MATONIACEOUS FERNS PRESERVED IN GROWTH POSITION IN LOWER JURASSIC DUNE SANDSTONES OF THE HOLY CROSS MOUNTAINS (POLAND)

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Abstract: The occurrence of the fern *Matonia braunii* (Goeppert) Harris, preserved in the growth position in sandstones of dune origin, is documented from the late Pliensbachian Szydłowiec Sandstone of the Drzewica Formation in the Holy Cross Mountains. This plant formed monotypic stands on coastal dunes during a marine highstand. The presence of this common Early Jurassic fern in such an unfavourable environment attests to the huge ecological plasticity of this species.

INTRODUCTION

Ferns were an important element of Mesozoic vegetation, with numerous taxa and a diversified ecology (e.g., Van Konijnenburg-van Cittert, 2002; Barbacka *et al*., 2014b). Families that today are of restricted occurrence as relicts (e.g., Dipteridaceae, Gleicheniaceae, Matoniaceae, Marattiaceae, Osmundaceae, Schizaeaceae) were then abundant (Taylor *et al*., 2009). They lived in a variety of environments, also colonising open areas and forming a Mesozoic analogue of today's meadows. This is in contrast to modern fern families (e.g., Pteridaceae, Athyriaceae, Blechnaceae, Aspleniaceae), which diversified in the Cretaceous in the shade of early arborescent angiosperms and today are mainly undergrowth plants (Schneider *et al*., 2004). As in some tropical areas today, Mesozoic ferns were early successional-stage colonisers of disturbed and open areas (Mehltreter *et al*., 2010; Barbacka, 2011). Ferns also constituted a significant part of the diet of dinosaurs, especially low browsers (e.g., Gierliński and Pieńkowski, 1999; Brown *et al*., 2020).

Among the typical Mesozoic fern families, Matoniaceae are especially frequent and well known (Harris, 1931, 1961; Van Konijnenburg-van Cittert, 1993; Popa, 1997; Klavins *et al*., 2004; Schmidt and Dörfelt, 2007; Kvaček and Dašková, 2010; Naugolnykh and Pronin, 2015; Pott *et al*., 2018; Badihagh and Uhl, 2019; Van Konijnenburg-van Cittert *et al*., 2020). This family was first known from the fossil record and secondarily from modern floras. The fossil

genus *Phlebopteris* was proposed in 1829 by Brongniart (Brongniart, 1828–1837) for several European Jurassic ferns. In 1830, Brown (in Wallich, 1830) proposed the genus *Matonia* for extant fern specimens, collected from the Malayan Peninsula. The family Matoniaceae was proposed by Presl (1848). Schenk (1871), Zeiller (1885) and Raciborski (1894) were among the first researchers to recognise that *Phlebopteris* Brongniart (= *Laccopteris* Presl in Sternberg) belongs to the Matoniaceae and referred other fossil species to this family. The Matoniaceae originated in the Triassic during the second fern radiation and had their widest range during the Mesozoic (Rothwell and Stockey, 2008; Pott *et al*., 2018). About twenty fossil genera have been described on the basis of foliage, petrified rhizomes and petioles, which were distributed on all continents (Schenk, 1865–1867; Seward, 1899; Harris, 1931, 1961; Hirmer and Hoerhammer,1936; Van Konijnenburg-van Cittert, 1993; Tidwell and Ash, 1994; Popa, 1997; Givulescu and Popa, 1998; Taylor *et al*., 2009; Barbacka *et al*., 2016). Today, this family is represented by two genera, *Matonia* (known since the Early Jurassic) and *Phanerosorus* Copeland, each represented by two species and confined to Indonesia, Borneo and New Guinea (Seward, 1899; Kramer, 1990; Taylor *et al*., 2009). The family is characterised by the presence of pedate fronds with pinnate or more rarely bipinnate pinnae and sporangia, arranged in sori, with a peltate indusium

(Kramer, 1990; Lindsay *et al*., 2003; Taylor *et al*., 2009; Van Konijnenburg-van Cittert *et al*., 2020).

Matoniaceae are well represented in Polish Mesozoic floras, especially the Early Jurassic of Holy Cross Mountains, with genera such as *Matonia* Brown in Wallich, *Matonidium* Schenk, *Phlebopteris* Brongniart (= *Laccopteris* Presl in Sternberg) and *Weichselia* Stiehler, numerous in species and specimens (Raciborski, 1891, 1892, 1894; Makarewiczówna, 1928; Reymanówna, 1963, 1965; Barbacka *et al*., 2010, 2014a, 2016; Pacyna, 2013).

This paper describes matoniaceous ferns, preserved in the growth position in Lower Jurassic coastal (foreshore) dune sandstones in the abandoned Podkowiński Quarry at Szydłowiec, in the Holy Cross Mountains (Fig. 1). Although *in situ* plants in the growth position are rather frequent in some strata, for example in the Carboniferous Coal Measures (Falcon-Lang, 2015), plants preserved in aeolian dune strata are exceptional and are rarely described in the palaeobotanical literature; more frequent are reports of fossil plants from interdune deposits (Gradziński and Uchman, 1994; Parrish and Falcon-Lang, 2007; Taylor *et al*., 2009; Florjan and Worobiec, 2016). Only very seldom are such preserved plant remains as taxonomically determinable as was possible for the material presented here.

GEOLOGICAL SETTING

During the Early Jurassic, terrigenous, continental, marginal-marine and marine deposits up to 1,400 m thick accumulated in a large epeiric basin, extending across Poland as a part of the Central European Basin (Pieńkowski, 1991, 2004, 2006; Pieńkowski *et al*., 2008, 2020; Barth *et al*., 2018). Sedimentation was mainly controlled by supraregional sea-level changes. Pieńkowski (2004) defined the deposits as the Kamienna Group and subdivided them into lithologic formations, showing regional facies differentiation, in a study using high-resolution sequence stratigraphic analysis, describing the lithofacies, identifying the depositional systems and subsystems, and determining their fluctuation in space and time. The Holy Cross Mountains are a marginal south-eastern part of the basin, but the strata of seven formations and ten discerned sequences are present (Fig. 2) and accessible for research in many outcrops and drill cores.

The plant fossils described here originate from the late Pliensbachian sequence VI, which belongs to the Drzewica Formation. The depositional sequence VI (Pieńkowski, 2004, 2006) lies on a prominent erosion surface; the sediments overlying the erosional sequence boundary (parasequence VIa) are coarse alluvial deposits. The depositional system is interpreted as a meandering river. The ensuing late Pliensbachian transgression was associated with the development of a foreshore-shoreface-barrier lagoon depositional system. Rapid inundation of the palaeorelief with alluvial valleys and coastal plains resulted in an embayed coastline with detached beach-barrier ridges and a nearshore depositional system with extensive shoreface deposits. The transitional deposits between the transgressive systems tract and the highstand systems tract (maximum flooding stage) are represented by very well sorted sandstone lithofacies, up to 20 m thick, with hummocky cross-stratification, horizontal bedding and tabular cross-bedding. They are known as the Szydłowiec Sandstone, exploited for construction use since medieval times (Karaszewski, 1960, 1962; Karaszewski and Kopik, 1970). These quartz sandstones occur in the Szydłowiec area, specifically in the lower parts
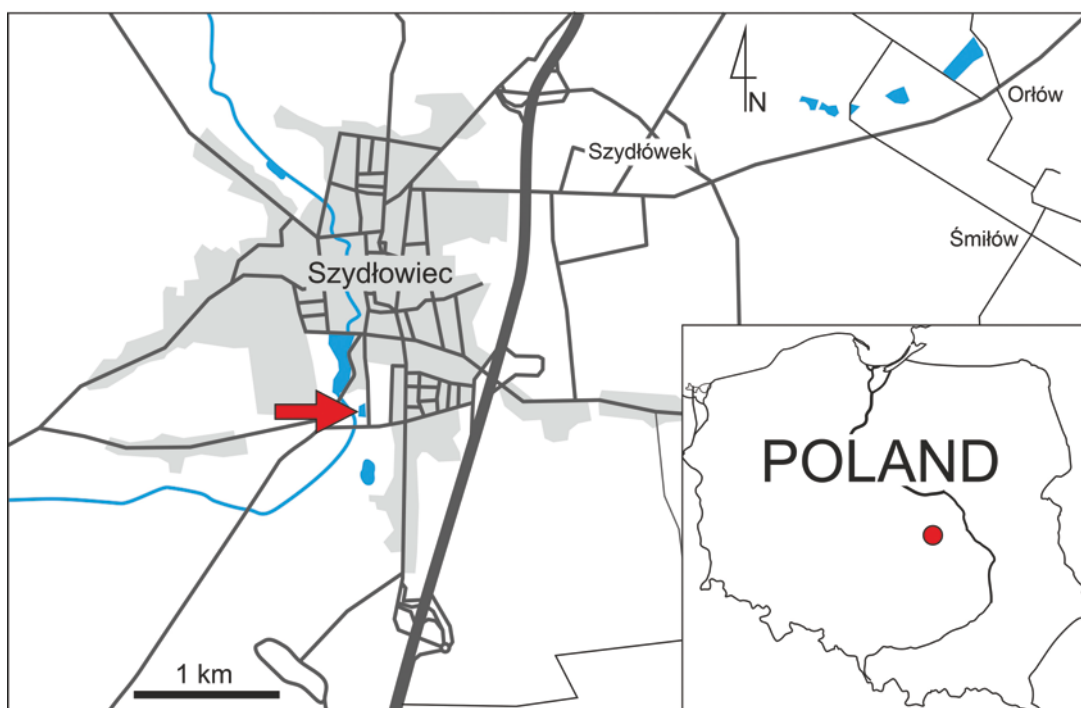

