

Matoniaceous ferns from Lower Jurassic strata of the Holy Cross Mountains (SE Poland). Revision of historical specimens and description of some new materials

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Received 9 April 2021; accepted for publication 7 June 2021

ABSTRACT. Ferns from the family Matoniaceae are characteristic but not very numerous elements of Early Jurassic floras of the Holy Cross Mountains. Based on historical specimens from the Geological Institute of the Polish Academy of Sciences, only partly published by Raciborski and Makarewiczówna, and a new collection gathered recently from the Gromadzice outcrop, two taxa are here recognised: *Matonia braunii* and *Phlebopteris angustiloba*, of which only *P. angustiloba* is rather frequent. Both species are represented by sterile and fertile specimens well comparable with historical and recently published material of these species from Greenland, Germany and Sweden. Specimens referred by Raciborski to *Laccopteris elegans* (illegitimate name) do not belong to Matoniaceae.

KEYWORDS: *Matonia*, *Phlebopteris*, Hettangian, Gromadzice

INTRODUCTION

The fern family Matoniaceae is a characteristic but only locally numerous and moderately taxonomically diversified element of Mesozoic floras from the Late Triassic to Cretaceous, becoming more and more relictual in the Cenozoic (Schweitzer, 1978; Tidwell and Ash, 1994; Popa, 1997; Taylor et al., 2009). The most characteristic features of the family include pedate fronds with pinnate pinnae and sporangia arranged in sori, with or without a peltate indusium (Kramer, 1990; Taylor et al., 2009). This family is well represented in Early and Middle Jurassic floras of southern Poland (Raciborski, 1894; Pacyna, 2013). The following genera were documented: *Matonia* R. Brown in Wallich, *Matonidium* Schenk and *Phlebopteris* Brongniart (= *Laccopteris* Presl in Sternberg) (Raciborski, 1891, 1892, 1894; Makarewiczówna, 1928; Reymanówna, 1963;

Barbacka et al., 2010, 2014, 2016; Pacyna, 2013). Published research (Barbacka et al., 2014, 2016) and ongoing work on Matoniaceae from the Polish Mesozoic (Holy Cross Mountains area, Grojec locality) has indicated the need to revise historical specimens, as new data about this family have been amassed in recent years (Van Konijnenburg-van Cittert, 1993; Badihagh and Uhl, 2019; Barbacka et al., 2019; Van Konijnenburg-van Cittert et al., 2020) and there has been progress on taxonomical issues (Harris, 1980; Klavins et al., 2004; Kvaček and Dašková, 2010).

Early Jurassic plants from the Holy Cross Mountains were among the first-described fossil plants from Polish territory. In two papers, M. Raciborski (1891, 1892) described several species from the Ostrowiec Świętokrzyski area. Makarewiczówna (1928) revised some

material published by Raciborski and described additional later-collected specimens. Modern research on this flora began with the discovery of the Odrowąż (Sołtyków) locality in the 1970s (Reymanówna et al., 1987). Based on these specimens and new material from boreholes, several papers have been published since then (Ziaja, 2006; Barbacka et al., 2010, 2014, 2016), and new specimens from historical localities such as Gromadzice have been collected recently (Pacyna and Zdebska, 2011; Pacyna et al., 2018). Pacyna (2013) summarised the history of that research and collated a list of recognised taxa. Despite this revival of research on Early Jurassic plants from the Holy Cross Mountains, the material published by Raciborski has not yet been revised. The collection gathered for him includes, besides the specimens he published, numerous specimens that were not registered and described. Revision of this material is important for many reasons. It includes specimens from now-inaccessible outcrops, some well-preserved examples, and some specimens on which Raciborski based proposals of new taxa. Some interpretations and the nomenclature used are outdated, however, and need revision. The historical collection of Early Jurassic plants from the Holy Cross Mountains stored in the Geological Institute of the Polish Academy of Sciences is the largest one still available. The fate of most specimens described

by Makarewiczówna (1928) is unknown; probably they are lost. In the mentioned collection I identified some of the specimens she illustrated. Her collection in the Institute of Botany of the Jagiellonian University probably is incompletely preserved; no specimen could be identified with confidence as illustrated by her. We do not know the whereabouts of specimens from the Polish Geological Institute in Warsaw (J. Czarnocki collection) and from the no-longer-existing S. Batory University (B. Rydzewski collection) in Wilno (today Vilnius Universitetas in Vilnius, Lithuania). Specimens collected and listed by Kuźniar (1923, 1924) probably were lost during World War II.

This paper revises published and unpublished historical specimens of matoniaceous ferns from Lower Jurassic strata of the Holy Cross Mountains. Some specimens published by Raciborski (1891) do not in fact belong to this family and will be the subject of forthcoming research; several specimens so far unpublished turned out to belong to the Matoniaceae and provided fine, important morphological details. Some historical specimens of this family from the region could not be revised for the reasons enumerated above. A matoniaceous specimen (positive and negative of one pinna) from a new collection from Gromadzice is also here described. This is the first paper describing material from recent excavations in Gromadzice in detail.

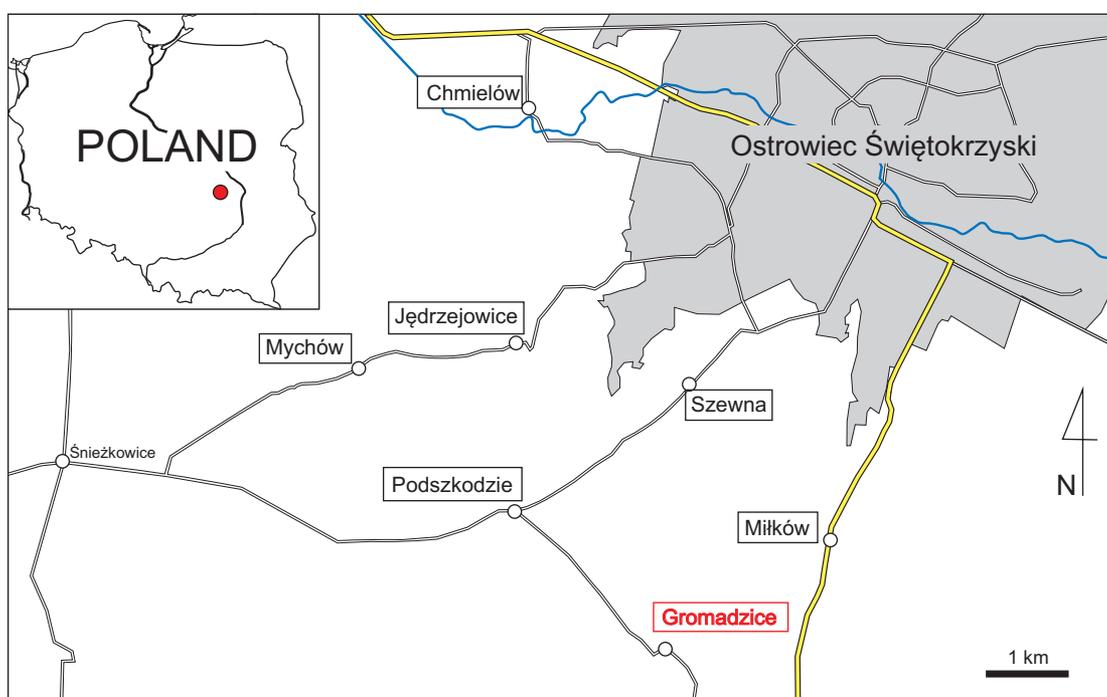


Fig. 1. Map showing Lower Jurassic plant-bearing localities in the Ostrowiec Świętokrzyski area, including those from which the described material originates (Gromadzice), and the location of the investigated area in Poland

