

# Fossil flora of Middle Jurassic Grojec clays (southern Poland). Raciborski's original material reinvestigated and supplemented. II. Pteridophyta. Osmundales

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**ABSTRACT.** In the second part of the series dealing with the flora of the Grojec clays (Poland, Middle Jurassic), macroremains of Osmundales are introduced. The re-examined and supplemented material originates from three collections: specimens collected and described in Polish by Raciborski in 1894; specimens preliminarily described by Stur (1888), housed at the Geological Survey of Austria; and Raciborski's still-unpublished material stored at the Institute of Botany of the Jagiellonian University. So far, 15 taxa of *Cladophlebis* have been described from the Osmundales of Grojec clays, and two species of *Todites* (*Todea*) and *Osmundopsis* (*Osmunda*) *sturii*. Detailed observations indicate that a large part of the material (12 taxa described by Raciborski) should be assigned to three widespread Jurassic species: *Cladophlebis denticulata*, *C. haiburnensis*, and *C. roessertii*. *Cladophlebis aurita* and *C. bartonecii*, created by Raciborski, should be retained. The occurrence of sterile and fertile fronds of *Todites williamsonii* (originally described as *Todea williamsonis*, *Cladophlebis whitbiensis*, and *Cladophlebis solida*) is confirmed for Grojec. Two species described by Raciborski (1894) required a change of generic names – *Osmundopsis* (*Osmunda*) *sturii* and *Todites* (*Todea*) *princeps*. This paper provides the taxonomical descriptions and considers the palaeoecology of 5 *Cladophlebis* species (*C. aurita*, *C. denticulata*, *C. haiburnensis*, *C. roessertii*, *C. bartonecii*) and other osmundaceous ferns such as *Osmundopsis sturii*, *Todites williamsonii*, and *T. princeps*.

**KEYWORDS:** *Cladophlebis*, *Osmundopsis*, *Todites*, Osmundaceae, ferns, palaeoecology

## INTRODUCTION

Osmundales are one of the oldest (since the Permian) existing orders of ferns, believed to be an intermediate stage between eusporangiate and leptosporangiate ferns (Tidwell & Ash 1994, Taylor et al. 2009). The fossil record shows their high diversity and worldwide distribution (e.g. Taylor et al. 2009, Barbacka et al. 2014b). Extant osmundaceous ferns are represented by four genera: *Todea*, *Osmunda*, *Leptopteris*, and *Osmundastrum*. *Osmunda* (ca 10 species) occurs primarily in the Northern Hemisphere in temperate climate, whereas *Todea* (2 species) and *Leptopteris* (6 species) prefer warmer conditions in Australia, New Zealand, South Africa, and the Pacific area.

*Osmundastrum cinnamomeum* is the only species of *Osmundastrum* (some authors consider it a subgenus of *Osmunda*), which occurs in North and South America, Siberia, and Asia (Metzgar et al. 2008, Singh 2010).

More than 150 osmundaceous fossil species (excluding *Cladophlebis* as a form genus) have been described worldwide, including ca 80 species of fronds, ca 50 species of stems and rhizomes, and ca 20 fossil spore species. Some authors considered *Cladophlebis* (*Osmunda*-like foliage) to be related to the Osmundaceae family (e.g. Raciborski 1894, Van Konijnenburg-van Cittert 1978, Van Konijnenburg-van Cittert & Morgans 1999, Bodor & Barbacka

2008), but similar morphology also is observed in other fern families (e.g. Villar de Seoane 1996, Escapa & Cúneo 2012). This genus is highly diverse, with more than 240 species and 21 varieties (Jongmans & Dijkstra 1959, 1967) and new species still reported (e.g. Czier 1995, Dai et al. 2012, Tian et al. 2016).

Osmundales, especially *Cladophlebis* and *Todites*, were present in almost all of Europe during the Triassic and Jurassic (Barbacka et al. 2014b): for example, in Poland (Makarewiczówna 1928, Pacyna 2013, Barbacka et al. 2014a), Serbia (Djordjević-Milutinović 2010), Germany (Schenk 1867, Gothan 1914, Kräusel 1958, Kustatscher & van Konijnenburg-van Cittert 2011, Kustatscher et al. 2012), the United Kingdom (Stopes 1907, Seward 1911, Harris 1961), Romania (Czier 1994, Popa 1997, Popa & Meller 2009), Hungary (Barbacka 2011; Barbacka & Bodor 2008), Greenland (Harris 1931, 1937), Sweden (Nathorst 1876, Antevs 1919, Johansson 1922, Lundblad 1950), Italy (Kustatscher & van Konijnenburg-van Cittert 2005, Petti et al. 2013), Denmark (Bartholin 1892, 1894, Möller 1902, Vajda & Wigforss-Lange 2009), and France (Saporta 1873).

The Middle Jurassic flora of Grojec has been studied since the 19<sup>th</sup> century. Details on the history of investigations were given in the first part of the Grojec flora series (sphenophytes, Jarzynka & Pacyna 2015). Ferns (Fig. 1) are the dominant element in the Grojec plant assemblage (Raciborski 1894, Reymanówna 1963,

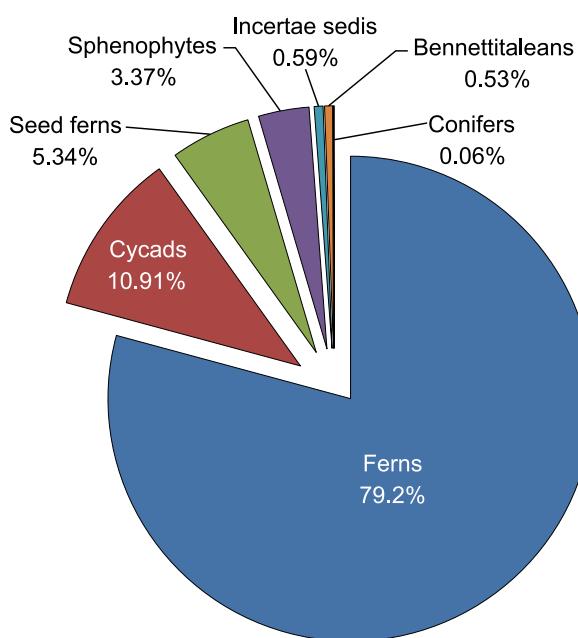


Fig. 1. Composition of the Grojec flora

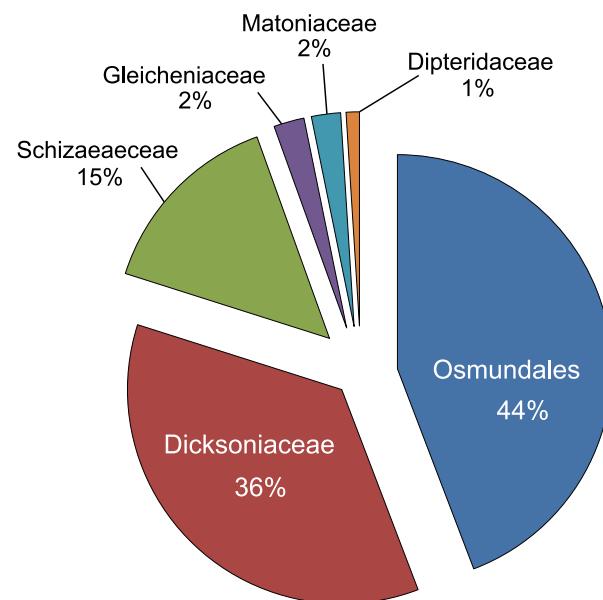


Fig. 2. Composition of the Grojec ferns

Jarzynka 2012, Jarzynka & Pacyna 2015). Osmundales are the most abundant (35%, Fig. 2) and diverse fern group (8 species).