Fig. 1.   Map showing the Podkowiński Quarry at Szydłowiec (red arrow), other localities discussed in the text, and the location of the study area in Poland

of the quarries at Szydłowiec (the Antecki and Podkowiński quarries) and the exposures at Szydłówek and Śmiłów (Pieńkowski, 2004). Higher in the sequence, a regressive trend, associated with a highstand systems tract, is developed in a foreshore-dune-backdune/lagoon environment. The Podkowiński Quarry is now abandoned and flooded. However, a detailed profile of this interval is known from the nearby Śmiłów Quarry (Pieńkowski, 2004). According to Karaszewski (1962), Karaszewski and Kopik (1970) and Pieńkowski (2004) the plants in the growth position were present at the bases of aeolian sandstone bodies, up to 2 m thick, which wedge out laterally and are covered by argillaceous strata of coastal lagoon origin with drifted plant remains. Plant macroremains are present at many levels of the Drzewica Formation, but in general are poorly preserved and undeterminable. Karaszewski (1962) observed
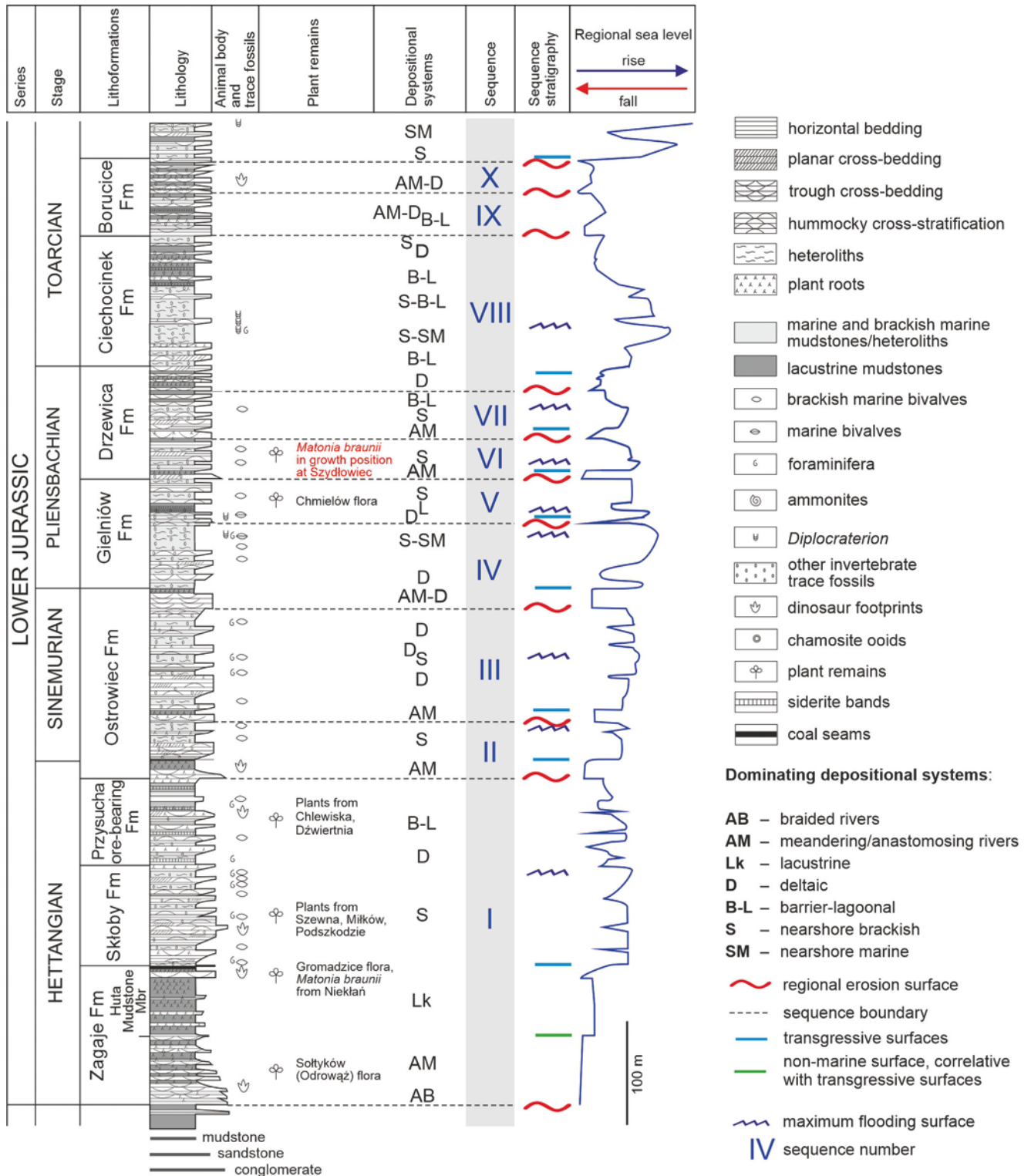

Fig. 2. Lithologic profile of Lower Jurassic deposits of the Holy Cross Mountains (Profile courtesy of G. Pieńkowski, based on Pieńkowski, 2004, fig. 67, modified), with source strata of material investigated and other fossil floras.

plant remains and rhizoids along the entire profile of this formation. Skurczyńska-Garwolińska and Woroncowa-Marcinowska (2015) illustrated several specimens, including those collected by Karaszewski, Ploch and Gierliński, with plant remains from the Szydłowiec Sandstones at Szydłowiec, Śmiłów and Mirzec, near Starachowice, from the collection of the Polish Geological Institute Museum; none of these, probably with one exception, are taxonomically determinable. Plants buried in the growth position (although difficult to determine) were found in the same dune interval in the Śmiłów Quarry (Pieńkowski, 2004; Gierliński *et al.*, 2006). Specimens from Szydłowiec (Skurczyńska-Garwolińska and Woroncowa-Marcinowska, 2015, p. 224, fig. 2) and from Mirzec (p. 224, fig. 1) probably contain plant shoots preserved in the growth position. The rest represent medium-sized detritus, preserved as moulds and casts of undeterminable shoots or twigs. The remains described here are unique in being taxonomically recognisable. Strata of the Drzewica Formation are well exposed today in exposures at Szydłówek and Śmiłów (Pieńkowski, 2004), and also are known from boreholes, such as the Gutwin (Rogalska, 1976) and Brody-Lubienia boreholes (Pieńkowski *et al.*, 2016). Depositional sequence VI deposits belong to the late Sinemurian–Pliensbachian megaspore *Horstisporites planatus* Zone (Marcinkiewicz, 1971; Marcinkiewicz *et al.*, 2014).

MATERIAL AND METHODS

The specimens were collected by the late Władysław Karaszewski in the 1950s, when the Szydłowiec Sandstone was exploited intensively in the Podkowiński Quarry. They are stored in the Institute of Botany of the Jagiellonian University, collection number Palaeobotanical Collection IB UJ 109. The plant fossils are preserved in orange-grey, medium-grained sandstone three-dimensionally, as voids after the decay of leaf stipes and as the impressions of leaf blades. The suprageneric classification follows Cronquist *et al.* (1966), Smith *et al.* (2006) and PPG I (2016). The plant remains were observed with a Technival 2 stereoscopic microscope and photographed with a Nikon NIKKOR AF-s DX Micro NIKKOR 85 mm f/3.5G ED VR camera.

SYSTEMATIC PALAEONTOLOGY

Class POLYPODIOPSIDA Cronquist, Takhtajan et Zimmermann, 1966
Order GLEICHENIALES Schimper, 1869
Family MATONIACEAE Presl, 1848

Genus *Matonia* Brown in Wallich, 1830

Type species: *Matonia pectinata* Brown in Wallich, 1830; Mount Ophir near Malacca, Malay Peninsula; extant

Matonia braunii (Goeppert, 1841) Harris, 1980
Figs 3–5

Selected synonyms:

1841 *Laccopteris brauni* sp. nov. – Goeppert, pp. 7–8, pl. 5, figs 1–7.