GEOLOGICAL SETTING

Lower Jurassic sediments are well exposed in the Ostrowiec Świętokrzyski region in the Holy Cross Mountains (Pieńkowski, 2004, 2006). Many outcrops with fossil plants were accessible at the end of the 19th century (e.g. Gromadzice, Miłków, Mychów, Jędrzejowice, Chmielów, Szewna, Podzgodzie; Fig. 1). Among these, Gromadzice provided most specimens of a well-preserved flora, but today it is not possible to determine with certainty the exact sites where the specimens Raciborski described were gathered. Two outcrops are still accessible: the Gromadzice lower outcrop with the uppermost part of the Zagaje Formation exposed, and the Gromadzice upper outcrop with sediments of the Skłoby Formation; identifiable plant remains are present only in the former (Fig. 2). The lower outcrop in Gromadzice is on the bank of Kamionka Stream. The outcrop reveals a sequence of an alluvial depositional system and an upper delta plain depositional subsystem (Pieńkowski, 2004: fig. 11, 2006: fig. B4.14). The change in the depositional system from alluvial plain to delta plain is gradual. The lower part of the outcrop comprises a meandering alluvial channel subsystem with trough-cross bedded sandstone filling channels. The overlying complex is composed of grey laminated mudstones, siltstones and grey fine-grained sandstones. Its characteristics point to an upper delta plain deposit, where the muddy overbank plain was periodically occupied by brackish water. Sandstone/siltstone layers represent deltaic, basinwards-prograding crevasse splay depositions. These features are consistent with rapid aggradation during which crevassing lacustrine/marsh sedimentation and avulsion dominated the delta plain/floodplain. Most plant macrofossils from the lower outcrop in Gromadzice are preserved in crevasse splay deposits. Numerous specimens were gathered from this outcrop recently (Pacyna et al., 2018), but only one matoniaceous fern specimen was found. This assemblage is dominated by leaves and cones of ginkgoaleans and czekanowskialean (*Sphenobaiera*, *Czekanowskia*). Other taxa such as sphenopsids (*Neocalamites*), ferns (*Cladophlebis*, *Matonia*, *Dictyophyllum*), seed ferns (*Sagenopteris*, *Pachypteris*), bennettitaleans, cycads (*Nilssonia*) and conifers (*Podozamites*,

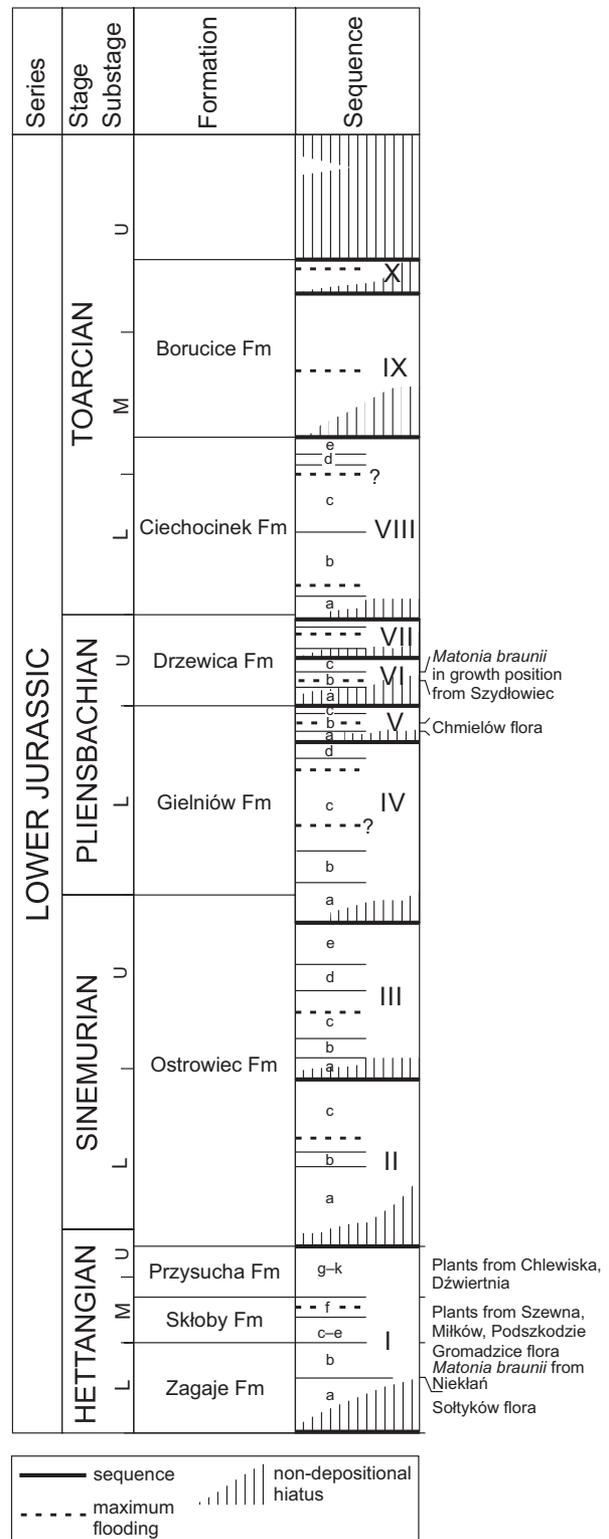


Fig. 2. Stratigraphy of the Lower Jurassic deposits of the Holy Cross Mountains (after Pieńkowski 2004: figs 3 and 72, modified), with source strata of the investigated material and other discussed fossil floras. Abbreviations used: L – lower, M – middle, U – upper

Brachyphyllum, *Pityophyllum*, *Stachyotaxus*) are rare. In contrast to the floral remains gathered recently from the lower outcrop in Gromadzice, Raciborski's collection is fern-dominated. The plant fossils originated from

two different sediment types: fine clay probably of lacustrine origin, and sandy mudstone of fluvial origin. In sandy mudstones the ferns are numerous: *Dictyophyllum* spp., *Marattiopsis muensteri*, *Thaumatopteris brauniana* and several specimens of pinnae fragments and isolated pinnules of *Phlebopteris angustiloba* and pinnae fragments of *Matonia braunii*. Also present are the sphenopsids *Neocalamites lehmannianus* and *Equisetites muensteri*, and the gymnosperms *Sagenopteris* sp., *Ixostrobus siemiradzki*, *Taeniopteris tenuinervis*, *Schizolepis follinii* and *Stachytaxus septentrionalis*. Fossils are much rarer in fine clays, but one specimen of *Phlebopteris angustiloba* pinnae and an isolated pinnule of *Matonia braunii* with sori preserved were found.

