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 succession-al-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 Dörflert, 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

Abstract: The occurrence of the fern Matonia braunii (Goepert) 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.

Key words: Pliensbachian, foreshore, aeolian dune, ferns in life position, Phlebopteris, Matonia.

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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 supraprovincial 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

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**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 Szydłowiek 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

![Lithologic profile of Lower Jurassic deposits of the Holy Cross Mountains](image_url)

**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 Szydlowiec Sandstones at Szydlowiec, 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 (Piekowski, 2004; Gierliński et al., 2006). Specimens from Szydlowiec (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 Szydlówek and Śmiłów (Piekowski, 2004), and also known from boreholes, such as the Gutwin (Rogalska, 1976) and Brody-Lubienia boreholes (Piekowski et al., 2016). Depositional sequence VI deposits belong to the late Sinemurian–Pliensbachian mega-spore *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 Szydlowiec 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 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 braunii* sp. nov. – Goeppert, pp. 7–8, pl. 5, figs 1–7.

1841 *Laccopteris germanns* 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 braunii* (Goeppert) Hirmer and Hoerhammer – Makarewiczówna, 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 – Makarewiczówna, 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 pinnae), 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 dune field) 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, Dźwiértinia, 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
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)

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.
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 mesicoides* 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; Barbacca 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 (Fuchs et al., 1991). 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 (Barbacca, 2011; Babarcza 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 Nekeňa borehole are interpreted as floodplain-backswamp, located at the transition between floodplain and lacustrine-back-swamp, associated with a fluvial environment (Barbacca 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 colonise 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 Prenz* 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) 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 drifts were found (Pieńkowski, 2004; Gierliński et al., 2006). They are not similar to the remains at the Podkowiński Quarry; they are larger, coalfied, 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 silicilastic foreshore zone, interfingerling 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 dunefields.

Szydłowiek 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 Schizaceae, seed ferns, conifers from the families Taxodiaceae, Podocarpaceae and Pinaceae, cycads, bennettitales 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.

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