1841 *Laccopteris germinans* sp. nov. – Goeppert, pp. 9–10, pl. 6, figs 1–12.

1865–1867 *Laccopteris göpperti* sp. nov. – Schenk, pp. 94–97, pl. 23, figs 1–12, pl. 24, figs 2–5.

1865–1867 *Laccopteris münsteri* sp. nov. – Schenk, pp. 97–98, pl. 24, figs 6–10, pl. 25, figs 1, 2a, b.

1891 *Laccopteris elegans* Presl in Sternberg – Raciborski, pp. 305–306, pl. 4, figs 1, 4.

1899 *Laccopteris elegans* Presl in Sternberg – Seward, pp. 193–196, text-fig. 8.

1928 *Laccopteris elegans* Presl in Sternberg – Makarewiczówna, p. 3.

1928 *Laccopteris Münsteri* Schenk 1867 – Makarewiczówna, p. 4, p. 1(10), figs 2, 2a.

1936 *Phlebopteris brauni* (Goeppert) Hirmer and Hoerhammer – Hirmer and Hoerhammer, pp. 7–17, text-figs 3, 4, 5, 1A–D, pl. 1, figs 1–12, pl. 2, figs 1–4, pl. 4, fig. 7.

1936 *Phlebopteris muensteri* (Schenk) Hirmer et Hoerhammer – Hirmer et Hoerhammer, pp. 17–26, text-figs B, 5, 2A–B, pl. 3, figs 1–7, pl. 4, figs 1–6, pl. 5, figs 1–6.

1980 *Matonia braunii* (Goeppert) Harris – Harris, pp. 295–310, figs 1–20.

2016 *Matonia braunii* (Goeppert) Harris – Barbacka *et al.*, pp. 860–865, figs 2–5.

2019 *Matonia braunii* (Goeppert) Harris – Barbacka *et al.*, pp. 167–169, figs 6h, 7a, b.

2020 *Phlebopteris muensteri* (Schenk) Hirmer et Hoerhammer – Van Konijnenburg-van Cittert *et al.*, pp. 9–11, pl. 5, figs 1–6.

Material: PC IB UJ 109/1 (isolated stipes, one frond, isolated pinnules), 109/2 (groups of stipes, one pinna).

Description: Frond fragments preserved in growth position (Figs 3–5). Frond palmately dissected with pinnatifid pinnae. More than twenty stipes preserved singly or in groups of ~6 (Fig. 5A, B). Stipes 1.5–2.0 mm in diameter, up to 20 cm long, incomplete, not attached to rhizomes (rhizomes not preserved). Only one frond reasonably close to complete, with at least 12 pinnae still attached to the stipe (Fig. 3A). Isolated pinnae also present (Fig. 5C, D). Preserved pinnae incomplete, up to 15 cm long, 15–18 mm wide. Pinnae rachis ~1 mm wide. Pinnules linear, opposite to subopposite, densely arranged, attached at 70–80° angles, slightly sickle-bent toward upper end of the pinnae. Pinnules 7–10 mm long, 2–4 mm wide, separated from each other by convex ridges of sandstone 1–1.5 mm wide (Fig. 3A–D). Pinnules of approximately uniform size along pinnae, smaller in basal and apical parts of pinnae, up to 3 mm wide and up to 5 mm long (Fig. 3C). Pinnule apices mostly poorly preserved, rather rounded. Pinnule venation indistinct, only central vein sometimes visible (Fig. 3B, C). Probably all pinnae sterile, no traces of sori detectable.

Fig. 3. *Matonia braunii* from Podkowiński Quarry. PC IB UJ 109/1. **A**. Palmately dissected frond with pinnatifid pinnae three-dimensionally preserved on several rock surfaces. **B**. Upper part of specimen from 3A, seen from above, void after stipe decay and several pinnae visible. **C**. Enlargement of pinnae fragments (detail from 3B), pinnules separated from each other by convex ridges of sandstone. **D**. Lower part of specimen from 3A, pinnae with pinnules separated from each other by prominent convex ridges of sandstone.

Remarks: The material described here is preserved well enough to be taxonomically determined. This is rather exceptional for plants growing in such an unfavourable environment (a dunefield) and found in a rock type that generally does not preserve fossils well (medium-grained sandstone). Palmately dissected fronds with pinnatifid pinnae and the characteristic shape of the pinnules allow this fossil to be assigned to the Matoniaceae family. In one specimen (PC IB UJ 109/1, Fig. 3A) the leaf is almost complete and

the pinnae are still attached to the stipe. There are also numerous isolated stipes (Fig. 4) and some isolated pinnae in both described specimens (Fig. 5C, D). The isolated stipes have the same shape and dimensions as stipes still connected to the pinnae, so most probably they also belong to this fern. No other plant remains are preserved in the two rock specimens.

Morphologically similar leaves were described and illustrated by Goeppert (1841), Schenk (1865–1867), Seward (1899), Hirmer and Hoerhammer (1936), Barbacka *et al.*
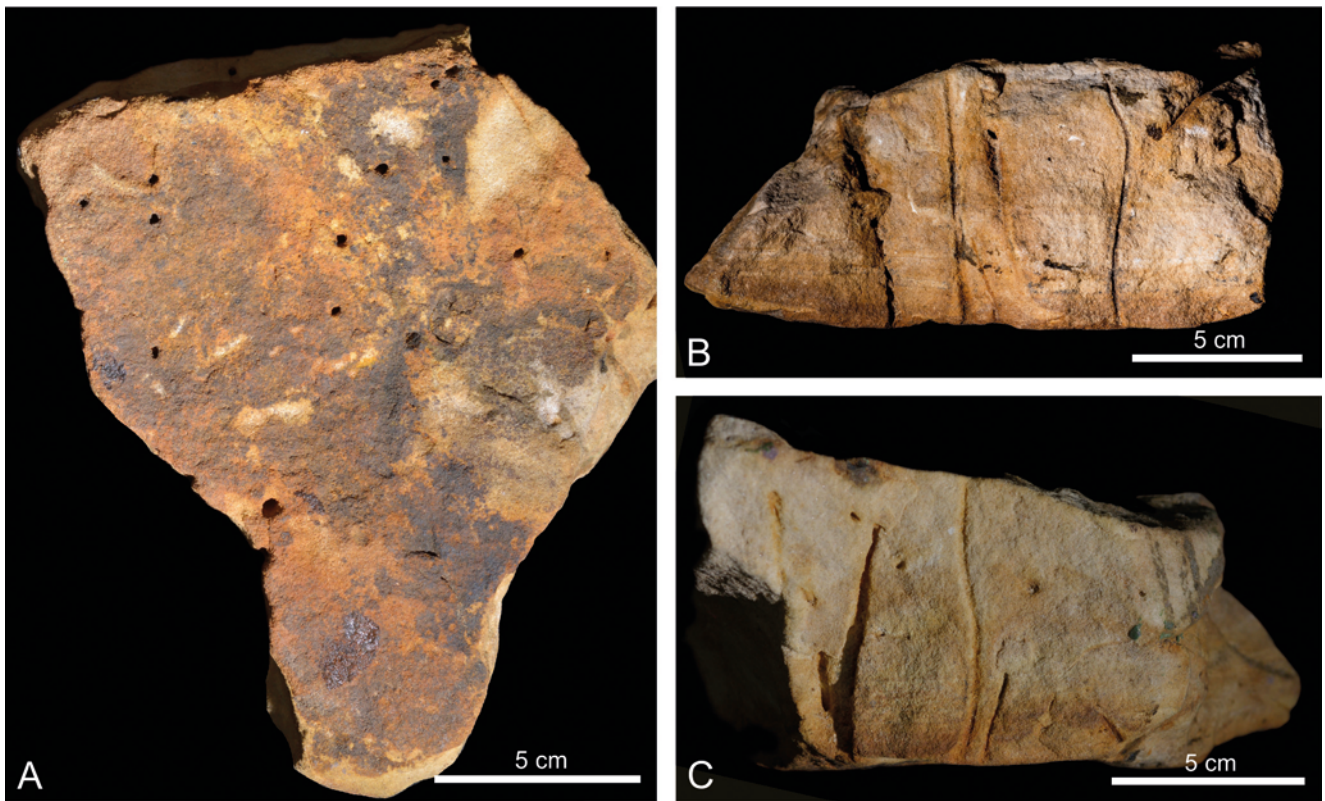
Fig. 4. *Matonia braunii* from Podkowiński Quarry. PC IB UJ 109/1. **A**. Specimen from 3A, lower side, flat surface, visible numerous voids after stipes decay. **B**. Side of specimen from 4A, visible moulds of stipes split lengthwise; note low-angle cross bedding of sandstone perpendicular to stipes. **C**. Opposite side of specimen from 4A, visible moulds of stipes split lengthwise.