Raciborski (1894) described 15 taxa belonging to *Cladophlebis* and two species of *Todea* (=*Todites*), and created two *Osmunda* (=*Osmundopsis*) species, *O. sturii* Raciborski 1894 and *O. microcarpa* Raciborski 1894. He also proposed to transfer *Pecopteris haiburnensis* Lindley et Hutton 1836 (=*Cladophlebis haiburnensis*) to *Thinnfeldia* as *Th. haiburnensis* (Lindley et Hutton) Raciborski 1894. In this paper the osmundaceous fern remains from Middle Jurassic flora of the Grojec clays are revised and their palaeoecological adaptations are discussed.

## MATERIAL AND METHODS

The studied material consisted of 594 fragments of sterile fern fronds and 19 fragments of fertile fronds from Grojec. All fragments are preserved in fine-grained light or dark kaolinite clay as impressions; organic matter is not preserved. Specimens belonging to the Osmundales include 2 fragments of *Cladophlebis aurita*, 251 fragments of *C. denticulata*, 121 fragments of *C. haiburnensis*, 72 fragments of *C. roessertii*, 120 fragments of *C. bartonecii*, 8 fragments of *Osmundopsis sturii*, 17 fragments of *Todites williamsonii*, and 3 fragments of *T. princeps*.

The majority of the samples (377) are stored in the Geological Museum of the Institute of Geological Sciences, Polish Academy of Sciences, Research Centre in Kraków, coll. acronym ZNG PAN A-III-12. Another 185 samples are stored in the Geologische Bundesanstalt (Geological Survey of Austria) in Vienna, Austria, coll. acronym GBA 2011/051, and 32 samples

are housed in the Department of Palaeobotany and Palaeoherbarium, Institute of Botany, Jagiellonian University, coll. acronym KRA-PALEO 105.

As noted in earlier work (Jarzynka & Pacyna 2015), neither Raciborski nor Stur used a numbering system for their hand specimens. Acronyms and specimen numbers were assigned to these collections many years after their publication. Moreover, Stur's short paper contains no illustrations. For specimens illustrated by Raciborski, here I give the original figure and plate numbers in parentheses after the inventory number: for example, "ZNG PAN A-12/382 (pl. XX, fig. 24)".

The re-examined specimens were studied using a Nikon SMZ 645 stereoscopic microscope and Nikon SMZ800 microscope with several different digital cameras and NIS software.

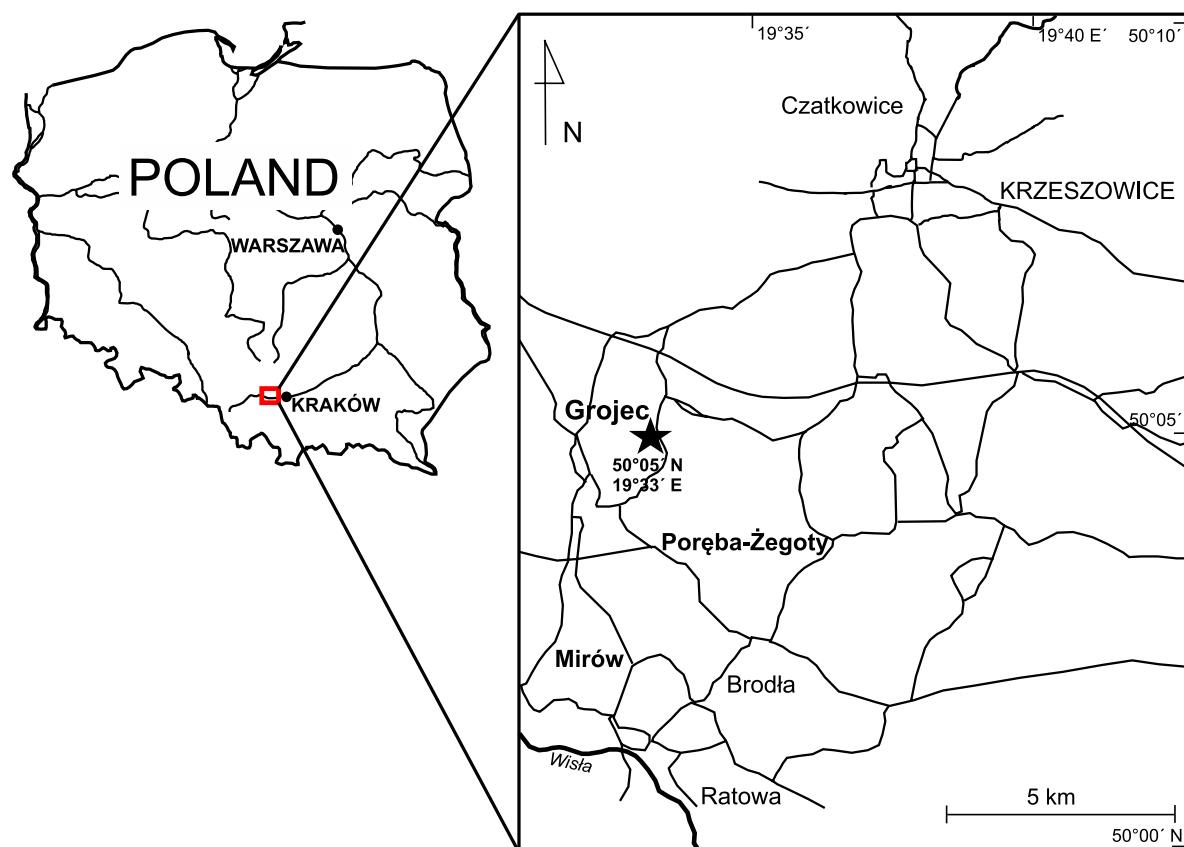
## GEOLOGICAL SETTING

Almost all the Middle Jurassic up to the Upper Bathonian of the Kraków area was a part of Małopolska Land and was an elevated landmass surrounded by shallow bays of the epicontinental sea (Jurkiewiczowa 1974). The marine transgression gradually expanded in the Upper Bathonian and reached maximum in the Oxfordian (Różycki 1953, Jurkiewiczowa 1974). In the 19<sup>th</sup> century, kaolinite clays were

mined in the Grojec area for the manufacture of ceramics and refractory materials (Fig. 3).

During the Bajocian and Bathonian the region between Grojec and Brodła was the most important basin for accumulation of kaolinite clays (Kozłowski 1957). The bottom of the profile (Fig. 4) is formed by layers of white non-laminated clays without plant macroremains (Jurkiewiczowa 1974, Biała 1985). They are followed by sandy deposits with beds of grey clays rich in fossil plant fragments and detritus. These deposits are up to 10 m thick, but in Poręba-Żegoty the average thickness is 6 m, and in the rest of the area ca 3 m. In the upper strata they pass into white fine-grained sands with calcareous intercalations containing plant remains (Różycki 1953, Kozłowski 1957, Jurkiewiczowa 1974). This section was interpreted as an estuarine-land series by Różycki (1953). A series of Callovian sediments such as ferriferous sandstone and limestone with ammonites and oolites reflects the transgression in this area (Różycki 1953).

More detailed descriptions of the palaeogeography, sedimentology, geological setting (with maps), and age are given in Jarzynka & Pacyna (2015).



**Fig. 3.** Location of the investigated area (after Kozłowski 1957 and Nosova & Wcisło-Luraniec 2007, modified)

Chrono-stratigraphy		Ammonite zones	Lithology
MIDDLE JURASSIC	UPPER CALLOVIAN	<i>Kosmoceras duncani</i> <i>Kosmoceras pollux</i> <i>Kosmoceras jason</i>	Grey and yellowish limestones with numerous ammonites and sparse ooliths (1 m)
	LOWER CALLOVIAN	<i>Kepplerites calloviensis</i> <i>Macrocephalites typicus</i> (?)	Ferriferous sandstones (3 m)
	? UPPER BATHONIAN		White finely-grained sands often calcareous (13 m)  Sandy deposits with grey clay intercalations with detritus and bigger plant remains  White clays without plant remains
? BAJOCIAN			

**Fig. 4.** Lithological section of Middle Jurassic sediments of Grojec (after Rózycki 1953, modified)

## SYSTEMATIC DESCRIPTION

Taxonomy follows Taylor et al. 2009.