MATERIALS AND METHODS

For this research, all available historical specimens of Matoniaceae from Lower Jurassic strata of the Holy Cross Mountains deposited in the Geological Museum of the Institute of Geological Sciences, Polish Academy of Sciences Research Centre in Cracow (formerly the collection of the Physiographical Commission of the Polish Academy of Arts and Sciences), were studied. These specimens were published only in part by Raciborski (1891, 1892) and Makarewiczówna (1928). They are stored under collection numbers ZNG PAN A-III-25 and 26. It should be mentioned that collection and specimen numbers were assigned to these specimens many years after Raciborski's work; he did not use a system of numbering for his hand specimens. This caused problems in identifying which specimens had been described and illustrated; sometimes identification is impossible. For specimens determined to have been illustrated by Raciborski, the original plate and figure numbers are given in parentheses after the collection acronym and specimen number. The shape of the stone slabs of some drawn specimens differs considerably from the reality. Some specimens were cropped for better alignment of the plate, and other drawings show the front and back of the specimen together in one plane. Another problem is that some specimens were wrongly assigned to source localities, even by Raciborski himself and probably also later by collection curators. Based on the lithology and the taxa preserved, it is evident that some specimens from Gromadzice were assigned to the Chmielów and even the Grojec localities (e.g. A-III-12/208), and vice versa. The following specimens that are revised here were undoubtedly examined by Raciborski and described in his papers: A-III-26/2, 4a+b, 20-21, 33-36, 48 (Raciborski, 1891, 1892). Some specimens identified by Raciborski as belonging to *Laccopteris elegans* (A-III-26/32-33) do not belong to Matoniaceae but probably to Osmundaceae. Specimens A-III-25/24-32, and PC IB UJ 106/54a+b have not been examined earlier. Raciborski's historical plant fossil remains from Lower Jurassic strata of the Holy Cross Mountains (belonging to the

Institute of Botany, Jagiellonian University) have also been examined; no matoniaceous fern was identified, however. In a large recently gathered collection of fossil plants from Gromadzice, only one specimen (positive and negative) belongs to the Matoniaceae. This collection is stored in the Institute of Botany, Jagiellonian University, collection number Palaeobotanical Collection IB UJ 106.

The specimens are preserved as impressions, sometimes with remnants of coaly matter (A-III-25/31, PC IB UJ 106/54a). Details of sori and sporangia are rare and poorly preserved. The specimens are very difficult to photograph due to the lack of contrast and the faintness of three-dimensional relief. The condition of the historical specimens is not good; they are heavily dusted. Many crucial details of, for example, sori and sporangia structure, which Raciborski observed, described and illustrated, are not visible today at all, probably due to small damages incurred during long storage. This hampers revision and reinterpretation of some important specimens. Important morphological details are more visible on recently discovered specimens. 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. Polarised light was used to increase the contrast.

The suprageneric classification follows Cronquist et al. (1966), Smith et al. (2006) and PPG I (2016).

SYSTEMATIC DESCRIPTION

Class: POLYPODIOPSIDA Cronquist,
Takhtajan et Zimmermann, 1966

Order: GLEICHENIALES Schimper, 1869

Family: MATONIACEAE Presl, 1848

Genus: *Matonia* R. Brown in Wallich, 1830

Matonia braunii

(Goeppert, 1841) Harris, 1980

Pl. 1, figs 1–5a

Selected synonyms:

- 1841 *Laccopteris brauni* Goeppert; Goeppert, pp. 7, 8, pl. 5, figs 1–7.
 1841 *Laccopteris germinans* Goeppert; Goeppert, pp. 9, 10, pl. 6, figs 1–12.
 1865–1867 *Laccopteris göpperti* Schenk; Schenk, pp. 94–97, pl. 23, figs 1–12, pl. 24, figs 2–5.
 1865–1867 *Laccopteris münsteri* Schenk; Schenk, pp. 97, 98, pl. 24, figs 6–10, pl. 25, figs 1, 2a, b.
 non 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.
 1926 *Laccopteris groenlandica* Harris; Harris, pp. 62–64, pl. 3, fig. 5, text-fig. 6.

- ? 1928 *Laccopteris elegans* Presl in Sternberg; Makarewiczówna, p. 3.
- 1928 *Laccopteris Münsteri* Schenk; Makarewiczówna, p. 4, p. 1(10), figs 2, 2a.
- 1931 *Laccopteris brauni* Goepfert; Harris, pp. 70–74, pl. 14, figs 1, 2, pl. 15, fig. 7, text-figs 24, 25.
- 1936 *Phlebopteris brauni* (Goepfert) Hirmer and Hoerhammer; Hirmer and Hoerhammer, pp. 7–17, text-figs 3, 4, 5, 1A–1D, 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–2B, pl. 3, figs 1–7, pl. 4, figs 1–6, pl. 5, figs 1–6.
- 1980 *Matonia braunii* (Goepfert) Harris; Harris, pp. 295–310, figs 1–20.
- 1997 *Matonia braunii* (Goepfert) Harris; Popa, p. 142, text-figs 19, 20, pl. 2, fig. 5.
- 2016 *Matonia braunii* (Goepfert) Harris; Barbacka et al., pp. 860–865, figs 2–5.
- 2019 *Matonia braunii* (Goepfert) 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. Pinnae fragments: A-III-25/28, 30, 32 (all sterile), PC IB UJ 106/54a+b (fertile); isolated fertile pinnule: A-III-25/31. All specimens from Gromadzice, uppermost part of Zagaje Formation, parasequence Ib, lower Hettangian.

Description. Only fragments of apical parts of sterile and fertile pinnae preserved, 7–65 mm long (Pl. 1, figs 1–5). Pinnae rachis 0.5–1.5 mm wide. Pinnae once pinnate, size of pinnules slightly decreasing towards pinna apex. Most pinnules incomplete, lacking apices, preserved length 15–18 mm. Pinnules 2.0–3.5 mm wide at base, towards apex slightly narrowing to 1.5–3.0 mm. Pinnules with straight margins, densely arranged, attached at ~80° angle, subopposite. Adjacent pinnules 0.5–1.5 mm apart, connected through gentle narrow wing, up to 0.5 wide along rachis. Pinnule venation difficult to recognise, only central vein visible (Pl. 1, figs 1–5). On fertile pinnules, rows of sori on both sides of central vein, occupying almost full width of pinnule lamina between vein and margin (Pl. 1, figs 1, 2, 5). Sori 0.7–1.0 mm in diameter, 0.2–0.5 mm apart (Pl. 1, figs 1a, 5). At least six sporangia per sorus. Sporangia oval, 0.1–0.2 mm in diameter with prominent annuli (Pl. 1, figs 1b, 5a).

Remarks. The material documented here is compatible with that described and illustrated by Harris (1980) and Barbacka et al.