(2016, 2019) and Van Konijnenburg-van Cittert *et al*. (2020) as belonging to *Phlebopteris braunii* (Goeppert) Hirmer and Hoerhammer, *Phlebopteris muensteri* (Schenk) Hirmer et Hoerhammer, *Matonia braunii* (Goeppert) Harris and some other clearly synonymous species (see list of selected synonyms). Harris (1980) considered the specimens classified as *Phlebopteris muensteri* as sun fronds and *Phlebopteris braunii* as shade fronds of the same species. He also demonstrated the presence of indusiate sori and on this basis referred both species to the extant genus *Matonia* and merged them under the name *Matonia braunii* (Goeppert) Harris. Worth noting is the usual co-occurrence of both of them at most localities (Schenk, 1865–1867). Barbacka *et al*. (2016, 2019) followed Harris' (1980) interpretation, when describing specimens from the Lower Jurassic of Poland and Hungary. However, some authors still question these species synonymy (see e.g., Van Konijnenburg-van Cittert, 1993; Schweitzer *et al*., 2009; Van Konijnenburg-van Cittert *et al*., 2020), based on subtle differences in leaf and sori morphology in forms from the two extremes of variability. Interestingly, the leaf morphology (especially the relatively short sterile pinnules) of the presently described plants, which most probably grew on dunes and were exposed to direct sunlight, rather resembles that of *P. braunii*, interpreted by Harris as shade leaves.

The only other species from the Matoniaceae present in the Lower Jurassic strata of the Holy Cross Mountains is the easily identifiable *Phlebopteris angustiloba* (Presl

in Sternberg) Hirmer and Hoerhammer, different in many aspects from *Matonia braunii* (Raciborski, 1891, 1892; Makarewiczówna, 1928; Pacyna, 2013). Members of other fern families present, such as the Osmundaceae and Dipteridaceae, are morphologically different enough not to be confused with the Matoniaceae.

Distribution: *Matonia braunii,* as understood here (*Phlebopteris braunii* and *P. muensteri* as its synonyms), is known from the Late Triassic to Early Cretaceous, mainly from Europe, but most frequent and characteristic for the Early Jurassic (Goeppert, 1836; Schenk, 1865–1867; Harris, 1980; Van Konijnenburg-van Cittert, 1993; Van Konijnenburg-van Cittert *et al*., 2020). In the Early Jurassic floras of Poland, this species is a characteristic but not very numerous element (Barbacka *et al*., 2014; Pacyna, 2021). Specimens similar to those described here were described and illustrated from the Lower Jurassic of the Holy Cross Mountains area (Chlewiska, Chmielów, Dźwiertnia, Gromadzice, Jędrzejowice, Szewna) by Raciborski (1891) and Makarewiczówna (1928), and referred mainly to *Laccopteris elegans* Presl in Sternberg (summarized in Pacyna, 2013). The species *Laccopteris elegans* was proposed by Presl in Sternberg (1838), on the basis of poorly preserved, rather indeterminate isolated pinnules (Jung and Knobloch, 1972; Kvaček and Straková, 1997). The species name *Laccopteris elegans* is a nomenclatural synonym of *Asterocarpus lanceolatus* Goeppert, 1836, and is an illegitimate name, as superfluous, including the
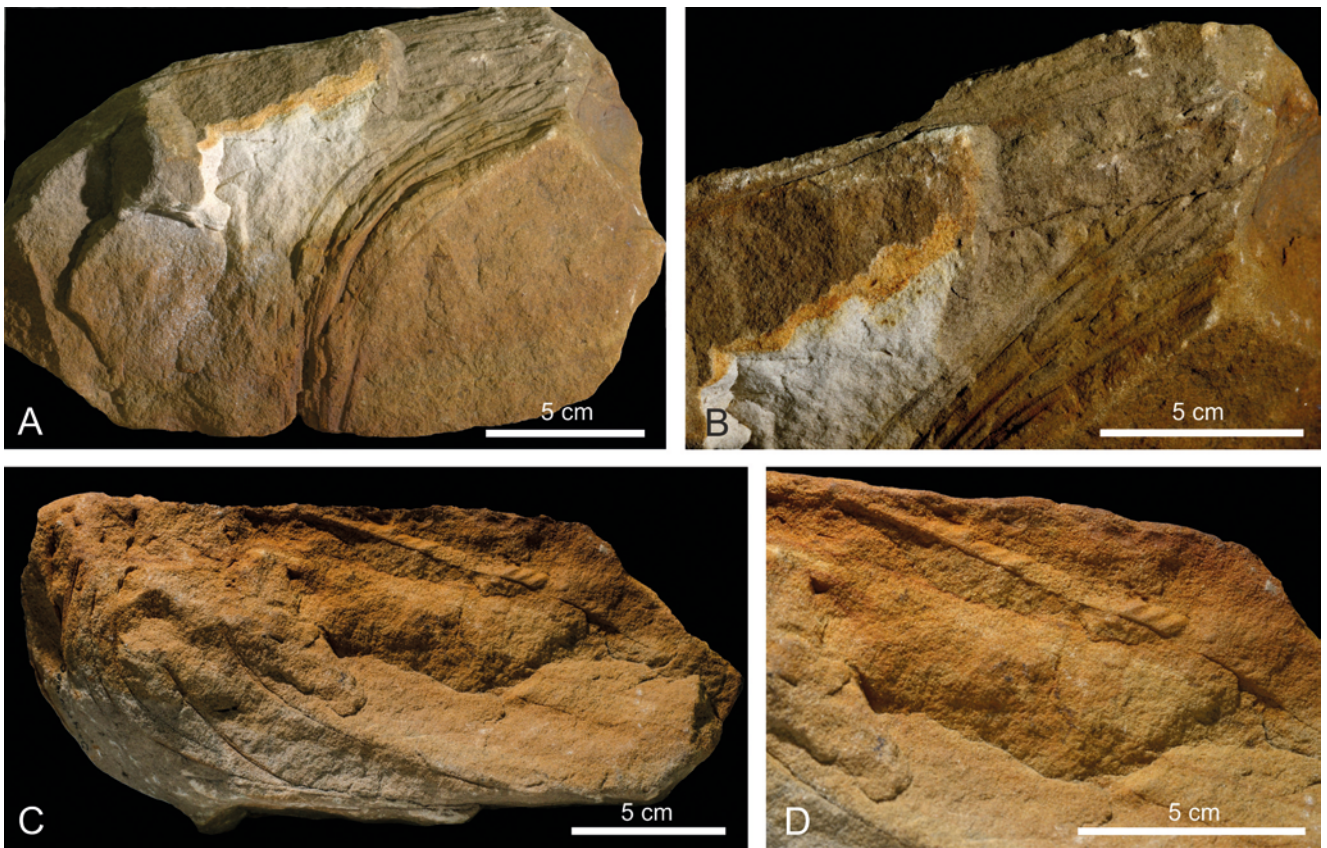
Fig. 5. *Matonia braunii* from Podkowiński Quarry. PC IB UJ 109/2 **A**. Two groups of stipes bent in one direction. **B**. Upper side of specimen from 5A, two groups of stipes bent in one direction. **C**. Opposite side of specimen from 5A, one pinna impression above several moulds of stipes. **D**. Detail from 5C, one pinnula visible; note low-angle cross bedding of sandstone.

type of the formerly validly published name (Goeppert, 1836; Turland *et al*., 2018). The species affiliation of the Polish material, historically referred to this species, needs revision. Material probably referable to *Matonia braunii* was described by Barbacka *et al*. (2014a) from strata of Toarcian–Aalenian age from the Ciechocinek IG 1 borehole as *Phlebopteris muensteri*. New well-preserved material of *Matonia braunii* from the Niekłań borehole in the Holy Cross Mountains was described by Barbacka *et al*. (2016).

DISCUSSION

Preservation of plant remains in growth position in dune sandstones

Plant remains are known from several horizons in the Lower Jurassic successions of the Holy Cross Mountains (Fig. 2); they are especially numerous in Hettangian and rarer in Sinemurian, Pliensbachian and Toarcian strata (for the most recent summary, see Pacyna, 2013). Only in the Drzewica Formation, they are frequently preserved in growth position, albeit for the most part poorly preserved in sandstones.

Karaszewski (1962) was the first to discover, describe and illustrate plants in the growth position from the Szydłowiec Sandstone in the Podkowiński Quarry. His specimens (Karaszewski, 1962, pl. 8, figs. 1–3) are very similar to the

material described here and were assigned by him as at least in part to the ferns, but without a detailed description and taxonomical determination. One specimen (Karaszewski, 1962, pl. 8, fig. 1), refigured by Skurczyńska-Garwolińska and Woroncowa-Marcinowska (2015, p. 223, fig. 2, inverted 180° in relation to Karaszewski's figure), may represent a frond of the same fern species as that identified here, but the photos are of poor quality and at very low magnification.