Order: OSMUNDALES

Family: OSMUNDACEAE ?

Genus: ***Cladophlebis*** Brongniart 1849

Type species: ***Cladophlebis albertii***  
(Dunker 1846) Brongniart 1849

The genus ***Cladophlebis*** is characterised by high variability of morphological characters (Bodor & Barbacka 2008) and a worldwide distribution from the Upper Palaeozoic to Mesozoic (Taylor et al. 2009). The fronds are usually bipinnate; the pinnae can be attached to the rachis oppositely, suboppositely, alternately, or subalternately (Harris 1961). Pinnules

have varied shapes even on the same frond: elongated, oblong, falcate, lanceolate, obovate, and so on. The pinnule margins are entire but many species have dentate, lobed, crenate, or serrate margins (e.g. Harris 1961, Barbacka & Bodor 2008).

Based on the characteristic venation and shapes of pinnules, within this plant assemblage Raciborski (1894) distinguished 15 taxa of ***Cladophlebis***: *C. aurita* Raciborski 1894, *C. bartonecii* Raciborski 1894, *Cladophlebis cf. nebbensis* (Brongniart) Nathorst 1876, *C. denticulata* (Brongniart) Fontaine 1889, *C. huttoniana* Raciborski 1894, *C. insignis* (Lindley et Hutton) Raciborski 1894, *C. recentior* Phillips 1829, *C. recentior* var. *dubia* Raciborski 1894, *C. solida* Raciborski 1894, *C. subalata* Raciborski 1894, *Cladophlebis* sp. (an forma *Cl. recentioris*) Raciborski 1894, *Cladophlebis* sp. indet., *C. tchihatchewi* Schmal. *similis* Raciborski 1894, *C. whitbiensis* Brongniart 1849, and *Cladophlebis whitbiensis* var. *crispata* Raciborski 1894. However, he noted at the same time that their morphological variability is high and that all described forms could represent only a few species. Table 1 compares the morphological features of all species described by Raciborski (1894).

### ***Cladophlebis aurita*** Raciborski 1894

Pl. 1, figs 1–6, Fig. 5A

1894 *Cladophlebis aurita* Raciborski, p. 80, pl. 20, figs 24–26.

**Holotype.** ZNG PAN A-III-12/383, “pl. XX, figs 24, 25” (Raciborski 1894), Pl. 1, figs 2–6 (recent paper); hic designates.

**Repository.** Geological Museum of the Institute of Geological Sciences of the Polish Academy of Sciences, Research Centre in Kraków.

**Type locality.** Grojec, southern Poland.

**Stratigraphic horizon.** Bathonian, Middle Jurassic.

**Etymology.** After the auricle at the base of pinnules, which is a diagnostic character for this species.

**Diagnosis.** (according to Raciborski 1894, p. 80). “Fronds bi- or tripinnate, rachis smooth, clearly longitudinally ribbed in middle. Pinnules smooth, sessile, alternate, broad, oblong. Upper pinnules directed upright, lower with small ovate auricles. Midrib straight, secondary

veins forking near base of pinnule, straight and parallel, in auricles straight. Width of rachis up to 1.5 mm, width of pinnules 7–8 mm, length of pinnules up to 25 mm, length of auricle 6–7 mm, width of auricle 2.5–3 mm, distance between secondary veins 0.75 mm”.

**Material.** Two small sterile frond fragments: ZNG PAN A-III-12\382 “pl. XX, fig. 24”, 383 “pl. XX, figs 25, 26”.

**Description.** Sterile fronds, probably bipinnate. Length of pinnae fragments (Pl. 1, figs 1, 4) up to 63 mm, width up to 26 mm. Pinna rachis ca 2 mm wide, smooth or slightly ribbed. Pinnules (Pl. 1, figs 2, 3, 5, 6) entire, arise alternately or subalternately from axis at 45–70° angle. Pinnule base asymmetrical, one base side expands to form basal lobe (Pl. 1, figs 1, 3, 6). Pinnules entire-margined, apex rounded but top of auricle subacute, 13–15 mm long, 9–10 mm wide. Basal lobes 2–4 mm × 2–3 mm. Length/width ratio of pinnules 1.85–2.6. Midrib straight, rises almost to apex. Secondary veins arise from midrib at ca 60° angle, divide once near midvein (Pl. 1, figs 2, 3, 5). Venation of auricle different (Pl. 1, fig. 6, Fig. 5A): in auricle, midvein arises from base near pinnule midrib and lateral veins arise from midvein of lobe at ca 60° angle, almost parallel, without forking.

**Discussion.** The set of features of the studied specimens, especially pinna shape, pinnule arrangement, and their shape and type of venation refer them to the genus *Cladophlebis*.

Because only two specimens of this species of Raciborski have been found in collections, not all the morphological features given in the Latin diagnosis (Raciborski 1894) are observable. Differences between Raciborski's diagnosis and description given above are seen in the pinnule dimensions and rachis ornamentation, but the rest of the morphological details are comparable. Except for the presence of the auricle, the material described here shows characters (e.g. venation, shape of pinnules) typical for *Cladophlebis*. Raciborski (1894) noted that only *C. aurita* is characterised by the presence of an auricle, which distinguishes this species from all other known forms of *Cladophlebis*. Due to the correspondence of all other features, a new species is justified and retained. Raciborski (1894) did not designate the holotype and illustrated only two specimens in his monograph. The better illustrated specimen by Raciborski

(ZNG PAN A-III-12\383, “pl. XX, fig. 25, 26”) is designated in this paper as the holotype of *Cladophlebis aurita* Raciborski 1894.

There are some similarities between *C. aurita* and *C. aktashensis* Turutanova-Ketova 1930. Pinnules of *C. aktashensis* are characterised by the base expansion on the acroscopic side of pinnules (Turutanova-Ketova 1930), but this character does not always occur and the base never forms an auricle (versus auricle typical for *C. aurita*). In the largest pinnules of *C. aktashensis* the base is even contracted (Harris 1961). Moreover, the species differ in pinnule size: *C. aktashensis* has longer and broader pinnules without basal lobes.

**Occurrence in Mesozoic floras.** *Cladophlebis aurita* is known only from the Middle Jurassic of Grojec, Poland.

#### *Cladophlebis bartonecii* Raciborski 1894

Pl. 2, figs 1–6, Figs 5B, C

- 1894 *Cladophlebis bartonecii* Raciborski, p. 83, pl. 23, figs 3, 5–7 (non pl. 22, figs 11, 12, pl. 23, fig. 4).  
 1894 *Cladophlebis recentior* Phillips: Raciborski, p. 76, non pl. 10, fig. 11b (lower), pl. 24, fig. 9, pl. 10, fig. 11b (upper), pl. 23, figs 1, 2.  
 1894 *Cladophlebis subalata* Raciborski, p. 85, non pl. 24, figs 15, 16, pl. 10, fig. 11c, pl. 24, fig. 14.  
 1894 *Cladophlebis whitbiensis* Brongniart: Raciborski, p. 73, non pl. 21, figs 1, 2, pl. 20, fig. 2, pl. 21, fig. 8, 9.

**Lectotype.** ZNG PAN A-III-12/391, Pl. 1, fig. 3 (present paper); hic designates.

**Repository.** Geological Museum of the Institute of Geological Sciences of the Polish Academy of Sciences, Research Centre in Kraków.