(2016, 2019) as *Matonia braunii* and by Goepfert (1841), Schenk (1865–1867), Seward (1899), Harris (1931), Hirmer and Hoerhammer (1936) and Van Konijnenburg-van Cittert et al. (2020) as belonging to *Phlebopteris braunii* and *Phlebopteris muensteri*. Harris (1980) interpreted these two latter species to be synonymous, considering the specimens classified as *Phlebopteris muensteri* to be sun fronds and *Phlebopteris braunii* to be shade fronds of the same species. Historically, most authors have referred mainly sterile leaves with rather short, even somewhat triangular pinnules to *Phlebopteris braunii*, and mainly fertile leaves with rather long linear pinnules to *Phlebopteris muensteri* (see e.g. Hirmer and Hoerhammer, 1936 for a very good illustration of this). However, intermediate specimens prevail or both morphologies co-occur in many published collections (e.g. Barbacka et al., 2016; Van Konijnenburg-van Cittert et al., 2020), and clear morphological differences on which separation on these species may be based are lacking. Harris (1980) also confirmed the presence of indusiate sori in his material, and on this basis referred both these species to the extant genus *Matonia* and combined them under the name *Matonia braunii* (Goepfert) Harris. This opinion is maintained here, though it should be mentioned that some authors still question their synonymy (see e.g., Van Konijnenburg-van Cittert, 1993; Schweitzer et al., 2009; Van Konijnenburg-van Cittert et al., 2020), based on elusive differences in leaf and sori morphology. According to these authors the most important difference between these species is the presence of indusiate sori in *Matonia* (*Phlebopteris*) *braunii* and their lack in *Phlebopteris muensteri*. This is in accordance with Hirmer and Hoerhammer's (1936) hypothesis that the oldest members of Matoniaceae (included in the genus *Phlebopteris*) are exindusiate and that the indusium evolved gradually in this family during the Mesozoic. However, both these species (exindusiate and indusiate) co-occur even in their oldest Upper Triassic records, and Klavins et al. (2004) documented indusiate sori in the oldest known Matoniaceae from the Middle Triassic of Antarctica. So even if Hirmer and Hoerhammer's (1936) hypothesis of the indusium's origin in Matoniaceae is correct, it cannot be documented based on available Mesozoic fossils, and this evolutionary change must have taken place before the first

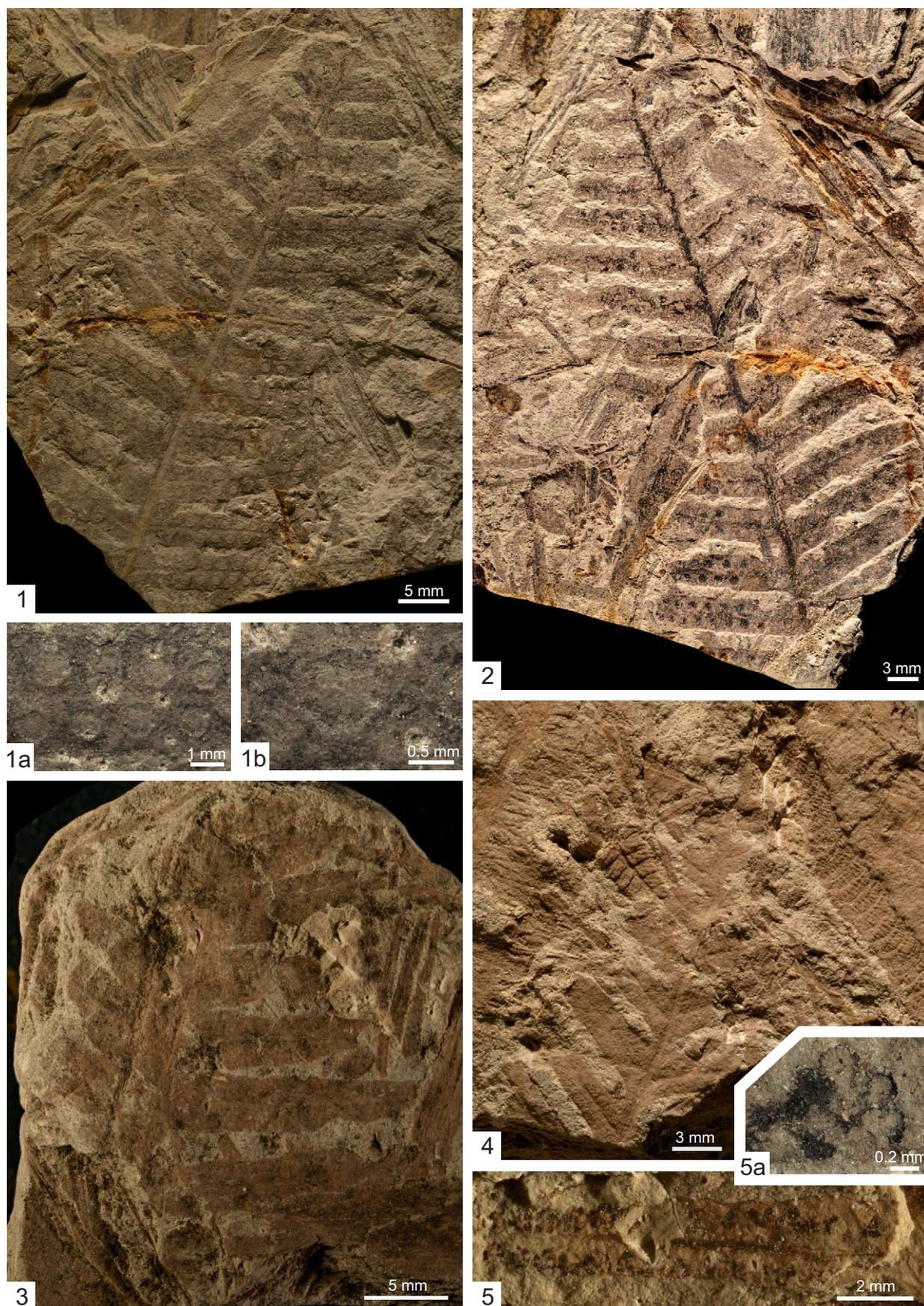


Plate 1. *Matonia braunii*. **1.** Fertile pinna, positive, PC IB UJ 106/54a; **1a.** Detail from 1, fragment of pinnule with sori visible, needle marks after preparation visible between sori; **1b.** Detail from 1a, one sorus, faint imprints of sporangia with annuli visible; **2.** Fertile pinna, negative, PC IB UJ 106/54b; **3.** Fragment of sterile pinna, A-III-25/30; **4.** Apical part of small sterile pinna, A-III-25/28; **5.** Isolated fertile pinnule, sori with sporangia visible, A-III-25/31; **5a.** Detail from 5, one sorus, sporangia with annuli visible

appearance of indusiate Matoniaceae in the Middle Triassic (Klavins et al., 2004).

The following features of this material confirm that it belongs to *Matonia braunii* as interpreted by Harris (1980) and Barbacka et al. (2016, 2019): pinnae shape, pinnule shape and dimensions, type of venation, size, and sori shape and arrangement. The specimens described here are in the middle range of variability limited by the morphotype margins described as the separate species *Phlebopteris braunii* and *Phlebopteris muensteri*. They have pinnules shorter and wider than most typical specimens referred historically to *P. muensteri*, and pinnule size decreasing lengthwise towards the pinna apex, which is most typical for specimens referred to *P. braunii*. Only naked sori without indusia were observed (Pl. 1, figs 1b, 5a). The indusia probably were lost before pinnae fossilisation, as the sporangia are well developed and hence probably mature and ready to disperse spores. This interpretation is based on Harris's (1980) careful observations of recent *Matonia*. In mature leaves the indusia are easily lost, revealing sporangia ready to disperse spores. The well-known Late Triassic species *Phlebopteris smithii* (Daugherty) Arnold was described as exindusiate, but the authors (Arnold, 1956; Ash et al., 1982; Litwin, 1985) could not exclude the possibility that indusia were present during the leaves' early ontogenetic stages, since they have at their disposal only mature fertile leaves with well-developed sporangia. New well-preserved material of *Matonia braunii* from the Niekłań borehole in the Holy Cross Mountains described by Barbacka et al. (2016) is also important for several reasons in the present context. First, it confirms Harris's (1980) suggestion that *Phlebopteris braunii* and *Phlebopteris muensteri* are conspecific based on their co-occurrence and indusiate sori details. The Niekłań material has well-visible indusia, which also concurs with Harris's referral of *Phlebopteris braunii* to the recent genus *Matonia*. Second, pinnules with morphology typical for *P. muensteri* have indusia preserved (Barbacka et al., 2016: figs 3E–G), a feature not observed before (compare Van Konijnenburg-van Cittert, 1993). In the sori of some mature pinnules from Niekłań not only are the indusia lost but even part of the sporangia fell off. This is also in line with Harris's neontological observations (Harris, 1980).