The bend of the groups of stipes in one direction in the material described here (Fig. 5A) may indicate wind blowing sand from one direction. Low-angle cross bedding, perpendicular to the vertically preserved stipes, indicates that the plants were still alive and in the growth position during the deposition of the sand. Two preserved groups of stipes (Fig. 5A, B) are not attached to rhizomes. The lack of rhizome preservation is interesting and needs explanation, as the plants are preserved in the growth position. Karaszewski (1962) did not mention the presence of rhizomes in his published material; no traces of them are present in the specimens described here. In extant *Matonia pectinata* the rhizomes are horizontal and produce fronds at certain distances (Seward, 1899; Schweitzer, 1978). Two groups of long stipes from specimen PC IB UJ 109/2 may have originated from one rhizome. In specimen PC IB UJ 109/1, the stipes are more scattered and one has pinnae still attached (Fig. 3). This sandstone block most probably preserves the upper parts of the stipes (Fig. 4). Karaszewski (1962)

suggested that the dune area was quickly inundated after plant burial, which allowed the plants to be fossilised and preserved. One possible explanation of the lack of rhizomes is that they would have been present in the soil layer beneath the frond-preserving sandstone and that they decayed after the plant was buried by sand and died. The presumed thin soil layer with rhizomes was not preserved. Fronds of the fern *Anomopteris* sp. from the Early Triassic Eifel region in Germany were similarly preserved in the growth position in sandstone of fluvial, not aeolian origin. Their rhizomes were rooted in siltstone lying below the sandstone and poorly preserved, unlike the well-preserved fronds (Fuchs *et al.*, 1991). In monotypic colonies of *Clathropteris meniscioides* Brongniart (Dipteridaceae) preserved *in situ* in the Early Jurassic of central Patagonia, horizontal rhizomes are also lacking (Choo *et al.*, 2016).

Palaeoecology of *Matonia braunii* at Szydłowiec with reference to the environmental preferences of ferns

Today, the Matoniaceae family is confined to tropical Thailand, Indo-Malaysia and Polynesia; the present distribution is a relict area. *Matonia pectinata* Brown in Wallich grows in exposed areas in relatively open scrub, on or near the tops of isolated mountains at 750–2,000 m a.s.l., but has also been found at sea level. It is a thicket-forming fern adapted to poor sandy soils (Piggott and Piggott, 1988; Kramer, 1990; Lindsay *et al.*, 2003).

The ecology of fossil Matoniaceae was more diversified and the family was more widespread (Van Konijnenburg-van Cittert, 2002; Wang, 2002; Barbacka *et al.*, 2014b) but probably connected mainly with warm and humid climates. Forms preferring humid conditions (especially having large fronds) and those more stress-adapted were certainly present and growing in the understorey along riverbanks and on open plains, forming assemblages similar to today's meadows. Only some species were adapted to an arid climate and rather dry localities (e.g., *Weichselia* or *Piazopteris* Lorch) and are frequently preserved as fusain (Tidwell and Ash, 1994). There were also species with quite variable ecology, the most spectacular being *Phlebopteris woodwardii* Leckenby. This fern was present in such different environments as coal-forming peatbogs, riverbanks, and fire-prone inland heaths (Raciborski, 1894; Harris, 1961). *Matonia braunii* also probably had a wide range of environmental preferences. In the Lower Jurassic coal-bearing strata of Hungary, this fern was interpreted as preferring the wettest, disturbed, alluvial habitats (Barbacka, 2011; Barbacka *et al.*, 2019). In the Polish age-coeval localities, it is present in river and deltaic or lagoonal settings at Gromadzice and Chmielów. The environmental conditions of the specimens from the Niekłań borehole are interpreted as flood-plain-backswamp, located at the transition between floodplain and lacustrine-back-swamp, associated with a fluvial environment (Barbacka *et al.*, 2016). The fern was found in a claystone bed separating two thin coal seams. The material described here at Szydłowiec considerably broadens the environmental tolerance of this species to include coastal dunes (very poorly developed sandy soils) and probably to include increased salinity, which is typical for such environments.

Active dunes are a very difficult habitat for plants (Podbielkowski and Podbielkowska, 1992; Warren, 2013; Sudnik-Wójcikowska and Krzyk, 2015). They are endangered by sand-blasting or burial in sand, and they have problems establishing on a loose substrate. Sand dunes are common features of shorelines. Beach dunes consist of the foredune, the angled side of which faces the sea, the sand plain at the top of the dune, and the backdune. Plants that thrive on the foredune are exposed to salt spray, strong wind, and burial by blowing and accumulating sand. Plants that thrive on the broad dune plain and backdune grow together into dense patches that hold the dune together. The presence of horizontal rhizomes of *Matonia braunii* could stabilise a dune, like rhizomes of the modern grass *Leymus arenarius* (Linnaeus) Hochstetter on the Baltic coast (Podbielkowski and Podbielkowska, 1992; Sudnik-Wójcikowska and Krzyk, 2015). As no other fossil plants were found associated with *Matonia braunii* fronds, it probably formed monotypic stands on coastal dunes, similar to the monotypic strands formed by *Matonia* today on sandy soils (Piggott and Piggott, 1988).

Generally ecological variability of ferns is narrower today than in the Mesozoic as a result of angiosperm competition (Rothwell and Stockey, 2008; Pšenička *et al.*, 2020). However, extant ferns tolerate a wide range of environmental conditions (Mehltreter *et al.*, 2010), and some species can colonize such highly disturbed habitats as lava flows, dunes, landslides as well as areas of forests that have been damaged by burning. Living Matoniaceae are relictual with a restricted number of species, ecology and range and certainly do not reflect ancient aptitudes of this fern family. Extant *Matonia* although adapted to poor sandy soils does not grow on coastal dunes (Piggott and Piggott, 1988; Kramer, 1990; Lindsay *et al.*, 2003). At least one fossil genus of Matoniaceae i.e. *Weichselia*, was salt tolerant and grew in tidal environments (Silantieva and Krassilov, 2006). Some extant ferns demonstrate a wide range of ecological tolerance, including possibility of growth on dunes. Bracken (*Pteridium* Scopoli) and scrambling ferns, *Gleichenia* Smith, *Dicranopteris* Bernhardi and *Sticherus* Presl, are often abundant on and characteristic of nutrient-poor sites such as heaths, landslides, recent fire scars and coastal sand dunes (Mehltreter *et al.*, 2010). *Pteridium* is one of the world's most widespread invasive vascular plant. Its success is explained by its broad survival strategies, it grows in woodlands and their edges, clearings, dunes, hedgerows and roadside verges (Mehltreter *et al.*, 2010). Southern bracken (*Pteridium esculentum* (Forster) Cockayne) grows on coastal sand dunes on the Kaitorete spit, southern New Zealand, and in subtropical eastern Australia, another species colonises sand dunes and coastal cliffs in UK (Walker *et al.*, 1981; Mehltreter *et al.*, 2010). Fossil *Matonia braunii* might have had wide ecological amplitude and colonised such disturbed habitats as floodplains, varied alluvial and deltaic settings and sand dunes. Numerous polypodiaceous ferns, normally associated with woodlands, were found growing on lake dunes in the Indiana Dunes National Park, in Indiana, USA (Tryon, 1936). Among angiosperms are species which grow not only on coastal dunes, but also in other habitats, e.g., sand sedge (*Carex arenaria* Linnaeus) grow

mainly on North Sea and Baltic Sea coasts, but also in the valleys of larger rivers in forests with sandy soils (Sudnik-Wójcikowska and Krzyk, 2015).

Matonia braunii in the growth position at Podkowiński Quarry in the context of Drzewica Formation biota

Additional data about plant cover during deposition of Drzewica Formation relevant for discussed here fossils provide nearby exposures and boreholes. The Śmiłów Quarry exploits fine-grained, very well sorted, quartz-cemented sandstones of the uppermost VIst sequence, which represent mostly nearshore facies (Pieńkowski, 2004, 2006). Aeolian reworking is present in the uppermost part of the profile, and undeterminable plants buried in growth position by barrier crest aeolian dunes were found (Pieńkowski, 2004; Gierliński *et al*., 2006). They are not similar to the remains at the Podkowiński Quarry; they are larger, coalified, up to 0.5 m high, and preserved only in the upright position. The remains may be interpreted as probably the basal parts of plants, although no roots or rooting structures were described or illustrated, with numerous basal branches that were interpreted by the authors as narrow bladed leaves. This may be a fern with an upright rhizome producing numerous fronds, from which only stipes are preserved, the blades having fallen off before fossilisation. Skurczyńska-Garwolińska and Woroncowa-Marcinowska (2015, p. 251, fig. 2) erroneously identified as ?*Neocalamites hoernensis* (sic) some indeterminable drifted plant remains from this quarry. Casts of large logs of drifted trees and dinosaur footprints were also found. Dinosaur footprints in the Śmiłów Quarry were formed in the siliciclastic foreshore zone, interfingering with backshore dunes; it seems that the footprints were formed on the coastal dunefield. On the basis of this locality, Niedźwiedzki *et al*. (2009) recognised a new type of dinosaur track assemblage in the Early Jurassic of the Holy Cross Mountains (compare with Gierliński and Pieńkowski, 1999). This association is characterised by the predominance of small- and medium-sized forms of theropods and early thyreophorans, but also contains footprints made by large sauropods (Gierliński and Niedźwiedzki, 2005). Fern thickets, formed by *Matonia braunii* on dunes, may have provided food for herbivorous dinosaurs crossing the coastal dune fields.

Szydłówek is a small quarry in the vicinity of Szydłowiec exploiting the Szydłowiec Sandstone and showing a succession comprised of nearshore-foreshore-backshore/eolian facies. Fossils from this outcrop include numerous vertebrate tracks, impressions of woody trunks, plant root moulds, brackish bivalves, and limuloids (Pieńkowski, 2004, 2006). Among the vertebrate tracks are well-preserved belonging to theropods, sauropods and ornithischians (Niedźwiedzki *et al*., 2008; Niedźwiedzki and Remin, 2008; Gierliński *et al*., 2009). Impressions of drifted woody trunks, probably of conifers, abundant in this outcrop, indicate the occurrence of vast coniferous forests around the track site, but have not been subjected to detailed palaeobotanical analysis (Pieńkowski, 2004, 2006).

Palynological data about the plant cover during sedimentation of the Drzewica Formation come from the Gutwin and Brody-Lubienia boreholes; the outcrops have not been analysed palynologically so far. These data provide a much wider picture of the vegetation. The following plant groups were confirmed by sporomorphs: bryophytes, lycophytes, ferns from the families Cyatheaceae, Dipteridaceae, Dicksoniaceae, Gleicheniaceae, Matoniaceae, Osmundaceae and Schizeaceae, seed ferns, conifers from the families Taxodiaceae, Podocarpaceae and Pinaceae, cycads, bennettitaleans and ginkgophytes (Rogalska, 1976; Pieńkowski *et al*., 2016). Pollen grains from seed ferns and conifers predominate over other sporomorphs. Spores of Matoniaceae (cf. *Matonisporites* sp.) are rather rare. Marine influences were confirmed by the presence of acritarchs (Rogalska, 1976).

CONCLUSIONS

The ecological range of the common Early Jurassic fern *Matonia braunii* (Goeppert) Harris was expanded to coastal dunes on the basis of specimens, preserved in the growth position, from the late Pliensbachian Szydłowiec Sandstone of the Drzewica Formation in the Holy Cross Mountains. The fern formed monotypic stands on coastal dunes during a marine highstand. From a taphonomical point of view, the fossil material is interesting as it is preserved well enough to be determined taxonomically. This is rather exceptional for plants growing in such an unfavourable environment as a dunefield and preserved in such a type of sediment (medium-grained sandstone). The leaf morphology (especially the relatively short, sterile pinnules) of the plants described, which grew on dunes and were exposed to direct sunlight, resembles that of the leaves of the ecological type of *Matonia braunii* previously interpreted as shade growing. Fern thickets, formed by *Matonia braunii* on coastal dunes, may have provided food for herbivorous dinosaurs crossing the dunefields.

REFERENCES

Badihagh, M. T. & Uhl, D., 2019. The first occurrence of *Phlebopteris dunkeri* and *P. woodwardii* (Matoniaceae) from the middle Jurassic of Iran. *Journal of Palaeogeography*, 8: 1–10.

Barbacka, M., 2011. Biodiversity and the reconstruction of Early Jurassic flora from the Mecsek Mountains (southern Hungary). *Acta Palaeobotanica*, 51: 127–179.

Barbacka, M., Bodor, E. R., Jarzynka, A., Kustatscher, E., Pacyna, G., Popa, M. E., Scanu, G. G., Thévenard, F. & Ziaja, J., 2014b. European Jurassic floras: statistics and paleoenvironmental proxies. *Acta Palaeobotanica*, 54: 173–195.

Barbacka, M., Kustatscher, E. & Bodor, E. R., 2019. Ferns of the Lower Jurassic from the Mecsek Mountains (Hungary): taxonomy and palaeoecology. *Paläontologische Zeitschrif*, 93: 151–185.

Barbacka, M., Pacyna, G., Feldman-Olszewska, A. Ziaja, J. & Bodor, E. W., 2014a. Triassic–Jurassic flora of Poland; floristical support of climatic changes. *Acta Geologica Polonica*, 64: 281–308.

Barbacka, M., Pacyna, G., Pieńkowski, G. & Ziaja, J., 2016. New data about *Matonia braunii* (Göppert) Harris from the Early Jurassic of Poland and its ecology. *Geological Quarterly*, 60: 857–868.

Barbacka, M., Ziaja, J. & Wcisło-Luraniec, E., 2010. Taxonomy and palaeoecology of the Early Jurassic macroflora from Odrowąż, central Poland. *Acta Geologica Polonica*, 60, 373–392.

Barth, G., Pieńkowski, G., Zimmermann, J., Franz, M. & Kuhlmann, G., 2018. Palaeogeographical evolution of the Lower Jurassic: high-resolution biostratigraphy and sequence stratigraphy in the Central European Basin. *Geological Society, London, Special Publications*, 469: 341–369.

Brongniart, A., 1828–1837. *Histoire des végétaux fossiles ou recherches botaniques et géologiques sur les végétaux renfermés dans les diverses couches du globe*. G. Dufour et Ed. d'Ocagne (Vol. I), Crochard et Compie (Vol. II), Paris, Vol. I, 488 pp., Vol. II, 72 pp., Atlas: 166 + 30 plates.

Brown, C. M., Greenwood, D. R., Kalyniuk, J. E., Braman, D. R., Henderson, D. M., Greenwood, C. L. & Basinger, J. F., 2020. Dietary palaeoecology of an Early Cretaceous armoured dinosaur (Ornithischia; Nodosauridae) based on floral analysis of stomach contents. *Royal Society Open Science*, 7, 200305.

Choo, T., Escapa, I. & Benjamin, B., 2016. Monotypic colonies of *Clathropteris meniscioides* (Dipteridaceae) from the Early Jurassic of central Patagonia, Argentina: implications for taxonomy and palaeoecology. *Palaeontographica, Abteilung B*, 294: 85–109.

Cronquist, A., Takhtajan, A. & Zimmermann, W., 1966. On the higher taxa of Embryobionta. *Taxon*, 15: 129–134.

Falcon-Lang, H. J., 2015. A calamitalean forest preserved in growth position in the Pennsylvanian coal measures of South Wales: implications for palaeoecology, ontogeny and taphonomy. *Review of Palaeobotany and Palynology*, 214: 51–67.

Florjan, S. & Worobiec, G., 2016. *Skamieniałości roślinne. Zarys tafonomii roślin*. Instytut Botaniki im. W. Szafera, Polskiej Akademii Nauk, Kraków, 220 pp. [In Polish.]

Fuchs, G., Grauvogel-Stamm, L. & Mader, D., 1991. Une remarquable flore à *Pleuromeia* et *Anomopteris* in situ du Buntsandstein moyen (Trias inférieur) de l'Eifel (R. F. Allemagne). Morphologie, paléoécologie et paléogéographie. *Palaeontographica, Abteilung B*, 222: 89–120.

Gierliński, G., Lockley, M. G. & Niedźwiedzki, G., 2009. A distinctive crouching theropod trace from the Lower Jurassic of Poland. *Geological Quarterly*, 53: 471–476.

Gierliński, G. & Niedźwiedzki, G., 2005. New saurischian dinosaur footprints from the Lower Jurassic of Poland. *Geological Quarterly*, 49: 99–104.

Gierliński, G. & Pieńkowski, G., 1999. Dinosaur track assemblages from the Hettangian of Poland. *Geological Quarterly*, 43: 329–346.

Gierliński, G. D., Ploch, I., Sabath, K. & Ziaja, J., 2006. An Early Jurassic problematical plant from the Holy Cross Mountains, central Poland. *Przegląd Geologiczny*, 54: 139–141. [In Polish, with English abstract.]

Givulescu, R. & Popa, M., 1998. *Aninopteris formosa* Givulescu et Popa, gen. et sp. nov., a new Liassic matoniaceous genus and species from Anina, Banat, Romania. *Review of Palaeobotany and Palynology*, 104: 51–66.

Goeppert, H. R., 1836. Die Fossilen Farrnkräuter. *Verhandlungen der Kaiserlichen Leopoldinisch-Carolinischen Academie der Naturforscher, Supplement*, 17: 1–488.

Goeppert, H. R., 1841. *Die Gattungen der fossilen Pflanzen. Lieferung 1–2*. Verlag von Henry und Cohen, Bonn, 70 pp.

Gradziński, R. & Uchman, A., 1994. Trace fossils from interdune deposits – an example from the Lower Triassic aeolian Tumlin Sandstone, central Poland. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 108: 121–138.

Harris, T. M., 1931. The fossil flora of Scoresby Sound, East Greenland. Part 1: Cryptogams (exclusive of Lycopodiales). *Meddelelser om Grønland*, 85: 1–102.

Harris, T. M., 1961. *The Yorkshire Jurassic Flora I. Thallophyta – Pteridophyta*. Trustees of the British Museum (Natural History), London, 212 pp.

Harris, T. M., 1980. The Yorkshire Jurassic fern *Phlebopteris braunii* (Goeppert) and its reference to *Matonia* R. Br. *Bulletin of the British Museum (Natural History), Geology Series*, 33: 295–311.

Hirmer, M. & Hoerhammer, L., 1936. Morphologie, Systematik und geographische Verbreitung der fossilen und rezenten Matoniaceen. *Palaeontographica, Abteilung B*, 81: 1–70.

Jung, W. & Knobloch, E., 1972. Die „STERNBERG-Originale" der Bayerischen Staatssammlung für Paläontologie und historische Geologie zu München. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie*, 12: 105–111.

Karaszewski, W., 1960. New division of the Święty Krzyż Lias. *Geological Quarterly*, 4: 899–920. [In Polish, with English summary.]

Karaszewski, W., 1962. The stratigraphy of the Lias in the northern Mesozoic zone surrounding the Święty Krzyż Mountains (Central Poland). *Prace Instytutu Geologicznego*, 30: 333–416. [In Polish, with English summary.]

Karaszewski, W. & Kopik, J., 1970. The Stratigraphy of the Mesozoic in the margin of the Góry Świętokrzyskie. Lower Jurassic. *Prace Instytutu Geologicznego*, 56: 65–98. [In Polish, with English summary.]

Klavins, S. D., Taylor, T. N. & Taylor, E. L., 2004. Matoniaceous ferns (Gleicheniales) from the middle Triassic of Antarctica. *Journal of Paleontology*, 78: 211–217.

Kramer, K. U., 1990. Matoniaceae. In: Kramer K. U. & Green P. S. (eds), *The Families and Genera of Vascular Plants. Vol. I. Pteridophytes and Gymnosperms*. Springer, Berlin, Heidelberg, pp. 183–185.

Kvaček, J. & Dašková, J., 2010. *Konijnenburgia*, a new genus of the fern family Matoniaceae. *Review of Palaeobotany and Palynology*, 158: 308–318.

Kvaček, J. & Straková, M., 1997. *Catalogue of fossil plants described in works of Kaspar M. Sternberg*. National Museum, Prague, 201 pp.

Lindsay, S., Suddee, S., Middleton, D. J. & Pooma, R., 2003. Matoniaceae (Pteridophyta) – a new family record for Thailand. *Thai Forest Bulletin (Botany)*, 31: 47–52.

Makarewiczówna, A., 1928. Étude sur la flore fossile du lias inférieur des environs d'Ostrowiec. *Travaux de la Société des Science et des Letters de Wilno, Travaux de L'Institut de Géologie de l'Université de Wilno*, 4: 1–49. [In Polish, with French summary.]

Marcinkiewicz, T., 1971. The stratigraphy of the Rhaetian and Lias in Poland based on megaspore investigations. *Prace Instytutu Geologicznego*, 65: 1–58. [In Polish, with English summary.]

Marcinkiewicz, T., Fijałkowska-Mader, A. & Pieńkowski, G., 2014. Megaspore zones of the epicontinental Triassic and Jurassic deposits in Poland – overview. *Biuletyn Państwowego Instytutu Geologicznego*, 457: 15–42. [In Polish, with English summary.]

Mehltreter, K., Walker, L. R. & Sharpe, J. M. (eds), 2010. *Fern Ecology*. Cambridge University Press, Cambridge, 444 pp.

Naugolnykh, S. V. & Pronin, A. P., 2015. A new matoniaceous fern from the Upper Triassic of the Caspian Depression in the context of florogenetic processes of transition from the Paleozoic to Mesozoic. *Paleontological Journal*, 49: 326–336.

Niedźwiedzki, G. & Remin, Z., 2008. Gigantic theropod dinosaur footprints from the Upper Pliensbachian of the Holy Cross Mountains, Poland). *Przegląd Geologiczny*, 56: 823–825. [In Polish, with English abstract.]

Niedźwiedzki, G., Remin, Z. & Pieńkowski, G., 2008. Preliminary report about spectacular Late Pliensbachian dinosaur tracksite from the Holy Cross Mountains, Poland. In: *5TH International Symposium of IGCP 506 on: Marine and Non-Marine Jurassic: Global Correlation and Major Geological Events. Abstract Volume. Tunisia (Hammamet), March 28–31, 2008*. UNESCO, Hammamet, pp. 110–111.

Niedźwiedzki, G., Remin, Z., Roszkowska, J. & Meissner, U., 2009. New finds of dinosaur tracks in the Liassic strata of the Holy Cross Mountains, Poland. *Przegląd Geologiczny*, 57: 252–262. [In Polish, with English abstract.]

Pacyna, G., 2013. Critical review of research on the Lower Jurassic flora of Poland. *Acta Palaeobotanica*, 53: 141–163.

Pacyna, G., 2021 (in press). Matoniaceous ferns from the Lower Jurassic of the Holy Cross Mountains (SE Poland). Revision of historical specimens and description of some new materials. *Acta Palaeobotanica*, 61.

Parrish, J. T. & Falcon-Lang, H. J., 2007. Coniferous trees associated with interdune deposits in the Jurassic Navajo Sandstone Formation, Utah, USA. *Palaeontology*, 50: 829–843.

Pieńkowski, G., 1991. Eustatically-controlled sedimentation in the Hettangian–Sinemurian (Early Jurassic) of Poland and Sweden. *Sedimentology*, 38: 503–518.

Pieńkowski, G., 2004. The epicontinental Lower Jurassic of Poland. *Polish Geological Institute Special Papers,* 12: 1–122.

Pieńkowski, G., 2006. Field trip B4 – Lower Jurassic marginal-marine and continental deposits – sedimentation, sequences, and ecosystems. In: Wierzbowski, A., Aubrecht, R., Golonka, J., Gutowski, J., Krobicki, M., Matyja, B. A., Pieńkowski, G. & Uchman, A. (eds), *Jurassic of Poland and Adjacent Slovakian Carpathians. Field Trip Guidebook of 7th International Congress of the Jurassic System*. Polish Geological Institute, Warszawa, pp. 207–235.

Pieńkowski, G., Hesselbo, S. P., Barbacka, M. & Leng, M. J., 2020. Non-marine carbon-isotope stratigraphy of the Triassic-Jurassic transition in the Polish Basin and its relationships to organic carbon preservation, pCO_2 and palaeotemperature. *Earth-Science Reviews*, 210, 103383. [15 pp.]

Pieńkowski, G., Hodbod, M. & Ullmann, C. V., 2016. Fungal decomposition of terrestrial organic matter accelerated Early Jurassic climate warming. *Scientific Reports*, 6, 31930. [11 pp.]

Pieńkowski, G., Schudack, M. E., Bosák, P., Enay, R., Feldman-Olszewska A., Golonka, J., Gutowski, J., Herngreen, G. F. W., Jordan, P., Krobicki, M., Lathuiliere, B., Leinfelder, R. R., Michalík, J., Mönnig, E., Noe-Nygaard, N., Pálfy, J., Pint, A., Rasser, M. W., Reisdorf, A. G., Schmid, D. U., Schweigert, G., Surlyk, F., Wetzel, A. & Wong, T. E., 2008. Jurassic. In: McCann, T. (ed.), *The Geology of Central Europe, Volume 2: Mesozoic and Cenozoic*. Geological Society, London, pp. 823–922.

Piggott, A. G. & Piggott, C. J., 1988. *Ferns of Malaysia in Colour*. Kuala Lumpur, Tropical Press, 458 pp.

Podbielkowski, Z. & Podbielkowska, M., 1992. *Przystosowania roślin do środowiska*. Wydawnictwa Szkolne i Pedagogiczne, Warszawa, 584 pp. [In Polish.]