**Type locality.** Grojec, southern Poland.

**Stratigraphic horizon.** Bathonian, Middle Jurassic.

**Etymology.** In honor of Franciszek Bartonec, a mining inspector in the kaolin clays mine, who called attention to the fossil plants and gave them to M. Raciborski.

**Diagnosis** (according to Raciborski 1894, p. 83). “Fronds bipinnate, up to 50 cm wide and more than 1 m long. Rachis thick, up to 8 mm wide in middle part of frond. Secondary axes attached suboppositely or alternately, up to 1.5 mm wide. Pinnules in lower part slightly convex and hirsute, in upper part slightly concave and smooth. Pinnules linear lanceolate,

**Table 1.** Comparison of features of *Cladophlebis* species described by Raciborski (1894) from the Grojec clays

Feature/ Taxon	<i>C. aurita</i>	<i>C. bartonecii</i>	<i>C. denticulata</i>	<i>Cladophlebis</i> cf. <i>nebbensis</i>	<i>C. insignis</i>	<i>C. recenior</i>	<i>Cladophlebis</i> sp. an forma <i>Cl. recentioris</i>
Length of pinnule [mm]	to 25	17–31	to 16	to 25	25–30	13–20	to 17
Width of pin-nule [mm]	7–8	5–6.5	6–7	to 7	7–9	5–7	to 5
Details of venation	secondary veins of auricle: straight, parallel	Midrib distinct, slightly curved near bottom	midrib recurvate	like <i>C. nebbensis</i>	secondary veins parallel	midrib distinct, subparallel; dense secondary veins	like <i>C. recentior</i>
Shape of secondary veins	straight, parallel	straight and parallel		like <i>C. nebbensis</i>	straight, parallel	curved	like <i>C. recentior</i>
Bifurcation of secondary veins of pinnule	once, near midrib	once, twice, three or even four times	once	like <i>C. nebbensis</i>	once, twice, sometimes three times	once near midrib/base of pinnule	like <i>C. recentior</i>
Other remarks/ comments	lamina without hair traces	numerous, irregularly arranged hair traces		lamina without hair traces; probably the “naked” form of <i>C. bartonecii</i> , or the small form of <i>C. insignis</i>	similar to <i>C. ligata</i> , <i>C. roessertii</i> , and <i>C. nebbensis</i>		

lanceolate or falcate, spreading or upright spreading, indistinct arcuate, parallel, with entire, slightly recurved (crenate), or more recurved (crenate) margin. Apex acute, subacute, rounded or obtuse, base slightly extended acroskopically and slightly contracted basiscopically, or only extended on acrosopic side, or straight. Sinuses between pinnules narrow. Midrib distinct, slightly curved near bottom. Secondary veins bifurcating first near base and then divided, reaching top of pinnules straight and parallel. Secondary veins arising from midrib at 60° angle. Hair traces well visible, numerous, and irregularly arranged; more numerous on axes than on pinnules, spaces between them 2/3–1 mm”.

**Material.** 120 fragments of sterile fronds: ZNG PAN A-III-12\29, 34–36, 64, 111, 114, 128, 133, 135, 152, 158.11, 229, 236, 280, 290, 292.1, 323–326, 329–331, 333–337, 339, 340.2, 357–359, 365, 375, 386–387, 389–390, 392, 396–399, 405, 408, 412–413, 416, 419–422, 424, 426, 428–431, 433–437, GBA 2011/051/0007/2, 0018/1, 0046/2–0047/2, 0051/1, 0105/2, 0149/2, 0163/2, 0166–0167/1, 0168/1–0174/1,

0175–0182/1, 0183/1, 0202, 0213/2–0214, 0223/2, 0225/2, 0229/1, KRA-PALEO 105/29, 33, 37, 43, 53, 60.

**Description.** Sterile fronds bipinnate (Pl. 2, figs 5, 6). Fragments 29–131 mm long, up to 67 mm wide. Rachis smooth, (1) 3–4 (6) mm wide. Fragments of pinnae 13–103 mm long, up to 43 mm wide, attached oppositely or subalternately. Pinna rachises smooth and 1–2 mm wide, arise from rachis at 45–60° (85°) angle.

Pinnules long and narrow, oblong, falcate, entire, rarely slightly crenate (Pl. 2, figs 1–6), attached oppositely or subalternately, arise from axis at 45–85° angle. Length of pinnules 10–25 mm, width 2–8 mm, length/width ratio (1) 2.25–4.5 (6). Base straight, apex acute (Pl. 2, figs 3, 4). Venation of pecopterid type (Pl. 2, figs 2, 3, 6). Secondary veins fork once (Fig. 5B), twice (Fig. 5C), rarely three or four times, first time close to midrib. Midrib straight, reaches apex. Secondary veins (16–18 near margin) arise from midrib at 50–70° angle.

**Discussion.** An examination of the specimens originally referred by Raciborski (1894)

<i>Cladophlebis</i> (recentior var.) <i>dubia</i>	<i>C. subalata</i>	<i>C. huttoniana</i>	<i>C. whitbiensis</i>	<i>Cladophlebis</i> (whitbiensis var.) <i>crispata</i>	<i>Cladophlebis</i> sp. indetem.	<i>Cladophlebis</i> sp. <i>thihatchewi</i> <i>similis</i>	<i>C. solida</i>
8–10	to 16	13	more than 15	like <i>C. whitbiensis</i>	to 20		7–8 (12)
6–7	3–5	7	to 6	like <i>C. whitbiensis</i>	to 5		ca 4 (5)
midrib slightly curved	midrib distinct	midrib recurvate, forked near apex	midrib distinct, secondary veins dense		midrib distinct	midrib distinct	secondary veins dense; midrib curved twice in pinnule
curved, parallel	straight or slightly recurved	straight, arcuate	straight, slightly curved in upper part of pinnule	like <i>C. whitbiensis</i>	straight		curved
once or twice; near midrib and near top of pinnule	once near midrib	once near midrib	usually once near base and midrib; veins subparallel	like <i>C. whitbiensis</i>	once in lower part of pinnule	twice or three times in lower part of pinnule, usually once in upper part	once in upper part of pinnule, twice and three times in lower part of pinnule
probably a form of <i>C. recentior</i> with shorter and wider pinnules; roughness of lamina observable	pinnule mor- phology like <i>C. denticulata</i> but no den- tate margin; possibly ster- ile fronds of <i>Osmundopsis</i> <i>sturii</i>	lamina distinctly longitudinally furrowed	lamina without hair traces	wrinkled and bent lamina	lamina is thick		

to the new species *Cladophlebis bartonecii*, revealed that the material is heterogeneous. Assigned to *C. haiburnensis* (Lindley et Hutton) Brongniart 1849 are the specimens characterised by lanceolate, oblong or falcate pinnules with slightly extended bases on the acroscopic side and subacute apices, a length/width ratio of 2–2.66, and having once- or twice-forked secondary veins. Specimens with oblong, dentate pinnules with a slightly extended base and an acute or subacute apex, a length/width ratio of 3–5, and vein density of 12–24/cm have been referred to *Cladophlebis denticulata* (Brongniart) Fontaine 1889.

Specimens corresponding to the diagnosis of *C. bartonecii*, that is, long and narrow pinnules with entire or slightly crenate margins, straight bases, acute apices, and veins bifurcating even four times were in fact assigned by Raciborski (1894) to three taxa: *Cladophlebis bartonecii*, *Cladophlebis recentior*, and *Cladophlebis subalata*.

The diagnosis of these species (Raciborski 1894) sometimes focused on characters that probably were related to the preservation state

or environmental conditions (e.g. presence of hair traces on pinnules and rachises, convex or concave surface of pinnules). Raciborski (1894) also emphasised the heterogeneity of venation patterns, shapes and margins of pinnules among the specimens he classified to *C. bartonecii*. To complicate matters, Raciborski (1894) did not designate any holotype, and almost all specimens illustrated as *C. bartonecii* in his monograph represent other species, in my opinion (see list of synonyms). Based on the morphological similarities between the above-mentioned species, I propose to include them in *C. bartonecii*.