Specimens from Poland that may belong to *Matonia braunii* were first mentioned by Raciborski (1891) and referred to *Laccopteris elegans*. During the present research and after an examination of the original specimens, it appeared that the two biggest specimens thoroughly described and illustrated by Raciborski (1891: pl. 4, fig. 1, 4, specimens A-III-26/32, 33) as *Laccopteris elegans* cannot not be referred to this poorly defined species, other *Phlebopteris* species, or even the family Matoniaceae. Those specimens, although poorly preserved and difficult to examine, show some important features incompatible with this family. Pinnule size changes gradually on most *Phlebopteris* or *Matonia* pinnae, but here they almost do not change along the pinna rachis. The pinnules in these specimens are not oblong as is typical for Matoniaceae, but rather somewhat triangular (especially in specimen A-III-26/33); however, this feature is not so prominent as in the genus *Cladophlebis*. The venation is of neuropterid type rather than pectopterid or pectopterid-reticulate as in *Phlebopteris*. These specimens may belong to Osmundaceae and will be the subject of forthcoming research to be published later.

The species *Laccopteris elegans* was proposed by Presl in Sternberg (1838), based on poorly preserved isolated pinnules. Actually the type specimen has only one pinnule preserved (Hirmer and Hoerhammer, 1936; Jung and Knobloch, 1972; Kvaček and Straková, 1997). However, before the last part of Sternberg's work was printed, Goeppert (1836) described and identified the same specimen as *Asterocarpus lanceolatus* Sternberg (proper species authorship should be *Asterocarpus lanceolatus* Sternberg in Goeppert). He did not publish an illustration himself, but referred to a plate in Sternberg's work, with an error (plate 31 instead of plate 32). Therefore the species name *Laccopteris elegans* is a nomenclatural synonym of *Asterocarpus lanceolatus* and an illegitimate name as superfluous, including the type of the formerly validly published name (Turland et al., 2018). Moreover, the type *Laccopteris elegans* is indeterminate and may not even belong to Matoniaceae (Hirmer and Hoerhammer, 1936). *Laccopteris elegans* Presl in Sternberg was treated for some time by many authors including Raciborski himself (Schimper, 1869–1874; Raciborski, 1891; Seward, 1899; Möller, 1902; Lilpop and Kostyniuk, 1957) as a synonym of *Phlebopteris braunii*.

Although the specimens described and illustrated by Raciborski (1891) were misidentified, historical specimens available to him but not described in his publication confirm the presence of *Matonia braunii* (= *Phlebopteris braunii*) in Gromadzice. These specimens are documented in the present paper for the first time, along with new material of that species from this locality. In fact, Raciborski (1981) mentioned along with two illustrated specimens the presence of other incomplete and worse-preserved specimens but did not describe them; perhaps he meant some specimens described here. Some specimens Raciborski described and illustrated are no longer in his collection. Among these lost specimens is one that may belong to *Matonia braunii*; it was figured on pl. 2, fig. 14 in Raciborski (1892). It is referred to in the text (p. 349) as *Dictyophyllum* aff. *dunkeri*, as *Thaumatopteris dunkeri* in the plate explanation, and as *Dictyophyllum dunkeri* in the plate caption. The shape of the pinnae and pinnules, their prominent central vein and the lack of mesh venation are congruent with the determination proposed here.

Occurrence. *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, most frequent and characteristic for the Early Jurassic. The best-preserved and the most numerous specimens were found in Lower Jurassic strata of Germany (Goepfert, 1841; Schenk, 1865–1867; Van Konijnenburg-van Cittert, 1993; Van Konijnenburg-van Cittert et al., 2020), Greenland (Harris, 1926, 1931), Sweden (Möller, 1902) and Romania (Popa, 1997) and in Middle Jurassic strata of England (Harris, 1961, 1980). In Polish Early Jurassic floras this species is a characteristic but not very numerous element (Pacyna, 2013, 2021; Barbacka et al., 2014, 2016). Raciborski (1891) wrote that the species *Laccopteris elegans* (which he treated as a synonym of *P. braunii*) is rather frequent in Gromadzice and rarer in Chmielów. In the revised collections only specimens from Gromadzice were found. Specimens documented here confirm the presence of *Matonia braunii* (= *Phlebopteris braunii*) in this locality. Makarewiczówna (1928) listed *Laccopteris elegans* from Gromadzice, Szewna and Jędrzejowice, but because she did not illustrate any specimen, her determinations were based on Raciborski (1891), and the specimens were lost, this

record cannot be checked. One illustrated fertile specimen from Chmielów which she determined as *Laccopteris Münsteri* most probably belongs to *Matonia braunii*. Specimens collected and listed by Kuźniar (1923, 1924) as *Laccopteris elegans* and revised by Lilpop and Kostyniuk (1957) as *Phlebopteris braunii* from Chlewiska near Szydłowiec probably were lost during World War II. This record is based on determinations alone, without any description or illustration, and its source locality is unavailable today, so it is not possible to verify the determination. A specimen probably referable to *Matonia braunii* was described by Barbacka et al. (2014) from strata of Toarcian–Aalenian age from the Ciechocinek IG 1 borehole as *Phlebopteris muensteri*. New well-preserved fertile and sterile material of *Matonia braunii* was described by Barbacka et al. (2016) from the Niekłań borehole in the Holy Cross Mountains. Pacyna (2021) recently described this fern preserved in the growth position from Upper Pliensbachian strata of the Drzewica Formation in Szydłowiec.

Genus: *Phlebopteris* Brongniart, 1829

Phlebopteris angustiloba

(Presl in Sternberg, 1838)

Hirmer and Hoerhammer, 1936

Pl. 2, figs 1–6, Pl. 3, figs 1–6

Selected synonyms:

- 1838 *Gutbiera angustiloba* Presl in Sternberg; Presl in Sternberg, p. 116, pl. 33, figs 13a–e.
- 1843 *Andriana baruthina* Braun; Braun, pp. 42–46, pl. 9, figs 3–12, pl. 10, figs 1–4.
- 1865–1867 *Gutbiera angustiloba* Presl in Sternberg; Schenk, pp. 64–66, pl. 18, figs 5–10.
- 1865–1867 *Andriana baruthina* Braun; Schenk, pp. 87–89, pl. 21, figs 1–8, pl. 24, fig. 1.
- 1891 *Laccopteris angustiloba* (Presl in Sternberg) Raciborski; Raciborski, pp. 306–308, pl. 2, figs 6–9, pl. 3, figs 1–3.
- 1892 *Laccopteris angustiloba* (Presl in Sternberg) Raciborski; Raciborski, pl. 2, fig. 22.
- 1914 *Gutbiera angustiloba* Presl in Sternberg; Gothan, pp. 99–100, pl. 17, fig. 5.
- 1914 *Andriana baruthina* Braun; Gothan, p. 102, pl. 17, fig. 8, pl. 18, figs 1, 2.
- 1914 *Andriana norimbergica* Gothan; Gothan, pp. 102, 103, pl. 17, figs 6, 7.
- 1931 *Laccopteris angustiloba* (Presl in Sternberg) Raciborski; Harris, pp. 74–77, pl. 14, figs 6–17, text-fig. 26.
- 1936 *Phlebopteris angustiloba* (Presl in Sternberg);

- Hirmer and Hoerhammer, pp. 26–33, pl. 6, figs 1–4, text-fig. 5, 3.
- 1950 *Phlebopteris angustiloba* (Presl in Sternberg) Hirmer et Hoerhammer; Lundblad, pp. 23, 24, pl. 2, fig. 14; pl. 3, figs 1–5, pl. 13, fig. 2, text-fig. 4.
- 1965 *Phlebopteris angustiloba* (Presl in Sternberg) Hirmer et Hoerhammer; Tralau, pp. 373–376, figs 1a–d.
- 1993 *Phlebopteris angustiloba* (Presl in Sternberg) Hirmer et Hoerhammer; Van Konijnenburg-van Cittert, pp. 241–243, pl. 1, figs 2, 5.
- 1997 *Phlebopteris angustiloba* (Presl in Sternberg) Hirmer et Hoerhammer; Popa, p. 142, text-fig. 13.
- 2019 *Phlebopteris angustiloba* (Presl in Sternberg) Hirmer et Hoerhammer; Barbacka et al., pp. 161–163, figs 4f, g, 5a, b.
- 2020 *Phlebopteris angustiloba* (Presl in Sternberg) Hirmer et Hoerhammer; Van Konijnenburg-van Cittert et al., p. 9, pl. 4, figs 4–6.

Material. Pinnae fragments: A-III-25/24, 25, 26, 27, A-III-26/2 (Raciborski, 1891: pl. 1, fig. 2b), 21 (Raciborski, 1892: pl. 2, fig. 22), 34 (Raciborski, 1891: pl. 2, fig. 8), 35 (probably Raciborski, 1891: pl. 2, fig. 9), 36; isolated pinnules: A-III-12-208, A-III-25/28 (sterile), 29, A-III-26/4a+b, 20 (Raciborski, 1891: pl. 4, fig. 2), 33, 48, numerous isolated pinnules on so-far uncatalogued specimens. All specimens probably from Gromadzice based on sample lithology and co-occurring taxa, on some specimen labels erroneously Miłków (A-III-25/25, 26, A-III-26/36), Chmielów (A-III-26/20, 48) and Grojec (A-III-12/208). All specimens fertile except when indicated as sterile. Lower Hettangian, upper part of Zagaje Formation, parasequence Ib.

Description. Only fragments of pinnae and numerous isolated pinnules preserved (Pl. 2, figs 1–6, Pl. 3, figs 1–6). All pinnae fragments fertile, 30–60 mm long (Pl. 2, figs 1–6, Pl. 3, figs 1–2). Pinnae rachis 0.3–0.8 mm wide. Isolated pinnules are both fertile and sterile (Pl. 3, figs 2–6). Pinnae once-pinnate, most pinnules incomplete, lacking apices (Pl. 2, figs 4–6), preserved length 18–30 mm. Pinnules linear, 1.8–3.5 mm wide, very slightly narrowing towards apices, densely arranged, touching each other, attached at 80°–85° angles, positioned slightly suboppositely, somewhat falcate towards pinna apex. Main pinnule vein gives rise to lateral secondary veins almost perpendicularly, producing a mesh consisting of rectangular to roundish depressions (if specimen preserved as negative, Pl. 1, figs 2, 3; Pl. 3, figs 1, 2), 0.9–1.4 mm wide (measured perpendicularly to

main pinnule vein) and 0.5–1.0 long (measured along pinnule length). These rectangular units represent the areas where sori were attached but the details of sori and sporangia generally are not preserved. Very faint remains of sori with sporangia possibly present only on specimen A-III-26/34 (Pl. 2, figs 1, 1a); they may be consistent with Raciborski's figure (1891: pl. 3, figs 1–3) in having at least four sporangia and an annulus consisting of cells smaller than in *Matonia braunii* (Pl. 2, fig. 1a). In specimen A-III-26/36, most basal rectangular units of pinnules adhering to pinnae rachis are prominent and slightly larger, 1.2 mm wide, 1.5 mm long (Pl. 2, fig. 2). Rectangular units distinctively convex on fertile fronds if pinnule preserved as positive (Pl. 2, figs 5, 6), sometimes with small hollow pit in centre, commonly interpreted as a receptacle, or maybe a trace of an indusium stalk if this species was indusiate (Pl. 2, fig. 5; Pl. 3, fig. 3). Rectangular units only slightly convex on sterile pinnules, also somewhat larger, 1.5 mm wide, 1.0 mm long (specimen A-III-25/28, Pl. 3, fig. 5). Higher-order venation visible on sterile pinnule, secondary veins branch nearly parallel to midrib and subsequently 2–3 times diagonally within the unit (Pl. 3, fig. 5).

Remarks. The species *Phlebopteris angustiloba* (Presl in Sternberg, 1838) Hirmer and Hoerhammer, 1936 was proposed by Presl as *Gutbiera angustiloba* (Presl in Sternberg, 1820–1838) based on reasonably good fertile material. Very similar specimens were described later under several names. Braun (1843) described numerous fertile and probably also sterile specimens under the binomen *Andriana baruthina* Braun, 1843. He described and illustrated a large frond fragment and numerous isolated pinnae, and documented details of sori and pinnule venation. In Schenk (1865–1867), material referable to *P. angustiloba* was described under both earlier-proposed names; he treated these as separate species. However, in 1888 he suggested that these two species might be synonymous. Only Raciborski (1891) formally synonymised these species, describing the specimens revised here. He assigned them to the genus *Lacopteris* as *Lacopteris angustiloba* (Presl in Sternberg, 1838) Raciborski, 1891. The genus *Lacopteris* Presl in Sternberg, 1838 (Sternberg, 1820–1838) is a heterotypic synonym (taxonomic synonym) of *Phlebopteris* Brongniart, 1829 (Brongniart, 1828–1837) so

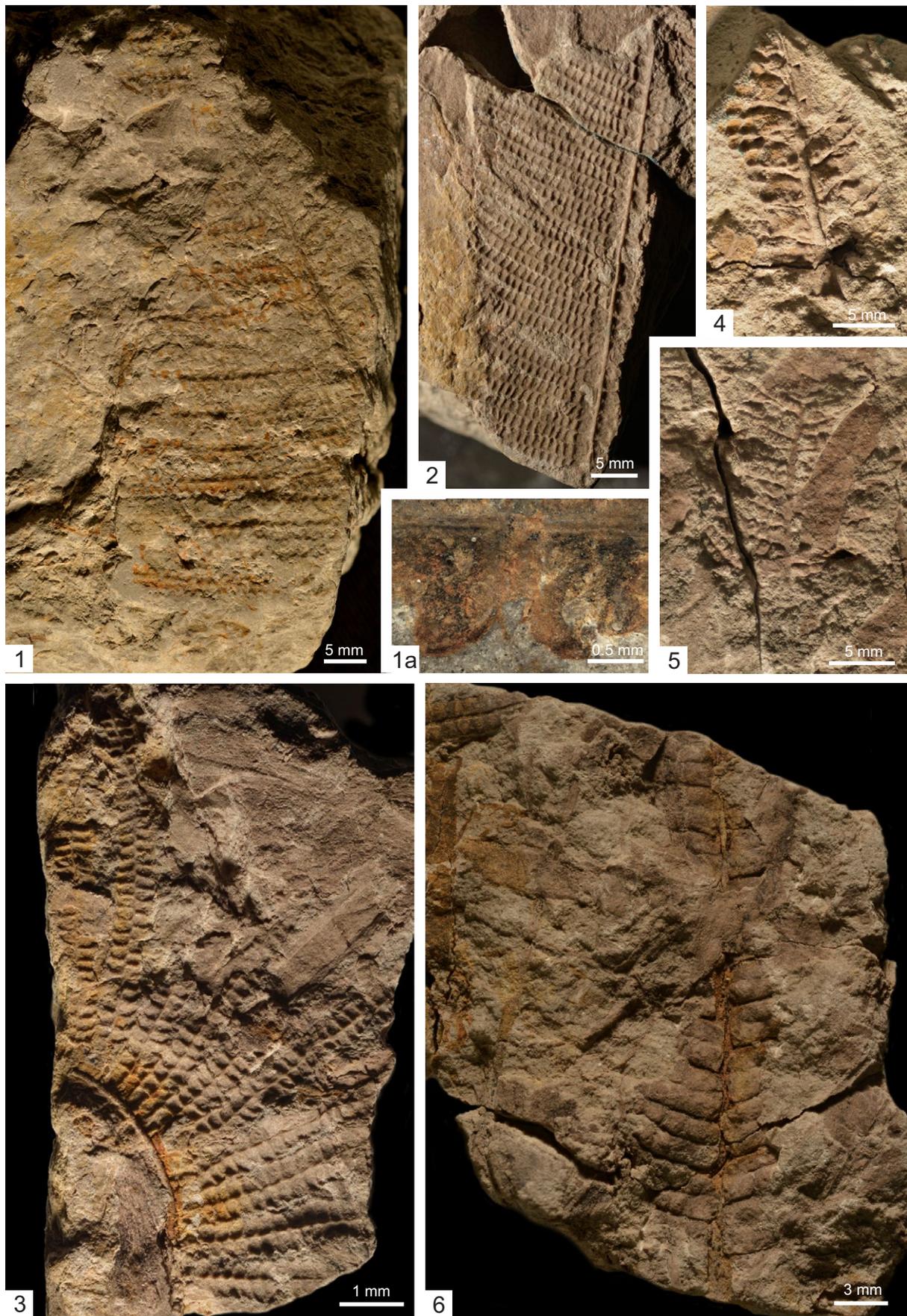


Plate 2. *Phlebopteris angustiloba*. **1.** Fragment of fertile pinna, A-III-26/34; **1a.** Detail from 1, pinnule fragment, margin damaged, sori and their details hardly visible; **2.** Fragment of fertile pinna, most basal rectangular units of pinnules adhering to pinna rachis, prominent and slightly larger, A-III-26/36; **3.** Fragment of arched fertile pinnule, A-III-25/21; **4.** Fragment of fertile pinna, pinnules incomplete, lacking apices, A-III-25/25; **5.** Fragment of fertile pinna, A-III-25/26; **6.** Fragment of fertile pinna, A-III-25/27

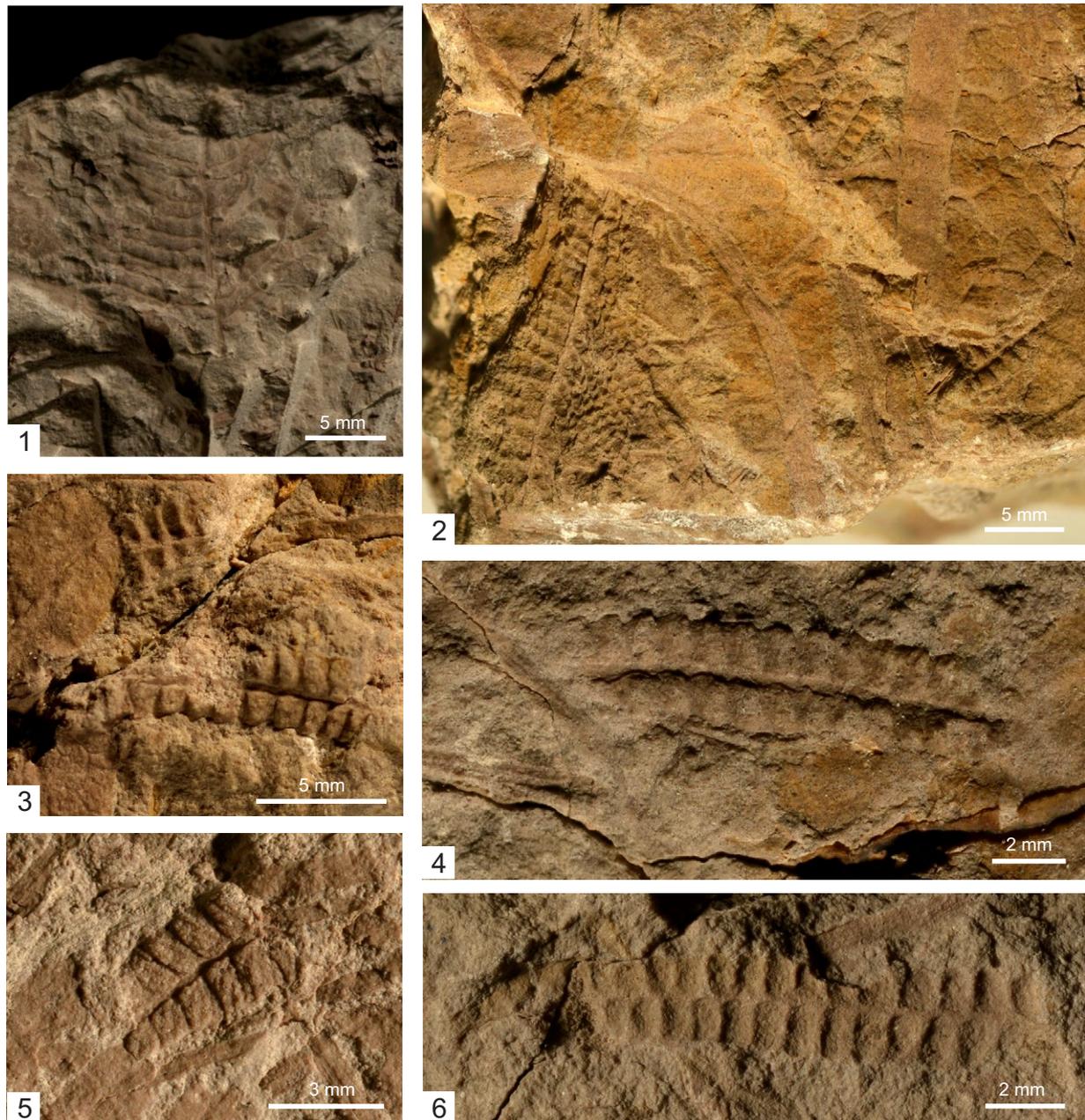


Plate 3. *Phlebopteris angustiloba*. 1. Fragment of fertile pinna, A-III-26/2; 2. Fragments of deformed fertile pinna and three isolated fertile pinnules with incomplete fragment of *Dictyophyllum* sp., A-III-25/24; 3. Two fragments of isolated fertile pinnules, upper negative, lower positive with small hollow pits in centre of sori, A-III-26/20; 4. Positive fragment of fertile pinnule, A-III-26/33; 5. Fragment of sterile pinnule with venation visible, A-III-25/28; 6. Negative fragment of fertile pinnule, A-III-12/208

Hirmer and Hoerhammer (1936) correctly proposed the currently accepted name.

The Polish material is very similar to specimens described by Presl in Sternberg (1838), Braun (1834), Hirmer et Hoerhammer (1936), Tralau (1965), Lundblad (1950), Barbacka et al. (2019) and Van Konijnenburg-van Cittert et al. (2020) in size, the shape of the pinnules and especially the mattress-like appearance of the pinnules. Recently, Barbacka et al. (2019) described and illustrated well-preserved material of this species from the Hettangian of Hungary, illustrating details of the pinnule venation

and sori. The here-revised material is not so well preserved but details of sterile pinnule venation were observed (Pl. 3, fig. 5). Raciborski (1981) described and illustrated (with drawings) details of the sori and sporangia based on this material. During the recent research it was not possible to confirm his observations. Raciborski (1891) did not indicate which specimen he used for his detailed observations. It could be specimen A-III-26/34, which Raciborski thoroughly described in the text and on which some remains of sori are still traceable today. Unfortunately, the details visible today (Pl. 2, figs. 1,

1a) are definitely worse than in his illustration. He mentioned that this specimen was damaged during transport, and damage is in fact visible on this specimen, so it cannot be ruled out that better details were visible before abrasion. Fertile specimens are numerically dominant in the revised material but there is also a sterile specimen (Pl. 3, fig. 5), though it was not recognised as such by Raciborski (1891). The sterile pinnule is compatible with those described by Antevs (1919), Harris (1931) and Barbacka et al. (2019). It has rectangular units less convex than in fertile pinnules, and third-order venation well visible.

This species is commonly considered to be exindusiate, like the whole genus *Phlebopteris*, but Harris (1980) convincingly showed that *Phlebopteris braunii* (and synonymised with it *Phlebopteris muensteri*, together named *Matonia braunii*) occasionally had an indusium, which was easily lost, as in modern *Matonia*. He described and illustrated both specimens with an indusium still in place, and specimens in which the indusium was lost so that sporangia were visible. This observation was confirmed by Barbacka et al. (2016) based on specimens from Niekłań. Specimens of *Matonia braunii* with indusia still in place have sori visible as bulges with a small hollow pit in the centre. Some specimens of *P. angustiloba* described here are preserved in that way (Pl. 3, fig. 3), and similar ones were earlier illustrated by Antevs (1919: pl. 1, fig. 9a). That sori with visible sporangia may be preserved in this species is confirmed by, for example, the specimen illustrated by Barbacka et al. (2019, fig. 5b). If an indusium was present in this *Phlebopteris* species, it can only be demonstrated by further research based on very well-preserved specimens. If it turns out that *Phlebopteris* as a whole is indeed indusiate, this will have far-reaching taxonomic consequences. The state of preservation of the present material is not good enough to settle this question for *P. angustiloba*. It is worth adding that the same mode of preservation of sori (bulges with a pit in the centre) is typical for *Matonidium goepperti*, which is considered to be indusiate (Harris 1961 and author's own observations based on Middle Jurassic Grojec material).

Occurrence. This species is characteristic for Rhaetian–Hettangian floras, predominantly distributed in Lower Jurassic strata of Europe, including Greenland (Harris, 1931), Sweden

(Antevs, 1919; Lundblad, 1950; Tralau, 1965), Denmark (Möller, 1902), Germany (Braun, 1843; Schenk, 1865–1867; Gothan, 1914; Weber, 1968; Van Konijnenburg-van Cittert et al., 2020), Hungary (Barbacka et al., 2019) and Romania (Popa, 1997). In Poland, Raciborski (1891) wrote that this species is common in Gromadzice but rare in Chmielów. Since some historical specimens from Gromadzice were wrongly attributed to Chmielów, based on the specimens available today the occurrence of this species in Chmielów cannot be confirmed. Makarewiczówna (1928) listed this species as *Gutbiera angustiloba* from Gromadzice and Chmielów. Her specimens from the collection of the Institute of Botany, Jagiellonian University, are lost. This species is moderately frequent in the slightly older early Hettangian flora of Sołtyków (Odrowąż) but represented only by isolated pinnules (Barbacka et al., 2010).

CONCLUSIONS

All available published and unpublished historical specimens (20 items) and some new material (one specimen preserved as positive and negative) of Matoniaceae ferns from Lower Jurassic strata of the Holy Cross Mountains were revised according to current views of the taxonomy of Mesozoic members of this family. The presence of *Matonia brauni* in the Hettangian of the Holy Cross Mountains was confirmed based on historical and newly collected specimens. This fern is a rather rare element in the flora. In contrast, *Phlebopteris angustiloba* is rather frequent, especially as isolated pinnules. However, the state of preservation of all available specimens prevents confirmation of Raciborski's (1891) observations about the sori and sporangial structure in this species. A sterile specimen has well-visible venation preserved, but this was not documented by Raciborski. Two large specimens illustrated by Raciborski (1891) and determined as *Lacopteris elegans* do not belong to Matoniaceae but probably to Osmundaceae. Only some specimens of *P. angustiloba* illustrated by Raciborski could be traced with certainty in the preserved collection. Some specimens historically referred to the Matoniaceae from the Holy Cross Mountains could not be revised based on illustrations alone, because they never were described and illustrated properly

and the specimens are lost. The reliability of historical labels in collections published by Raciborski, especially with regard to the origin of the specimens, must be treated with caution. Also, after long storage of the specimens (more than a century) some subtle morphological and anatomical details may have been lost.

ACKNOWLEDGEMENTS

I am grateful D. Zdebska (Institute of Botany, Jagiellonian University, Cracow), M. Barbacka and especially J. Ziaja (W. Szafer Institute of Botany, Polish Academy of Sciences, Cracow) for help and discussions, G. Pieńkowski (Polish Geological Institute – National Research Institute, Warsaw) for taking me to the outcrop in Gromadzice and for discussions about the geological context and age of Early Jurassic floras of the Holy Cross Mountains, M. Szewczyk and K. Stachowicz for photos of the specimens, A. Sojka for preparing the figures, and the journal referees Johanna H.A. van Konijnenburg-van Cittert (Naturalis Biodiversity Center, Leiden and Laboratory of Palaeobotany and Palynology, Utrecht, the Netherlands) and Emese R. Bodor (Eötvös Loránd University, Budapest, Hungary) for their helpful comments and suggestions. Special thanks for the curators of the palaeobotanical collections in the Geological Museum of the Institute of Geological Sciences, Polish Academy of Sciences, Research Centre in Cracow, Agata Jarzynka and Barbara Kietlińska-Michalik (ret.), for the loan of Raciborski's specimens, access to comparative collections, and their hospitality and help during research. The study was financed by funds from the National Science Centre, Poland (grant no. 2017/25/B/ST10/01273) and the Institute of Botany of the Jagiellonian University (N18/DBS/000002).

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