Popa, M., 1997. Liassic ferns from the Steierdorf Formation, Anina, Romania. In: Herngreen G. F. W. (ed.), *Proceedings of the 4th European Palaeobotanical and Palynological Conference. Mededelinger Nederlands Instituut voor Toegepaste Geowetenschappen TNO*, 58: 139–147.

Pott, C., Bouchal, J. M., Choo, T., Yousif, R. & Bomfleur, B., 2018. Ferns and fern allies from the Carnian (Upper Triassic) of Lunz am See, Lower Austria: A melting pot of Mesozoic fern vegetation. *Palaeontographica. Abteilung B*, 297: 1–101.

PPG I, 2016. A community-derived classification for extant lycophytes and ferns. *Journal of Systematics and Evolution*, 54: 563–603.

Presl, K. B., 1848. Die Gefässbündel im stipes der farrn. *Abhandlungen der Königlichen Böhmischen Gesellschaft der Wissenschaften*, 5 (5): 307–356.

Pšenička, J., Wang, J., Rößler, R., Popa, M. E. & Kvaček, J., 2020. Long-lasting morphologies despite evolution: Ferns (Monilophytes) throughout the Phanerozoic. In: Martinetto, E., Tschopp, E. & Gastaldo, R. A. (eds), *Nature Through Time.*

Virtual Field Trips Through the Nature of the Past. Springer, Cham, pp. 269–290.

Raciborski, M., 1891. Flora retycka północnego stoku Gór Świętokrzyskich. *Rozprawy Wydziału Matematyczno-Przyrodniczego Akademii Umiejętności w Krakowie*, 23: 292–326. [In Polish.]

Raciborski, M., 1892. Przyczynek do flory retyckiej Polski. *Rozprawy Wydziału Matematyczno-Przyrodniczego Akademii Umiejętności w Krakowie*, 22: 345–360. [In Polish.]

Raciborski, M., 1894. The fossil flora of Kraków's refractory clays. Part I. Cryptogamous plants (Archaegoniatae). *Pamiętnik Matematyczno-Przyrodniczy Akademii Umiejętności*, 18: 1–101. [In Polish.]

Reymanówna, M., 1963. The Jurassic flora from Grojec near Cracow in Poland. Part I. *Acta Palaeobotanica*, 4: 9–48.

Reymanówna, M., 1965. On *Weichselia reticulata* and *Frenelopsis hoheneggeri* from the Western Carpathians. *Acta Palaeobotanica,* 6: 15–25.

Rogalska, M., 1976. Stratigraphy of the Lower and Middle Jurassic in the Polish Lowlands on the basis of spore and pollen analysis. *Prace Instytutu Geologicznego*, 78: 1–61. [In Polish, with English summary.]

Rothwell, G. W. & Stockey, R. A., 2008. Phylogeny and evolution of ferns: a paleontological perspective. In: Ranker, T. A. & Haufler, C. H. (eds), *Biology and Evolution of Ferns and Lycophytes*. Cambridge University Press, Cambridge, pp. 332–366.

Schenk, A., 1865–1867. *Die fossile Flora der Grenzschichten des Keupers und Lias Frankens*. Kreidel, Wiesbaden, 231 pp.

Schenk, A., 1871. Beiträge zur Flora der Vorwelt, IV. Die Flora der nordwestdeutschen Wealdenformation. *Palaeontographica*, 19: 203–276.

Schimper, W. P., 1869–1874. *Traite de Paleontologie vegetale ou la flore du monde primitif dans ses rapports avec les formations geologiques et la flore du monde actuel*. Vol. 1 (1869), 738 pp.; Vol. 2 (1870- 1872), 869 pp.; Vol. 3 (1874), 966 pp.; Atlas (1874), 110 pls. J. B. Baillere et Fils, Paris.

Schmidt, A. R. & Dörfelt, H., 2007. Evidence of Cenozoic Matoniaceae from Baltic and Bitterfeld amber. *Review of Palaeobotany and Palynology*, 144: 145–156.

Schneider, H., Schuettpelz, E., Pryer, K. M., Cranfill, R., Magallón, S. & Lupia, R., 2004. Ferns diversified in the shadow of angiosperms. *Nature*, 428: 553–557.

Schweitzer, H-J., 1978. Die Raeto-Jurassischen Floren des Iran und Afghanistans: 5. *Todites princeps, Thaumatopteris brauniana* und *Phlebopteris polypodioides. Palaeontographica, Abteilung B*, 168: 17–60.

Schweitzer, H-J., Schweitzer, U., Kirchner, M., van Konijnenburg-van Cittert, J. H. A., van der Burgh, J. & Ashraf, R. A., 2009. The Rhaeto-Jurassic flora of Iran and Afghanistan. 14. Pterophyta – Leptosporangiatae. *Palaeontographica, Abteilung B*, 279: 1–108.

Seward, A. C., 1899. On the structure and affinities of *Matonia pectinata*, R. Br., with notes on the geological history of the Matonineae. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 191: 171–209.

Silantieva, N. & Krassilov, V., 2006. *Weichselia* Stiehler from Lower Cretaceous of Makhtesh Ramon, Israel: new morphological interpretation and taxonomical affinities. *Acta Palaeobotanica*, 46: 119–135.

Skurczyńska-Garwolińska, K. & Woroncowa-Marcinowska, T., 2015. *Katalog zbiorów Muzeum Geologicznego. Dział III. Rośliny kopalne*. Państwowy Instytut Geologiczny - Państwowy Instytut Badawczy, Warszawa, 286 pp.

Smith, A. R., Pryer, K. M., Schuettpelz, E., Korall, P., Schneider, H. & Wolf, P. G., 2006. A classification for extant ferns. *Taxon*, 55: 705–731.

Sternberg, K. M., 1820–1838. *Versuch einer geognostisch botanischen Darstellung der Flora der Vorwelt*. Fr. Fleischer, Leipzig und Prag, 220 pp.

Sudnik-Wójcikowska, B. & Krzyk, A., 2015. *Flora Polski. Rośliny wydm, klifów, solnisk i aluwiów*. MULTICO Oficyna Wydawnicza, Warszawa, 320 pp. [In Polish.]

Taylor, T. N., Taylor, E. L. & Krings, M., 2009. *Paleobotany, The Biology and Evolution of Fossil Plants, Second Edition*. Academic Press, Amsterdam, 1230 pp.

Tidwell, W. D. & Ash, S. R., 1994. A review of selected Triassic to Early Cretaceous ferns. *Journal of Plant Research*, 107: 417–442.

Tryon, R. M., 1936. Ferns of the dune region of Indiana. *American Midland Naturalist*, 17: 425–429.

Turland, N. J., Wiersema, J. H., Barrie, F. R., Greuter, W., Hawksworth, D. L., Herendeen, P. S., Knapp, S., Kusber, W.-H., Li, D.-Z., Marhold, K., May, T. W., McNeill, J., Monro, A. M., Prado, J., Price, M. J. & Smith, G. F. (eds), 2018. *International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. Regnum Vegetabile 159*. Koeltz Botanical Books, Glashütten, 254 pp.

Van Konijnenburg-van Cittert, J. H. A., 1993. A review of the Matoniaceae based on in situ spores. *Review of Palaeobotany and Palynology*, 78: 235–267.

Van Konijnenburg-van Cittert, J. H. A., 2002. Ecology of some Late Triassic to Early Cretaceous ferns in Eurasia. *Review of Palaeobotany and Palynology*, 119: 113–124.

Van Konijnenburg-van Cittert, J. H. A., Pott, C., Schmeißner, S., Dütsch, G. & Kustatscher, E., 2020. Ferns and fern allies in the Rhaetian flora of Wüstenwelsberg, Bavaria, Germany. *Review of Palaeobotany and Palynology*, 273, 104147. [21 pp.]

Walker, J., Thompson, C. H., Fergus, I. F. & Tunstall, B. R., 1981. Plant succession and soil development in coastal sand dunes of subtropical eastern Australia. In: West, D. C., Shugart, H. H. & D. B. Botkin (eds), *Forest Succession: Concepts and Application*. Springer Verlag, New York, pp. 107–131.

Wallich, N., 1830. *Plantae Asiaticae Rariores: or, Descriptions and Figures of a Select Number of Unpublished East Indian Plants. Vol. 1*. Richard Taylor, London, 100 pp.

Wang, Y., 2002. Fern ecological implications from the Lower Jurassic in western Hubei, China. *Review of Palaeobotany and Palynology*, 119: 125–141.

Warren, A., 2013. *Dunes: Dynamics, Morphology, History*. John Wiley & Sons, West Sussex, 227 pp.

Zeiller, R., 1885. Sur les affinités du genre *Laccopteris. Bulletin de la Société botanique de France*, 32: 21–25.