*C. bartonecii* differs from other *Cladophlebis* species from the Grojec clays in having narrower and longer pinnules (see Table 2) and more frequent bifurcation. The length/width ratio of *C. denticulata* and *C. bartonecii* is similar, but *C. denticulata* has broader pinnule bases, and the margin of the pinnules is usually dentate or entire. *C. bartonecii* has long and falcate pinnules and narrower bases. Similar falcate pinnules are characteristic for *C. haiburnensis*, but there the pinnules are

**Table 2.** Comparison of pinnule features of *Cladophlebis* species from the Grojec clays, described on the basis of this study

Feature / Species	<i>Cladophlebis aurita</i>	<i>Cladophlebis bartoneei</i>	<i>Cladophlebis denticulata</i>	<i>Cladophlebis haiburnensis</i>	<i>Cladophlebis rossertii</i>	<i>Todites williamsoni</i> sterile frond
Frond	bipinnate	bipinnate	bipinnate	bipinnate (?)	bipinnate	bipinnate
Width of rachis [mm]	2	(1) 3–4 (6)	(2) 4–6 (8)	2	2	3–4
Rachis ornamentation	smooth or slightly ribbed	smooth, sometimes slightly ribbed	slightly ribbed	smooth, sometimes slightly ribbed	smooth	usually smooth
Arrangement of pinnules	alternate, subalternate	opposite, subopposite	opposite, subopposite	oppositely, subalternately	oppositely, suboppositely	alternately
Pinnule shape	asymmetrical, oblong	long and narrow, oblong, falcate	oblong	lanceolate, oblong, falcate	elongated, triangular, very rarely falcate	falcate (dominant), oval
Angle of arising of pinnules	45°–70°	45°–85°	45°–90°	40°–60° (85°)	60°–85°	
Base of pinnule	asymmetrical, expands to basal lobe/auricle	straight		straight, only sometimes extended acroskopically	straight	contracted
Pinnule apex	rounded	acute	acute or subacute	subacute	acute	subacute, rounded
Margin of pinnule	entire with basal lobe/ auricle	entire, rarely slightly crenate	entire, rarely dentate in upper part of pinnule	entire	entire	entire, rarely slightly cre- nate near apex
Length of pinnule [mm]	13–15	10–25	5–28	4–20	5–12	5–8
Width of pinnule [mm]	9–10	2–8	2–9	3–7	3–6	3–4
Length/width ratio of pinnule	1.85–2.6	(1) 2.25–4.5 (6)	(1.6) 3.16–4.75 (5.25)	(1.6) 2–2.66 (3.66)	1.2–2.66	1.2–2.25
Type of venation	pecopterid	pecopterid	pecopterid	pecopterid	pecopterid	neuropterid
Vein density/10 mm or *5 mm	6–10	16–18	6–12*	8–21	5–13	10–15*
Angle of arising of secondary veins [°]	ca 60	50–70	(25) 55–60 (75)	40–50 (55–75)	ca 60	30–60
Bifurcation of secondary veins of pinnule	usually once, near midrib	once or twice, rarely three or four times	once, usually near midrib	twice	once or twice	usually twice, sometimes three times in basal part of pinnules, once in apical part

significantly shorter than in *C. bartonecii* and the venation pattern does not correspond in the two species.

The specimens of *C. bartonecii* resemble *Cladophlebis nebbensis* and *C. denticulata*. In some cases *C. nebbensis* has length/width ratio, pinnule width and length, and margins similar to those of *C. bartonecii*, but the venation differs, especially the bifurcations of the secondary veins. The features most distinguishing between *C. denticulata* and *C. bartonecii* are pinnule shape and venation pattern, while the length/width ratio, pinnule length and width, and angle of arising of secondary veins can be similar.

**Occurrence in Mesozoic floras.** Species known only from Grojec, Middle Jurassic (Raciborski 1894).

### *Cladophlebis denticulata* (Brongniart 1828) Fontaine 1889

Pl. 3, figs 1–8, Pl. 5, Figs 5D, E

#### Selected synonyms.

- 1828 *Pecopteris denticulata* Brongniart, p. 301, pl. 98, figs 1, 2.
- 1828 *Pecopteris phillipsii* Brongniart, p. 304, pl. 109, fig. 1.
- 1876 *Cladophlebis denticulata* Brongniart: Nathorst, p. 19 (note).
- 1889 *Cladophlebis denticulata* (Brongniart) Fontaine, p. 71, pl. 7, figs 7–7a.
- 1894 *Cladophlebis cf. nebbensis* Brongniart: Raciborski, p. 85, pl. 22, figs 5, 6.
- 1894 *Cladophlebis denticulata* Brongniart: Raciborski, p. 82, pl. 22, figs 4 (non pl. 22, fig. 3).
- 1894 *Cladophlebis insignis* Lindley et Hutton: Raciborski, p. 81, pl. 22, figs 9, 10.
- 1894 *Cladophlebis bartonecii* Raciborski, p. 83, pl. 23, fig. 4 (non pl. 22, figs 11, 12, pl. 23, figs 3, 5–7).
- 1894 *Cladophlebis recentior* Phillips: Raciborski, p. 76, pl. 10, fig. 11b (lower), pl. 24, fig. 9 (non pl. 10, fig. 11b – upper, pl. 23, figs 1, 2).
- 1894 *Cladophlebis* sp. (an forma *Cl. recentioris* Phillips?): Raciborski, p. 78, pl. 22, figs 7, 8.
- 1894 *Cladophlebis subalata* Raciborski, p. 85, pl. 24, figs 15–16 (non pl. 10, fig. 11c, pl. 24, fig. 14).
- 1961 *Todites denticulatus* (Brongniart) Krasser: Harris, pp. 78–86, figs 25–27 (with synonyms)
- 1997 *Cladophlebis denticulata* (Brongniart) Nathorst: Schweitzer et al., p. 179, text-figs 25C, 28A–C, 29, pl. 22, figs 1–4.
- 2004 *Cladophlebis denticulata* (Brongniart) Harris: Rees and Cleal, pp. 26–28, text-fig. 3D, pl. 6, fig. 4, pl. 7, figs 1, 2.
- 2004 *Cladophlebis antarctica* Halle: Rees and Cleal, p. 25, text-fig. 3C, pl. 25, fig. 2, pl. 7, fig. 3.
- 2008 *Cladophlebis denticulata* (Brongniart) Harris:

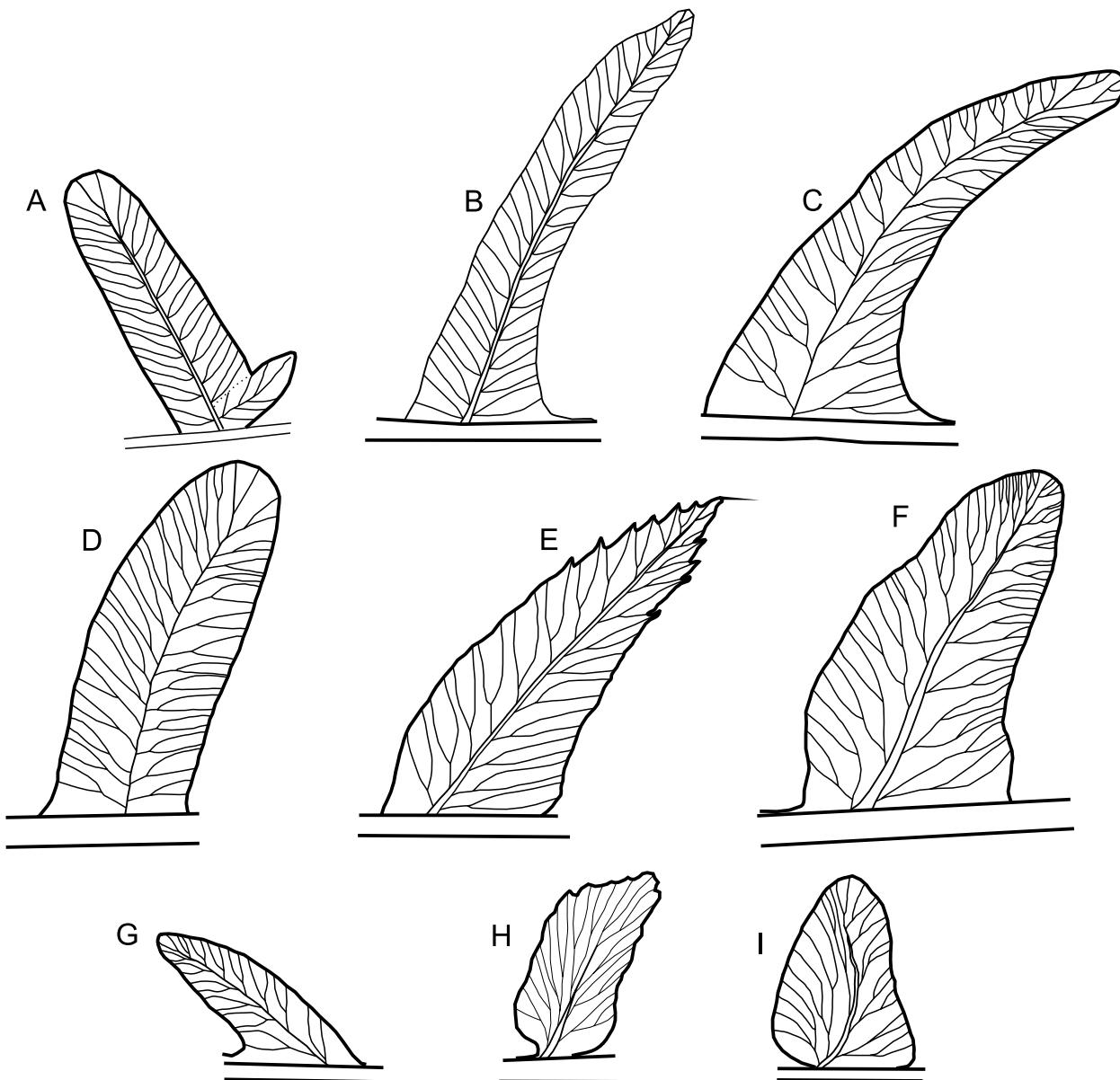
Ociepa in Birkenmajer and Ociepa, p. 34, figs 15A, 17F–G.

- 2008 *Cladophlebis antarctica* Halle: Ociepa in Birkenmajer and Ociepa, p. 32, figs 15B, 16, 17B.
- 2008 *Cladophlebis denticulata* (Brongniart) Fontaine: Barbacka and Bodor, pp. 135–138, pl. 2, fig. 5–9.
- 2009 *Cladophlebis denticulata* (Brongniart) Nathorst: Popa and Meller, pl. 2, fig. 1.

**Material.** 251 fragments of sterile fronds: ZNG PAN A-III-12\12, 19, 22.1, 32, 34, 58–59, 64–65, 97, 106.1, 123, 125, 127, 132, 135–137, 139–140, 142.2, 142.9, 143.6, 143.10, 146.3, 147, 148.3, 149, 151.1, 157–158, 167.2, 178, 190–191, 195, 197, 199–200, 217, 222, 235, 241, 245–246, 249, 254–255, 260–261, 267, 268.1, 272, 278, 280.1, 283, 288, 290.1, 292, 297–300, 306.1, 309, 316, 327, 332, 340, 340.1, 343, 345, 349–356, 358.1–2, 360–362, 363–364, 367–369, 370.1, 372–373, 375, 375.1, 384, 386, 391, 393–395, 400–401, 403–404, 406–407, 409–411, 414, 415–419, 423, 425, 432, 443, 445–446, 449–450, 455, 456.14, 457, 459, 461, 471–473, 476, 496, 498–499, 501, 503, GBA/051/0016/1, 0022–0023/2, 0025/2, 0026/3, 0027/1–2, 0028/1–2, 0032/2, 0035/1, 0037/2–0038, 0047/2, 0051/2, 0057/2, 0059, 0084/1–2, 0096, 0123/2, 0124/2, 0125/2, 0128–0129/1, 0130/1–0133/1, 0134–0139/1, 0140–0142/1, 0143/1–0149/1, 0150–0158/1, 0159/1, 0160/1–0162/1, 0163/1, 0164–0165, 0188/2, 0205/1–2, 0209/2, 0212, 0216/1, 0226/2, KRA-PALEO 105/24/2, 51, 80/1–2, 84.

**Description.** Sterile fronds, bipinnate (Pl. 3, figs 1, 8). Fragments 59–186 mm long, up to 150 mm wide. Rachis usually slightly ribbed, width (2) 4–6 (8) mm. Pinna fragments 11–95 mm long, up to 35 mm wide, attached oppositely, alternately, or subalternately to rachis. Pinna axes arise from rachis at 45–70° angle and angle decreases towards frond apex.

Pinnules oblong, entire (Pl. 3, figs 1–8), rarely dentate (Fig. 5E), length 5–28 mm, width 2–9 mm, length/width ratio (1.6) 3.16 to 4.75 (5.25). Pinnules arranged oppositely or suboppositely (Pl. 3, figs 1–5), arise from axis at 45–90° angle. Pinnule bases usually as wide as lamina, sometimes extended on acroscopic side; apex acute or subacute. Venation distinct (Pl. 3, figs 6, 7), midrib reaches pinnule apex, secondary veins dichotomise once, usually near midrib (Figs 5D, E). Secondary veins arise from midrib at (25°) 55–60° (75°) angle. Density of secondary veins near margin 6–12 per 5 mm length.



**Fig. 5.** Schematic drawing of sterile pinnules of various osmundaceous ferns from the Grojec clays. **A** – *Cladophlebis aurita*; **B, C** – *C. bartonecii*; **D, E** – *C. denticulata*; **F** – *C. haiburnensis*; **G** – *C. roessertii*; **H, I** – *Todites williamsonii*

**Discussion.** Raciborski (1894) described *Cladophlebis denticulata* from the Grojec clays based on one specimen, but he noted that there were several taxa of *Cladophlebis* characterised by slightly dentate pinnule margins, such as *Cladophlebis cf. nebbensis*, *C. recentior*, and *Cladophlebis* sp. “*an forma Cl. recentioris*”, as well as several specimens of *C. bartonecii*. He noted the high morphological variability of this genus and suggested that *Cladophlebis cf. nebbensis* might be a “naked” form of *C. bartonecii* or small form of *C. insignis* (Lindley et Hutton) Raciborski 1894. According to him, the specimens of *C. subalata* from Grojec are morphologically similar to *C. denticulata*; only the dentate margin of the pinnules and length/

width ratio distinguish the two species. Raciborski also suggested that *C. subalata* could be sterile fronds of *Osmundopsis sturii*.

The high variability of frond morphology observed by Raciborski, especially in numerous details, suggests unification of some species from Grojec into *C. denticulata*.

In his work on the Middle Jurassic flora of Yorkshire, Harris (1961) synonymised *Cladophlebis insignis* from Grojec with *C. denticulata*. Later, specimens of *Cladophlebis cf. nebbensis* described by Raciborski were included in the list of synonyms of *C. denticulata* (Barbacka & Bodor 2008).

I suggest that one specimen originally ascribed by Raciborski (1894) to *C. denticulata*,

as well as several other specimens from Grojec, should also be included in this species: all specimens figured by Raciborski as *Cladophlebis cf. nebbensis*, *C. insignis*, *Cladophlebis* sp. “an forma *Cl. recentioris*”, as well as some specimens of *C. subalata* and *C. recentior* with dentate pinnule margins. The differences between them involve details of the pinnule margins and the shape of the secondary veins (see Tables 1 and 2); other morphological features of all those taxa correspond, such as the length/width ratio, type of bifurcation, and angle of arising of secondary veins. The differences could be an effect of intraspecific variability and/or environmental conditions (Harris 1961, Barbacka & Bodor 2008, Bodor & Barbacka 2008), and their taxonomical significance is low.

Pinnules morphologically similar to *Cladophlebis denticulata* also belong to some Triassic and Jurassic *Cladophlebis* species such as *C. denticulata* var. *asiatica* Kiritchkova 1962 and *C. antarctica* Halle 1913. *Cladophlebis denticulata* var. *asiatica* has the smallest pinnules of all species. It corresponds to the non-dentate forms of *C. denticulata* from Grojec in its rounded apices, subalternate and opposite arrangement of the pinnules, entire pinnule margins, and number of bifurcations of secondary veins. Other morphological features slightly differ in these taxa, such as pinnule length and width and number of secondary veins at the pinnule margin. The difference between *Cladophlebis antarctica* and *C. denticulata* is very slight. The material from Grojec has slightly lower density of secondary veins (6–12) and a larger angle of arising of secondary veins (usually 55–60°), whereas the mode of bifurcation of secondary veins, length/width ratio, and the margins, apex, and base of pinnules correspond in the two taxa.

**Occurrence in Mesozoic floras.** Sweden, Late Triassic–Early Jurassic (Nathorst 1876, Lundblad 1950), Japan, Late Triassic–Early Jurassic (Oishi & Takahashi 1935, Kimura 1959), Afghanistan and Iran, Late Triassic–Early Jurassic (Kilpper 1964, Schweitzer et al. 1997), Romania, Early Jurassic (Popa 1997, Popa & Meller 2009), Hungary, Early Jurassic (Barbacka & Bodor 2008), China, Early–Middle Jurassic (Sun et al. 2004, 2006, 2010, Wang et al. 2005, Tian et al. 2016), Antarctica, Early Jurassic–Early Cretaceous (Gee 1989, Rees & Cleal 2004), the United Kingdom,

Middle–Late Jurassic (Stopes 1907, Seward 1911, Harris 1961), the United States of America, Jurassic (Fontaine 1889, Ward 1905), Russia, Jurassic (Thomas 1911, Kiritchkova 1962), Argentina, Jurassic (Frenquelli 1947), and India, Early Cretaceous (Goswami et al. 2006). In the Polish Mesozoic it occurred only in the Holy Cross Mts (Makarewiczówna 1928, Pacyna 2014).

### *Cladophlebis haiburnensis*

(Lindley et Hutton 1836) Brongniart 1849

Pl. 4, figs 1–6, Fig. 5F

#### Selected synonyms.

- 1836 *Pecopteris haiburnensis* Lindley et Hutton, p. 97, pl. 187.  
 1849 *Cladophlebis haiburnensis* (Lindley et Hutton) Brongniart, p. 105.  
 1894 *Thinnfeldia haiburnensis* (Lindley et Hutton) Raciborski, p. 67, pl. 20, figs 3–6.  
 1894 *Cladophlebis bartonecii* Raciborski, p. 83, pl. 22, figs 11, 12 (non pl. 23, figs 3–7).  
 1894 *Cladophlebis huttoniana* Presl: Raciborski, p. 83, pl. 10, fig. 11d, pl. 22, figs 13, 14.  
 1894 *Cladophlebis* sp. indet.: Raciborski, p. 78, pl. 24, figs 3, 4.  
 1894 *Cladophlebis recentior* Phillips: Raciborski, p. 76, pl. 10, fig. 11b (upper), pl. 23, figs 1, 2 (non pl. 10, fig. 11b (lower), pl. 24, fig. 9).  
 1894 *Cladophlebis recentior* var. *dubia* Raciborski, p. 77, pl. 24, figs 1, 2.  
 1894 *Cladophlebis tchihatchewi* Schmal. *similis* Raciborski, p. 78, pl. 24, figs 5–8.  
 1894 *Cladophlebis whitbiensis* var. *crispata* Raciborski, p. 76, pl. 22, figs 1, 2.  
 1961 *Cladophlebis haiburnensis* (Lindley et Hutton) Brongniart: Harris, p. 187, text-fig. 69 (with synonyms).  
 2008 *Cladophlebis haiburnensis* (Lindley et Hutton) Brongniart: Barbacka and Bodor, p. 138, pl. 2, figs 10–13.  
 2008 *Cladophlebis haiburnensis* (Lindley et Hutton) Brongniart: Bodor and Barbacka, figs 25H–L.

**Material.** 121 sterile frond fragments: ZNG PAN A-III-12\64, 72, 98, 108–109, 112, 126, 133–134.1, 135.9, 135.11, 143.2, 143.7, 146.3, 150, 152, 156–157, 177, 216, 229, 232, 236, 254, 277, 290, 293, 301, 304, 314–315, 323–327, 329–337, 340, 340.1, 340.2, 341–345, 347–349, 363, 366–367, 369–371, 374–377, 380–381, 385, 388, 427, 454, 456.3, 459, 461–462, 490, 496–497, GBA/051/0030, 0036/2, 0041–0043/1, 0047/3, 0053, 0055/2, 0062/2, 0104/1–0105/1, 0106–0107/1, 0108–0113/1, 0114–0120/1, 0121/1–0123/1, 0124/1, 0125/1, 0126–0127, 0158/2, 0162/2, KRA-PALEO 105/46, 48, 60/2.

**Description.** Fronds bipinnate (Pl. 4, fig. 1). Fragments 18–96 mm long, up to 173 mm wide. Rachis smooth, width (1) 4–6 mm. Pinnae attached to rachis oppositely or suboppositely, length 11–88 mm and width reaches 41 mm. Pinna axes 1–2 mm wide, arise from rachis at (25°) 45–60° (90°) angle. Pinnules entire, shapes various but usually lanceolate, oblong and falcate (Pl. 4, figs 2–6), attached closely, oppositely or subalternately (Pl. 4, figs 2, 4), arise from axis at 40–60° (85°) angle. Pinnule length 4–20 mm, width 3–7 mm, length/width ratio (1.6) 2–2.66 (3.66). Base usually straight, only sometimes slightly extended acroscopically, apex subacute. Venation of pecopterid type (Pl. 4, figs 3, 5, 6). Midrib straight, runs to apex. Secondary veins arise from midrib at 40–50° (55–75°) angle and fork twice (Fig. 5F). Density of secondary veins 8–21 veins per 1 cm of pinnule length.

**Discussion.** A key to typical species of ferns from the Middle Jurassic Yorkshire flora (Harris 1961) shows that *Cladophlebis haiburnensis* is characterised by its entire pinnule margin, twice-forked secondary veins, elongated pinnules, opposite arrangement of pinnae, and slender rachises.

*Thinnfeldia haiburnensis* (Lindley et Hutton) Raciborski 1894 (originally *Pecopteris haiburnensis* Lindley et Hutton 1836) was a new combination based on its specific, “more membranous texture” of the pinnules and the bifurcation pattern of secondary veins. Harris (1961) noted that specimens from Grojec assigned by Raciborski (1894) to this species show some differences in the pinnule venation pattern and described them as *C. haiburnensis* distinct or indeterminable, with the suggestion that these specimens could represent “true *Thinnfeldia*”, whereas Barbacka and Bodor (2008) included specimens of *Th. haiburnensis* from Grojec in the synonym list of *Cladophlebis haiburnensis*. Detailed study of original specimens of *Th. haiburnensis* from Grojec showed that their morphology, that is, their pinnule venation (pecopterid type, with twice-forked secondary veins), pinnule shape, entire margin of the pinnules, base straight or slightly extended acroscopically, and subacute apex correspond with that of *Cladophlebis haiburnensis*; in my opinion they should be assigned to this species.

Raciborski (1894) distinguished many species of *Cladophlebis* on the basis of

insignificant features such as “crumpled and wrinkled lamina” (*Cladophlebis whitbiensis* var. *crispata* Raciborski 1894), slightly broader pinnules (*Cladophlebis recentior* var. *dubia* Raciborski 1894), “more delicate lamina” (*Cladophlebis tchihatchewi*) or “traces of hairs” (*Cladophlebis huttoniana*). Considering the frond structure, some other specimens identified by Raciborski (1894) and described as *Cladophlebis huttoniana*, *Cladophlebis tchihatchewi* Schmal *similis*, *Cladophlebis* sp. indet., *Cladophlebis bartonecii*, *Cladophlebis recentior*, *Cladophlebis subalata*, and *Cladophlebis whitbiensis* should be included in *Cladophlebis haiburnensis*. No noticeable differences between these specimens can be observed in their lamina morphology and venation patterns. There is close similarity between *Cladophlebis haiburnensis* from the Grojec clays and *C. aktashensis*, *C. harrisii* Van Konijnenburg-van Cittert 1966, and *C. nebbensis*. The slight differences relate to venation and rachis pattern, pinnule size, the shape of pinnule bases and apices, and the length/width ratio.

*Cladophlebis aktashensis* (Turutanova-Ketova 1930, Harris 1961, Schweitzer et al. 1997) is characterised by having pinnules with contracted, slightly expanded or straight bases, rounded, acute, and obtusely angular apices, length 25 mm (maximum 34), width 7 mm (even 10), length/width ratio ca 3, vein density 18–21, and twice-bifurcating secondary veins. Pinnules of *C. haiburnensis* from Grojec are smaller (4–20 mm) and usually narrower (3–7 mm), with an acute apex and straight or slightly extended base, and lower length/width ratio and vein density (8–21). This species should have an alternate arrangement of pinnae and stout pinnae rachises (Harris 1961).

Material described by Van Konijnenburg-van Cittert (1966, 1996) and assigned to *C. harrisii* is characterised by having an obtuse pinnule apex, entire margin, length of 10–15 mm, width of 2–4 mm, length/width ratio of 3–5, and secondary veins not forked or forked once. Similarities with Grojec specimens are seen in the angle of arising of secondary veins (ca 40°), width of the pinna rachis (ca 2 mm), and margin of the pinnules.

Features of the typically Rhaeto-Liassic species *Cladophlebis nebbensis* correspond with those of the Grojec specimens in having slightly extended bases, subacute apices,

an entire pinnule margin, a length/width ratio of ca 2, and bifurcation of the secondary veins only once (basal vein sometimes twice) (Nathorst 1876, Yokoyama 1906, Oishi 1940, Johansson 1922, Frenquelli 1947), but *C. nebbensis* pinnules are 15 mm long and 7–9 mm wide, and the apices are rounded, while the material from Grojec clays shows more variable pinnule size, subacute apices, straight or slightly restricted bases, and the secondary veins bifurcate even three times.

Some similarities are observed between *C. haiburnensis* and *Todites williamsonii*, especially in pinnule shape and type of venation, but the pinnules of *T. williamsonii* from Grojec are significantly smaller (5–8 mm × 3–4 mm) than those of *C. haiburnensis* (4–20 mm × 3–7 mm) and are characterised by neuropterid type of venation with once- or twice-forked secondary veins.

**Occurrence in Mesozoic floras.** Greenland, Early Jurassic (Harris 1931), Romania, Early Jurassic (Popa 1997), Hungary, Early Jurassic (Barbacka & Bodor 2008, Bodor & Barbacka 2012), the United Kingdom, Middle Jurassic (Harris 1961). In Poland, *Cladophlebis haiburnensis* was noted from Early Jurassic strata in the Holy Cross Mts by Makarewiczówna (1928), but probably these specimens represents another species of *Cladophlebis*.

### *Cladophlebis roessertii* (Schenk 1867) Saporta 1873

Pl. 5, figs 1–3, Fig. 5G

- 1867 *Asplenites roessertii* Schenk, p. 49, pl. 7, fig. 7, pl. 10, figs 1–4.
- 1873 *Cladophlebis roessertii* (Schenk) Saporta, p. 301, pl. 31, fig. 4.
- 1878 *Cladophlebis (nebbensis var.) roessertii* Presl: Nathorst, p. 42, pl. 2, figs 1–3.
- 1890 *Cladophlebis roessertii* (Presl) Saporta: Raciborski, p. 11, pl. 3, figs 26–29.
- 1890 *Cladophlebis roessertii* forma *parvifolia* Raciborski, p. 12, pl. 3, figs 24, 25.
- 1894 *Cladophlebis subalata* Raciborski, p. 85, pl. 10, fig. 11c, pl. 24, fig. 14 (non pl. 24, figs 15, 16).
- 1894 *Cladophlebis whitbiensis* Brongniart: Raciborski, p. 73, pl. 21, figs 1, 2 (non pl. 20, fig. 23, pl. 21, figs 8, 9).
- 1919 *Cladophlebis roessertii* Presl: Antevs, p. 18, text-fig. 2, pl. 8, fig. 1.
- 1922 *Cladophlebis roessertii* (Presl) Saporta: Johansson, p. 18, pl. 5, figs 4–9.

- 1926 *Cladophlebis roessertii* (Schenk) Saporta: Harris, p. 57, text-figs 3A–D.
- 1989 *Cladophlebis* sp., Gee, p. 169, pl. 2, fig. 20.
- 2008 *Cladophlebis roessertii* (Schenk) Saporta: Barbacka and Bodor, p. 139, pl. 2, fig. 14.

**Material.** 72 fragments of sterile fronds: ZNG PAN A-III-12\64, 70, 73, 135.7, 143.3, 143.9, 149, 179.2, 217, 221, 257.1, 265, 275.1, 329, 339, 365, 424–425, 426.3, 427–428, 430–438, 461, 463, GBA/051/0012/1, 0047/1, 0056, 0077/2, 0100/1, 0184–0188/1, 0189/1, 0190–0192/2, 0209/1, 0225/1, KRA-PALEO 105/1/6, 27–28, 30, 32, 34–36, 39, 41–42, 45, 47, 49–50, 57, 60–60.2.

**Description.** Sterile fronds bipinnate (Pl. 5, fig. 1). Fragments up to 63 mm long, up to 45 mm wide. Rachis smooth, 2 mm wide. Pinnae attached to rachis oppositely, 32–42 mm long, up to 21 mm wide. Pinnae arise from rachis at 45–65° angle.

Pinnules entire, usually triangular, very rarely falcate (Pl. 5, figs 1–3), arise closely, oppositely, or suboppositely from axis at (45°) 60–85° angle. Pinnules 5–12 mm long, 3–6 mm wide, length/width ratio 1.2–2.66. Base straight, apex acute. Venation of pecopterid type (Pl. 5, fig. 1, Fig. 5G). Midrib straight, reaches the apex. Secondary veins arise from midrib at 60° angle and fork usually once or twice. Density of secondary veins 5–13 veins per cm of pinnule length.

**Discussion.** The set of morphological features, especially the small, triangular, elongated and narrow pinnules with entire margins, a straight base and acute apex, and pecopterid venation pattern closely corresponds to *Cladophlebis roessertii* described from France by Saporta (1873). This species is easily recognisable among the other *Cladophlebis* species, and its morphology is rather uniform and well distinguishable.

Specimens from the Grojec clays here attributed to *Cladophlebis roessertii* were assigned by Raciborski (1894) to two different taxa: *C. subalata* