continued

Taxon as originally described, selected nomenclatural synonyms	Botanical affinity, taxon validity, taxonomical synonyms	Location	Horizon, age	References, comments
<i>Coniopteris lobata</i> (Oldham & Morris 1863) Halle 1913 (= <i>Pecopteris lobata</i> Oldham & Morris 1863)	Pterophytina, probably valid species referable to genus <i>Coniopteris</i> (Harris 1961)	Czerwone Żlebki (Tatra Mountains)	Tomanová Formation; Upper Triassic, Rhaetian	Raciborski 1890a*, b, c (as <i>Pecopteris lobata</i> ), Reymanówna 1986
<i>Czekanowskia</i> Heer 1876 cf. <i>Czekanowskia</i> sp.	Czekanowskiales	Patoka (Upper Silesia)	Jarkowo/ Zbąszynek Beds; Upper Triassic, Norian	Barbacka et al. 2012
<i>Desmiophyllum</i> Lesquereux 1878 <i>Desmiophyllum</i> sp.	Coniferales	Krasiejów (Opole Silesia)	Drawno Beds?; Upper Triassic, Upper Carnian	Dzik & Sulej 2007*
<i>Dicranopteris roemeriana</i> Schenk 1867	Pterophytina, species needs revision	Dobiercice (Upper Silesia)	Wilmsdorfer Schichten; Upper Triassic, Rhaetian	Schenk 1867 <sup>^</sup> * (as <i>Dicranopteris Römeri</i> in text, as <i>Dicranopteris Römeriana</i> in plate caption), Roemer 1870 (as <i>Dicranopteris Roemeriana</i> )
<i>Dictyophyllum</i> aff. <i>dunkeri</i> Nathorst 1878	Pterophytina	Czerwone Żlebki (Tatra Mountains)	Tomanová Formation; Upper Triassic, Rhaetian	Raciborski 1890a*, b, c, Reymanówna 1986 (poorly preserved small leaf fragment)
<i>Equisetites arenaceus</i> (Jaeger 1827) Schenk 1864	Equisetales, valid taxon	Majków area (north part of Holy Cross Mts.)	Lower Keuper, Lettenkohle; Middle Triassic, Ladinian	Samsonowicz 1929 (as <i>Calamites arenaceus</i> , record without description or illustration)
<i>Equisetum chaluhiński</i> Raciborski 1890	Equisetales, valid taxon, proper taxon orthography <i>Equisetum chaluhiński</i> Raciborski 1890	Czerwone Żlebki (Tatra Mountains)	Tomanová Formation; Upper Triassic, Rhaetian	Raciborski 1890a*, b, c, Reymanówna 1986. Species very similar to <i>Equisetites muensteri</i> Sternberg 1833; should properly be referred to genus <i>Equisetites</i>
<i>Equisetum</i> an <i>bunburyanum</i> ? Zigno 1856	Equisetales, specimens need revision	Czerwone Żlebki (Tatra Mountains)	Tomanová Formation; Upper Triassic, Rhaetian	Raciborski 1890a*, b, c, Reymanówna 1986
<i>Equisetites</i> Sternberg 1833 <i>Equisetites</i> sp./ <i>Equisetum</i> sp.	Equisetales, specimens never illustrated or revised	Western Holy Cross Mts.	Lower Buntsandstein; Lower Triassic	Czarnocki 1925 (only record, without description or illustration)
		Western Holy Cross Mts.	Lower Keuper, Lettenkohle; Middle Triassic, Ladinian	Czarnocki 1925 (only record, without description or illustration)
		Nowa Wieś (Upper Silesia)	Woźniki Limestone; Upper Triassic, Norian	Różycki 1930, Znosko 1955 (only record, without description or illustration)
		Kołaczkowice near Rawicz (Lower Silesia)	Wielichowo Beds; Upper Triassic, Rhaetian	Piwocki 1970 (only record, without description or illustration)
<i>Ginkgoites acosmia</i> Harris 1935	Ginkgoales, valid taxon	Gradzanowo 3 borehole (Central Poland)	Upper Triassic, Rhaetian	Barbacka & Wcisło-Luraniec 2002*, 2003*
<i>Glossopteridium czarnockii</i> Bocheński 1957	<i>Incertae sedis</i> , originally stated as <i>Glossopteridales</i> , specimen probably lost	Radoszyce 3 borehole (Holy Cross Mts.)	Middle Buntsandstein; Lower Triassic	Bocheński 1957 <sup>^</sup> * (original proposed species name <i>Glossopteridium J. Czarnockii</i> )
<i>Knorripteris mariana</i> (Michael 1895) Potonié 1897 (= <i>Knorria mariana</i> Michael 1895)	Pterophytina – fern stem, older synonym of <i>Adelophyton jutieri</i> Renault 1900 according to Hörich (1910)	Krapkowice (Upper Silesia)	Lower Muschelkalk, Chorzów beds; Middle Triassic	Michael 1895b <sup>^</sup> *, Potonié 1897*, Hörich 1910* (description of specimen anatomy; Hörich questioned age determination of specimen by Michael)

Table 1. Continued

Taxon as originally described, selected nomenclatural synonyms	Botanical affinity, taxon validity, taxonomical synonyms	Location	Horizon, age	References, comments
<b><i>Lepidopteris ottonis</i></b> (Goepfert 1836) Schimper 1869 (= <i>Alethopteris ottonis</i> Goepfert 1836, basonym) (= <i>Pecopteris ottonis</i> (Goepfert 1836) Goepfert 1846a) (= <i>Aspidites ottonis</i> Schenk in Roemer 1867) (= <i>Asplenites ottonis</i> (Goepfert 1836) Schenk 1867)	Pteridospermopsida, Peltaspermales, valid taxon	Biadacz, Dobiercice, Gosław, Maciejów (Upper Silesia)	Wilmsdorfer Schichten/ Gorzów Beds; Upper, Triassic, Rhaetian	Goepfert 1846a*, Schenk 1867, Roemer 1867, 1870*, Gothan 1909a*, Harris 1932, Marcinkiewicz 1969, Reymanówna & Barbacka 1981*, Barbacka 1991*
		Wieluń (Upper Silesia)	Upper Triassic, Rhaetian	Goepfert 1836 <sup>^*</sup>
		Kończakowice borehole near Rawicz (Lower Silesia)	Wielichowo Beds; Upper Triassic, Rhaetian	Piwocki 1970*
		Gostyń 46 G borehole (Central Poland)	Zbąszynek/Jarkowo Beds; Upper Triassic, Rhaetian <i>sensu polonico</i> , Norian?	Marcinkiewicz & Orłowska-Zwolińska 1985, 1994 (only isolated cuticles determined as cf. <i>Lepidopteris ottonis</i> )
		Gradzanowo 1 borehole (Central Poland)	Wielichowo Beds; Upper Triassic, Rhaetian	Barbacka 1980, Barbacka 1991*
		Gradzanowo 3 borehole (Central Poland)	Wielichowo Beds; Upper Triassic, Rhaetian	Marcinkiewicz & Orłowska-Zwolińska 1994 (only isolated cuticles determined as cf. <i>Lepidopteris ottonis</i> )
		Chabowo 2 borehole (Western Pomerania)	Upper Triassic, Rhaetian	Ociepa et al. 2008
		Lipie Śląskie-Lisowice, (Upper Silesia)	Upper Triassic, Rhaetian	Staneczko 2007*, Wawrzyniak & Ziaja 2009 (only isolated cuticles), Wawrzyniak 2010b
<b><i>Neocalamites</i></b> Halle 1908 <b><i>Neocalamites</i></b> sp.	Equisetales	Gacki 1 borehole (Holy Cross Mts.)	Lower Keuper, Lettenkohle; Middle Triassic, Ladinian	Pawłowska 1979*
		Studzianna borehole (Holy Cross Mts.)	Lower Keuper, Lettenkohle; Middle Triassic, Ladinian	Barbacka et al. 2009, Barbacka et al. in prep. (as <i>Neocalamites merianii</i> (Brongniart 1828) Halle 1908)
<b><i>Neuropteris</i></b> sp. conf. <b><i>N. remota</i></b> Presl in Sternberg 1838	Pterophytina, valid name <i>Cladophlebis remota</i> (Presl in Sternberg 1838) Zeiller 1911	Ligota near Woźniki (Upper Silesia)	Woźniki Limestone; Upper Triassic, Norian	Roemer 1870*
<b><i>Pachylepis quinques</i></b> (Linck 1951) Kräusel 1952 (= <i>Voltzia? quinques</i> Linck 1951)	Coniferales, valid species	Krasiejów (Opole Silesia)	Drawno Beds?; Upper Triassic, Upper Carnian	Dzik & Sulej 2007*
<b><i>Pachylepis</i></b> Kräusel 1952 <b><i>Pachylepis</i></b> sp.	Coniferales	Patoka (Upper Silesia)	Jarkowo/Zbąszynek Beds; Upper Triassic, Norian	Barbacka et al. 2012
<b><i>Pagiophyllum</i></b> sp.	Coniferales	Lipie Śląskie-Lisowice (Upper Silesia)	Wielichowo Beds; Upper Triassic, Rhaetian	Wawrzyniak & Ziaja 2010
<b><i>Palaeohepatica roemeri</i></b> Raciborski 1892 (= <i>Hepaticites roemeri</i> (Raciborski 1892) Oostendorp 1987)	Hepaticopsida, species never illustrated or revised. Type specimen found by M. Reymanówna in Wrocław University collection (Wcisło-Luraniec 1984).	Ligota near Woźniki (Upper Silesia)	Woźniki Limestone; Upper Triassic, Norian	Raciborski 1892, 1893 (original Roemer label identification – <i>Thaumatopteris Münsteri</i> β. <i>longissima</i> ), Wcisło-Luraniec 1984, Oostendorp 1987 (she referred

Table 1. Continued

Taxon as originally described, selected nomenclatural synonyms	Botanical affinity, taxon validity, taxonomical synonyms	Location	Horizon, age	References, comments
	Harris (1942) referred type species of genus <i>Paleohepatica</i> Raciborski 1889 – <i>P. rostafinskii</i> Raciborski 1889 to genus <i>Thallites</i> Walton 1925 as <i>Thallites rostafinskii</i> (Raciborski 1889) Harris 1942			species <i>Palaeohepatica roemeri</i> to genus <i>Hepaticites</i> and provided its diagnosis in English based on Raciborski's description in Polish (1892)
<b><i>Palissya braunii</i></b> Endlicher 1847	Coniferales, valid species	Czerwone Żlebki (Tatra Mountains)	Tomanová Formation; Upper Triassic, Rhaetian	Raciborski 1890a*, b, c, Reymanówna 1986
<b><i>Pecopteris</i></b> (Brongniart 1822) Sternberg 1825 <b><i>Pecopteris</i></b> sp.?	Pterophytina or Pteridospermopsida, genus erroneously identified	Gacki 4 borehole (South-eastern Holy Cross Mts.)	Muschelkalk, transitional beds; Middle Triassic, Ladinian	Pawłowska 1979*
<b><i>Peltaspermum rotula</i></b> Harris 1932	Pteridospermopsida, Peltaspermales, valid taxon	Dobiercice (Upper Silesia)	Gorzów Beds; Upper Triassic, Rhaetian	Barbacka 1991* (cupulate disc and isolated seeds)
<b><i>Pinites jurassicus</i></b> Goepfert 1846a (= <i>Peuce jurassica</i> (Goepfert 1846a) Endlicher 1847)	Coniferales, probably valid species, specimens need revision, according to Seward (1919) could be referable to genus <i>Cedroxylon</i>	Kamienica Polska (in original paper misspelt as Kaminika Polska) (north part of Upper Silesia)	Upper Triassic (Rhaetian) or (Middle? – Oolite) Jurassic	Goepfert 1846a <sup>^</sup> *, Mercklin 1852, 1855, Schenk 1867, Schimper 1870–1872, Seward 1919, Jongmans & Dijkstra 1973
<b><i>Pinites pertinax</i></b> Goepfert 1846a (= <i>Peuce pertinax</i> (Goepfert 1846a) Endlicher 1847) (= <i>Cedroxylon pertinax</i> (Goepfert 1846a) Kraus in Schimper 1870–1872)	Coniferales, probably valid species, specimen needs revision	Sumpen, Gorzów Śląski (?) (north part of Upper Silesia)	Upper Triassic (Rhaetian) or (Middle?) Jurassic	Goepfert 1846a <sup>^</sup> *, Endlicher 1847, Mercklin 1855, Schenk 1867, Schimper 1870–1872, Seward 1919, Jongmans & Dijkstra 1973
<b><i>Pinites</i></b> Lindley & Hutton 1831 <b><i>Pinites</i></b> sp.	Coniferales	Lofkowitz, Sumpen (?) (Upper Silesia)	Keuper; Upper Triassic	Roemer 1867, 1870
<b><i>Pleuromeia</i></b> cf. <b><i>sternbergi</i></b> (Münster 1839) Corda 1852	Isoetales, specimens never illustrated or revised	North-west part of Holy Cross Mts.	Upper Middle Buntsandstein; Lower Triassic	Czarnocki 1931 (only record without description)
<b><i>Pleuromeia</i></b> Corda 1852 <b>?<i>Pleuromeia</i></b>	Isoetales	Otyń IG-1 borehole (Fore-Sudetic Monocline)	Supra-Oolitic Beds, Middle Buntsandstein; Lower Triassic	Fuglewicz 1980b* (strobile with megaspores <i>Pusulospirites</i> Fuglewicz 1973 <i>in situ</i> )
<b><i>Pseudohirmerella</i></b> Arndt 2002 <b><i>Pseudohirmerella</i></b> sp. n.	Coniferales	Krasiejów (Opole Silesia)	Drawno Beds?; Upper Triassic, Upper Carnian	Dzik & Sulej 2007*
<b><i>Pterophyllum braunianum</i></b> Goepfert 1844	Bennettitales	Gosław (Upper Silesia)	Wilmsdorfer Schichten, Keuper; Upper Triassic, Rhaetian	Schenk 1867, Roemer 1870* (as synonym of <i>Pterophyllum oeynhausianum</i> Goepfert 1844)
<b><i>Pterophyllum carnallianum</i></b> Goepfert 1844	Bennettitales	Biadacz, Dobiercice, Gosław (Upper Silesia)	Wilmsdorfer Schichten, Keuper; Upper Triassic, Rhaetian	Goepfert 1844 <sup>^</sup> *, 1845, 1846a, Schenk 1867*, Roemer 1867, 1870* (as synonym of <i>Pterophyllum propinquum</i> Goepfert 1844)
<b><i>Pterophyllum compressum</i></b> Lundblad 1950	Bennettitales	Extra-Carpathian area of Poland	Wielichowo beds; Upper Triassic, Rhaetian	Marcinkiewicz 1969 (only isolated cuticules)

Table 1. Continued

Taxon as originally described, selected nomenclatural synonyms	Botanical affinity, taxon validity, taxonomical synonyms	Location	Horizon, age	References, comments
<i>Pterophyllum</i> cf. <i>jaegeri</i> Brongniart 1828	Bennettitales	Gacki 3 borehole (South-eastern Holy Cross Mts.)	Lower Keuper, Lettenkohle; Middle Triassic, Ladinian	Pawłowska 1979*
<i>Pterophyllum muensteri</i> (Presl in Sternberg 1838) Goeppert 1844 (= <i>Nilssonia muensteri</i> (Presl in Sternberg 1838) Schimper in Zitel 1880)	Cycadales, synonym of <i>Nilsonia acuminata</i> (Presl in Sternberg 1838) Goeppert 1844	Dobiercice (Upper Silesia)	Wilmsdorfer Schichten; Upper Triassic, Rhaetian	Schenk 1867, Roemer 1870, Raciborski 1892 (Raciborski referred this specimen to <i>Ptilozamites nilsonii</i> )
<i>Pterophyllum oeynhausianum</i> Goeppert 1844	Bennettitales	Biadacz (Upper Silesia)	Wilmsdorfer Schichten; Upper Triassic, Rhaetian	Goeppert 1844 <sup>^*</sup> , 1845, 1846a, Schenk 1867, Roemer 1867, 1870
<i>Pterophyllum propinquum</i> Goeppert 1844	Bennettitales	Biadacz (Upper Silesia)	Wilmsdorfer Schichten; Upper Triassic, Rhaetian	Goeppert 1844 <sup>^*</sup> , 1845, 1846a, Schenk 1867*, Roemer 186
<i>Pterophyllum</i> Brongniart 1828 <i>Pterophyllum</i> sp.	Bennettitales	Krasiejów (Opole Silesia)	Drawno Beds?; Upper Triassic, Upper Carnian	Dzik & Sulej 2007
		Nowa Wieś (Upper Silesia)	Woźniki Limestone; Upper Triassic, Norian	Znosko 1955 (only record, without description or illustration)
<i>Schizoneura hoerensis</i> (Hisinger 1840) Schimper 1869	Equisetales, synonym of <i>Neocalamites lehmannianus</i> (Goeppert 1846a) Weber 1968	Czerwone Żlebki (Tatra Mountains)	Tomanová Formation; Upper Triassic, Rhaetian	Raciborski 1890a*, b, c, Reymanówna 1986
<i>Sphaerococcites blandowskianus</i> Goeppert 1846b	<i>Nomen dubium</i> , originally stated as alga, most probably trace fossil	Tarnowskie Góry (Upper Silesia)	Muschelkalk; Middle Triassic	Goeppert 1845, 1846b <sup>^*</sup> , Eck 1865
<i>Stachyotaxus septentrionalis</i> (Agardh 1823) Nathorst 1886	Coniferales, illustrated by Dzik et al. (2008a), remains most probably belong to genus <i>Elatocladus</i>	Lipie Śląskie-Lisowice (Upper Silesia)	Wielichowo Beds; Upper Triassic, Rhaetian	Dzik et al. 2008a*, b, Świło et al. 2014
<i>Taeniopteris gigantea</i> Schenk 1867	Cycadales	Dobiercice (Upper Silesia)	Wilmsdorfer Schichten; Upper Triassic, Rhaetian	Schenk 1867 <sup>^*</sup> , Roemer 1867, 1870*
<i>Voltzia krappitzensis</i> Kunisch 1886	Coniferales, species needs revision	Krapkowice (Upper Silesia)	Muschelkalk; Middle Triassic, Anisian	Kunisch 1886 <sup>^*</sup>
<i>Voltzia</i> Brongniart 1828 <i>Voltzia</i> sp.	Coniferales, specimens never illustrated or revised	North-west part of Holy Cross Mts.	Upper Middle Buntsandstein; Lower Triassic	Czarnocki 1931 (only record, without description)
<i>Widdringtonites</i> Endlicher 1847 <i>Widdringtonites</i> sp.	Coniferales	Czerwone Żlebki (Tatra Mountains)	Tomanová Formation; Upper Triassic, Rhaetian	Raciborski 1890a*, b, c, Reymanówna 1986
<i>Xylomites irregularis</i> Goeppert 1846a	Originally stated as epiphyllous fungi on leaves	Dobiercice (Upper Silesia)	Wilmsdorfer Schichten; Upper Triassic, Rhaetian	Goeppert 1846a <sup>^*</sup> , Roemer 1870 (as fungi on <i>Pterophyllum carnallianum</i> leaf fragments)

**Table 2.** Proposed approximate zonation and correlation of Triassic floras of Poland

Age	Germanic Triassic division (Kozur & Bachmann 2008, Franz 2009, Kozur & Weems 2010)	Polish Triassic division (Orłowska-Zwolińska 1985, Mader 1997, Fijałkowska-Mader 1999)	German/French floral assemblages (Dobruskina 1988, 1994, Kelber 1998)	Polish macrofloral assemblages and assemblage zones (here proposed)
Rhaetian	Upper Keuper/ Rhätkeuper/ Exter Formation	Upper Rhaetian sensu polonico/ Wielichowo Beds and perhaps Upper (most) Zbąszynek Beds (?)	Rhät-Flora/ <i>Lepidopteris ottonis</i> zone	<i>Lepidopteris ottonis</i> zone
Norian	Middle Keuper/ Steinmergelkeuper/ Arnstadt Formation	Lower Rhaetian sensu polonico/Zbąszynek Beds, Jarkowo Beds (Grabowa Formation), Drawno Beds	Stubensandstein/ Burgsandstein Flora	<i>Brachyphyllum</i> zone
Carnian	Middle Keuper/ Upper Gipskeuper/ Weser Formation	Upper Keuper sensu polonico/Upper Gipskeuper	Coburger Sandstein Flora	(Younger) <i>Voltzia</i> zone
	Middle Keuper/ Schilfsandstein/ Stuttgart Formation	Upper Keuper sensu polonico/Schilfsandstein	Schilfsandstein Flora	Lack of macroscopic plant remains in Poland
	Middle Keuper/ Lower Gipskeuper/ Grabfeld Formation	Upper Keuper sensu polonico/Lower Gipskeuper and Grenz dolomit	Gipskeuper Flora	Lack of macroscopic plant remains in Poland
Upper Ladinian	Lower Keuper/ Lettenkeuper/ Erfurt Formation	Lower Keuper/ Sulechów Beds	Unterkeuper (Lettenkohle) Flora	Equisetales-flora
Middle and Lower Ladinian	Upper Muschelkalk	Upper Muschelkalk	Lack of macroscopic plant remains in Germanic Basin	Lack of macroscopic plant remains in Poland
Upper Anisian	Middle Muschelkalk	Middle Muschelkalk		
	Lower Muschelkalk	Lower Muschelkalk		
Lower Anisian/ Upper Buntsandstein- Röt	Upper Buntsandstein-Röt	Upper Buntsandstein-Röt	Grés à <i>Voltzia</i> flora	(Older) <i>Voltzia</i> -flora
Scytian/ Lower and Middle Buntsandstein	Middle Buntsandstein	Middle Buntsandstein	<i>Pleuromeia</i> -flora	<i>Pleuromeia</i> -flora
	Lower Buntsandstein	Lower Buntsandstein		

## CONCLUSIONS AND FUTURE PROSPECTS

The Triassic floras of the Northern Hemisphere are rare and poorly known. Each new site with plant macroremains fills a gap in our knowledge of plant evolution in this period (Kustatscher & van Konijnenburg-van Cittert 2005, Roghi et al. 2006, van Konijnenburg-van Cittert et al. 2006, Kustatscher & van Konijnenburg-van Cittert 2008, Kustatscher et al. 2012). Good, complete descriptions of the floras of Upper Triassic localities in Poland will help researchers study Triassic ecosystems in Poland and worldwide, and will be useful in analysing the evolution of floras in the Triassic. Some taxa found in Poland may have large implications for reconstruction of the gymnosperm phylogeny, particularly for conifers.

These floras will also fill in the palaeoecological and palaeoenvironmental background of the vertebrates, especially the dinosaurs at Polish localities. A better understanding of the dinosaurs' environment will help expand our knowledge about their biology and explain their evolutionary success. Such interdisciplinary dinosaur research has been very intense lately, particularly in North America (Sampson 2012), but has not included the dinosaurs of Poland; they have yet to take their rightful place in the European Triassic.

The very few descriptions of the Triassic floras of Poland come mainly from the 19<sup>th</sup> century. They require modern revisions incorporating current nomenclature and meeting current standards of fossil description. Expert investigations begun in the 19<sup>th</sup> century were not continued in the 20<sup>th</sup> century, except for a very few



Table 2. Continued

Palynological zones (spores and pollen grains) in Poland (Orłowska-Zwolińska 1985)	Megaspore zonation in Poland (Marcinkiewicz 1978, 1992)	Most typical plant macrofossil taxa in Poland	Localities in Poland	Evolutionary events in Polish macroflora
<i>Riccisporites tuberculatus</i>	<i>Trileites pinguis</i>	<i>Lepidopteris ottonis</i> , <i>Neocalamites lehmannianus</i> , <i>Pterophyllum</i> spp.	Kluczbork area (Goepert's sideritic nodules flora) Lipie Śląskie-Lisowice, Czerwone Żlebki	During stage rise of floral biodiversity, growing similarity to Lower Jurassic floras
<i>Corollina meyeriana</i>		<i>Brachyphyllum</i> , <i>Pterophyllum</i> , <i>Equisetites</i>	Poręba, Patoka, Woźniki Limestone (Ligota, Myszaków, Poręba), Marciszów-Zawiercie	Appearance of modern conifer families ( <i>Brachyphyllum</i> leaves appearing)
Hiatus in pollen zones in Poland, upper <i>Camerosporites secatus</i> zone in German part of Germanic Basin		<i>Voltzia</i> , <i>Glyptolepis</i> , <i>Desmiophyllum</i> , <i>Pseudohirmerella</i> , <i>Pachylepis</i> , <i>Sphenopteris schoenleiniana</i>	Krasiejów, Woźniki claypit	Decrease of diversity and extinction of Voltziales
<i>Aulisporites astigosus</i>	<i>Narkisporites harrisi</i>			
<i>Porcelispora longdonesis</i>				
<i>Heliosaccus dimorphus</i>	<i>Dijkstraisorites beutleri</i>	<i>Neocalamites merianii</i>	Holy Cross Mountains	Floras very rare and impoverished in Poland
Hiatus				
<i>Tsugaepollenites oriens</i>				
<i>Perotrilites minor</i>				
<i>Voltziacaesperites heteromorphia</i>	<i>Trileites validus</i>	<i>Voltzia</i> , ferns and equisetalean remains	Krapkowice, Pałęgi	Floras very rare and impoverished in Poland
<i>Densoisporites nejburgii</i>	Hiatus	<i>Pleuromeia</i> and equisetalean remains only	Holy Cross Mountains	Floras very rare and impoverished in Poland
	<i>Talchirella daciae</i>			
	<i>Trileites polonicus</i>			
	Hiatus			
<i>Lundbladispora obsoleta-Protohaploxypinus pantii</i>	<i>Otynisporites eotriassicus</i>			

papers and excerpts in publications on stratigraphy. There is a good record of Polish Lower and Middle Triassic floras in the palynological data but not in data on macroremains. Upper Triassic macrofloras are better known but their descriptions are outdated. Most determinations of macroremains from the Polish Triassic should be revised. The plants described by Goepert (1836, 1844, 1845, 1846a) were revised by Schenk alone (1867). Later only *Lepidopteris ottonis* was redescribed (Barbacka 1991). As is clear from Schenk's (1867) revision, some species Goepert described are junior synonyms of previously described species, some new species were described from small, badly preserved remains, and species in some genera are oversplit (e.g. *Pterophyllum*).

Palynological research on Triassic strata in Poland intensified in the 1970s and produced

a useful palynological biostratigraphic scheme for the Polish Triassic (Orłowska-Zwolińska 1985). New palynological data gathered from Poland fits this scheme perfectly (Fijałkowska-Mader 1999). Orłowska-Zwolińska's scheme is congruent with Western European palynological biostratigraphy (Fijałkowska-Mader 1999, Cirilli 2010, Kürschner & Hengreen 2010). Correlating dispersed spores and pollen grains with their parent plants in Triassic floras presents great difficulties not just in Poland but worldwide. The true botanical affiliation of even index taxa such as *Riccisporites tuberculatus* is disputed (Mader et al. 2012). This presents problems, as broad palaeoecological conclusions are based on this palynological data (e.g. Dzik et al. 2008b). The newly discovered floras, especially those in Krasiejów, Patoka and Lipie Śląskie-Lisowice, contain

**Table 3.** Complete taxonomical composition of Upper Triassic macrofloral assemblage zones here proposed for main localities

Age	Assemblage zones (here proposed)	Formation/ Beds	Locality	Floral assemblage composition
Rhaetian	<i>Lepidopteris ottonis</i> assemblage zone	Wilmsdorfer Schichten	Kluczbork area (Goepfert's sideritic nodule flora) Biadacz, Dobiercice, Gosław, Maciejów (Upper Silesia)	<i>Neocalamites lehmannianus</i> , <i>Alethopteris insignis</i> , <i>Cladophlebis roesserti</i> , <i>Clathropteris meniscoides</i> (= <i>Camptopteris jurassica</i> = <i>Clathropteris muensteriana</i> ), <i>Carpolithes cardiocarpoides</i> , <i>Dicranopteris roemeriana</i> , <i>Lepidopteris ottonis</i> , <i>Peltaspermum rotula</i> , <i>Pterophyllum braunianum</i> , <i>Pterophyllum carnallianum</i> , <i>Pterophyllum muensteri</i> , <i>Pterophyllum oeynhausianum</i> , <i>Pterophyllum propinquum</i> , <i>Taeniopteris gigantea</i> , <i>Xylomites irregularis</i>
		Wielichowo Beds	Lipie Śląskie-Lisowice (Upper Silesia)	<i>Lepidopteris ottonis</i> , <i>Brachyphyllum</i> sp., <i>Pagiophyllum</i> sp., <i>Cheirolepidiaceae</i>
		Tomanová Formation	Czerwone Żlebki (Tatra Mountains)	<i>Neocalamites lehmannianus</i> , <i>Equisetum chalubinskii</i> , <i>Equisetum an bunburyanum</i> , <i>Cladophlebis roesserti</i> , <i>Cladophlebis roesserti</i> forma <i>parvifolia</i> , <i>Clathropteris meniscoides</i> (= <i>Clathropteris platyphylla</i> ), <i>Dictyophyllum</i> aff. <i>dunkeri</i> , <i>Pecopteris lobata</i> , <i>Palissyia braunii</i> , <i>Widringtonites</i> sp.
Norian	<i>Brachyphyllum</i> assemblage zone	Woźniki Limestone	Woźniki area (Ligota, Myszków, Nowa Wieś, Poręba) (Upper Silesia)	<i>Clathropteris meniscoides</i> (= <i>Clathropteris muensteriana</i> ), <i>Neuropteris</i> sp. conf. <i>N. remota</i> , <i>Palaeohepatica roemeri</i> , <i>Pterophyllum</i> sp., <i>Brachyphyllum</i> sp., <i>Equisetites muensteri</i>
Carnian	<i>Voltzia</i> assemblage zone	Upper Gipskeuper	Krasiejów (Opole Silesia)	<i>Sphenopteris schoenleiniana</i> , <i>Pterophyllum</i> sp., <i>Desmiophyllum</i> spp., <i>Glyptolepis keuperiana</i> , <i>Pachylepis quinques</i> , <i>Pseudohirmerella</i> sp., <i>Voltzia</i> spp.

many new taxa yet to be described, and some of them could have great evolutionary importance. A complete description of the Woźniki limestone flora, which has been on record since the end of the 19<sup>th</sup> century, is urgently needed.

The Triassic is an exceptionally interesting period as it witnessed rapid evolution of conifers. The oldest representatives of modern conifer families occurred in the Upper Triassic (Rothwell et al. 2012). The stages of transformation from the primitive *Votziales* to evolutionarily advanced families of modern conifers in the Triassic are insufficiently documented. The newly discovered Silesian sites (Krasiejów, Patoka, Lipie Śląskie-Lisowice), containing Upper Triassic floras rich in conifer taxa, can shed new light on this poorly known stage of conifer evolution. The flora from Krasiejów contains relatively primitive conifers: they fall into the genus *Voltzia* based on twig morphology and into the genus *Glyptolepis* based on seed scales. Further research is needed to identify the Krasiejów conifers to species level based upon twig, seed scale, and pollen cone morphology, because these specimens represent genera and species new to science. The Krasiejów conifers hold clues to the evolution of these plants in the early Upper Triassic. In the flora of Patoka, which is slightly younger geologically, relatively advanced *Brachyphyllum*-type shoots characteristic of Jurassic or

Cretaceous conifers are accompanied by a new type of seed scale which may have evolved from primitive *Voltzia*-type scales. This is a plant of evolutionary significance for modern conifers. Preliminary work indicates that it will be possible to fully reconstruct a conifer from Patoka with trunks, twigs, male and female cones – and pollen grains. Completely reconstructed extinct plants can be used in developing phylogenetic hypotheses. The discovery of a plant with primitive female cones accompanied by evolutionarily advanced shoots at the Patoka site may form the basis for erecting a new family of conifers and revising current views on the taxonomy of this group of plants. This find could also have far-reaching implications for the taxonomy of conifers.

The task of correlating Triassic floras worldwide is hampered by stratigraphical problems and regional differences in floral composition. Some approximate correlations are possible regionally on the continental scale, however. Such biostratigraphical and lithostratigraphical correlations of the Polish Triassic floras from the main localities with other well-known European Triassic floras are provided here (Tab. 2), and new macrofloral assemblages for the Lower and Middle Triassic and macrofloral assemblage zones for the Upper Triassic in Poland (Tabs 2 and 3), corresponding to Orłowska-Zwolińska's palynological zonation

**Table 4.** Main Polish Triassic macrofossil and selected microfossil plant localities with basic palaeobotanical, palaeozoological and geological references

Locality of fossil plant remains	References
Chabowo 2 borehole	Ociepa et al. 2008, Barbacka et al. in prep.
Czerwone Żlebki	Raciborski 1890a, b, c, Michalík et al. 1976, 1988, Reymanówna 1984, 1986, Niedźwiedzki 2005, 2008, 2011, Niedźwiedzki & Sulej 2007
Gacki 1, 3 and 4 boreholes	Pawłowska 1979
Gorzów Śląski area	Goepfert 1846a, Endlicher 1847, Mercklin 1855, Roemer 1867, 1870, Schenk 1867, Schimper 1870–1872, Seward 1919, Znosko 1955, Jongmans & Dijkstra 1973
Gostyń 46 G borehole	Marcinkiewicz & Orłowska-Zwolińska 1985, 1994
Gradzanowo 1 and 3 boreholes	Barbacka 1980, Barbacka 1991, Marcinkiewicz & Orłowska-Zwolińska 1994, Barbacka & Wcisło-Luraniec 2002, 2003
Holy Cross Mts.	Samsonowicz 1924, 1929, Czarnocki 1925, 1931, Fijałkowska 1989, 1992a, b, 1994a, b, Rdzanek 1982, Fijałkowska-Mader 1999
Kluczbork area (Biadacz, Dobiercice, Gosław, Maciejów)	Goepfert 1836, 1841–1846, 1844, 1845, 1846a, b, Roemer 1867, 1870, Schenk 1867, Michael 1893, 1894, 1895a, Gallinek 1894, Gothan 1909a, Znosko 1955, Orłowska-Zwolińska & Senkowiczowa 1970, Barbacka 1980, 1991, Reymanówna & Barbacka 1981, Mader 1997, Kiritchkova 2006, 2008
Kamienica Polska	Goepfert 1846a, Mercklin 1852, 1855, Schenk 1867, Schimper 1870–1872, Seward 1919, Jongmans & Dijkstra 1973
Kamień Pomorski IG 1 borehole	Pieńkowski 2004, Pieńkowski et al. 2012
Kołaczkowice near Rawicz	Piwocki 1970
Krapkowice	Kunisch 1886, Michael 1895b, Potonié 1897, Hörich 1910, Rieppel & Hagdorn 1997, Rieppel 2000
Krasiejów	Dzik et al. 2000, Dzik 2001, 2002, 2003a, b, 2008, Sulej 2002, 2003, 2004, 2005, 2007, 2010, Zatoń & Piechota 2003, Dzik & Sulej 2004, 2007, Olempska 2004, 2011, Sulej & Majer 2005, Szulc 2005, Zatoń et al. 2005, Barycka 2007, Konietzko-Meier & Wawro 2007, Lucas et al. 2007, Szulc & Becker 2007, Gruszka & Zielinski 2008, Brusatte et al. 2009, Fostowicz-Frelik & Sulej 2009, Mazurek & Słowiak 2009, Kozur & Weems 2010, Piechowski & Dzik 2010, Racki 2010, Skawina 2010, 2013, Sues & Fraser 2010, Skawina & Dzik 2011, Bodzioch & Kowal-Linka 2012, Desojo et al. 2013, Konietzko-Meier & Klein 2013, Konietzko-Meier & Sander 2013, Konietzko-Meier et al. 2013
Lipie Śląskie-Lisowice	Fuglewicz & Śniezek 1980, Marcinkiewicz 1981, Staneczko 2007, Dzik et al. 2008a, b, Niedźwiedzki & Sulej 2008, Ociepa et al. 2008, Marynowski & Simoneit 2009, Gorzelak et al. 2010, Wawrzyniak & Ziaja 2009, 2010, Wawrzyniak 2010a, b, c, d, Racki 2010, Niedźwiedzki et al. 2011, 2012, Skawina & Dzik 2011, Świło et al. 2014
Majków	Samsonowicz 1929
Mechowo IG I borehole	Marcinkiewicz 1962
Otyń IG-1 borehole	Fuglewicz 1980b
Pałęgi	Kuleta et al. 2006, Żyła et al. 2013
Patoka	Znosko 1955, Barbacka et al. 2012
Poręba	Znosko 1955, Brzyski & Heflik 1994, Sulej et al. 2012
Radoszyce 3 borehole	Bocheński 1957
Ratajów	Samsonowicz 1929
Studzianna	Karaszewski 1962, Reymanówna 1986, Barbacka et al. 2009, Barbacka et al. in prep.
Wieluń	Goepfert 1836, Znosko 1955
Woźniki Limestone (Ligota, Myszków, Nowa Wieś, Poręba, Woźniki)	Roemer 1870, Raciborski 1892, 1893, Różycki 1930, Znosko 1955, Wcisło-Luraniec 1984, Reymanówna 1986, Szulc et al. 2006, Szulc & Becker 2007

(Orłowska-Zwolińska 1985), are proposed. The Lower and Middle Triassic floras are too poor in taxa for macrofloral assemblage zones to be defined. Only the Upper Triassic strata have a plant macrofossil record rich enough for assemblage zones to be delineated. Three macrofossil assemblage zones are proposed and defined here for the Polish Upper Triassic:

The **Voltzia assemblage zone**, in which *Voltzia* (sensu lato) leaf species predominate,

with their seed scales *Glyptolepis*. *Pseudohirmerella*, *Pachylepis*, and a new genus. Coniferous foliage incertae sedis *Desmiophyllum*, is also present. *Pterophyllum* leaves are very rare. This zone comprises the Upper Gipskeuper strata and corresponds to the Carnian. In the palynological zonation of Poland there is a hiatus, but it corresponds to the upper *Camerosporites secatus* zone in other parts of Europe (Cirilli 2010, Kürschner & Hengreen 2010).

The *Brachyphyllum* assemblage zone is dominated by conifers with *Brachyphyllum*-type foliage, probably signalling the emergence of modern conifer families. Whole-plant reconstructions of those conifers are possible, based on new findings (wood, seed scales with ovules, male cones with pollen in situ, shoots). Other plant taxa are very rare; single fern leaves of *Cladophlebis* and *Clathropteris meniscoides*, and bennettitalean foliage *Pterophyllum* and *Equisetites muensteri* shoots have been found. This zone comprises the Lower Rhaetian sensu polonico (Zbąszynek, Jarkowo and Drawno beds) and corresponds to the Norian. In the palynological zonation of Poland it corresponds to the *Corollina meyeriana* zone.

The *Lepidopteris ottonis* assemblage zone (*Lepidopteris* zone of Harris 1937) is characterised by the index species *Lepidopteris ottonis* and very abundant *Neocalamites lehmannianus*, or locally *Equisetum chalubinskii* (Tatra Mountains). The genus *Pterophyllum* is widespread and species-rich. The ferns *Cladophlebis roesserti* and *Clathropteris meniscoides* were also found. There are conifers typical of the Triassic (*Pseudohirmerella*) with species more evolutionarily advanced than in the *Voltzia* assemblage zone, and species of Lower Jurassic type (*Palissya*). The plant assemblage is taxonomically rich and somewhat similar in composition to Lower Jurassic floras (pers. observ. of Lipie Śląskie-Lisowice flora). This zone comprises the Upper Rhaetian sensu polonico (Wielichowo Beds) and corresponds to the Rhaetian. In the palynological zonation of Poland it corresponds to the *Riccisporites tuberculatus* zone.

The abrupt change in flora at the Carnian-Norian boundary could be connected with the mass extinction observed in faunas worldwide (Benton 1994a, b), but this needs to be investigated more carefully, as new data based on the Polish Upper Triassic vertebrates may challenge this conclusion (Dzik et al. 2008a, b).

Full analyses of the floras from the Triassic sites in Poland will extend our knowledge (still very scant) of Triassic palaeoecosystems in Poland and generally in the Northern Hemisphere. Recent new finds of taxonomically rich, well-preserved floras with numerous specimens accompanying vertebrate remains in Silesia provide researchers studying Polish Triassic floras with an opportunity to upgrade the taxonomy and describe them in

an evolutionary and palaeoecological context. The new research on these localities is in its infancy (Dzik & Sulej 2007, Staneczko 2007, Dzik et al. 2008a, b, Wawrzyniak & Ziaja 2009, Wawrzyniak 2010a, b, Barbacka et al. 2012, Pacyna et al. 2013a, b). Intensive research on plant remains from drill cores is also in progress (Ociepa et al. 2008, Barbacka et al. 2009, 2011, Krupnik et al. 2011, Pieńkowski et al. 2012). When good, comprehensive taxonomic descriptions have been completed, the floras from these sites may serve as reference floras for future evolutionary and palaeoecological studies of the world's Triassic plants.

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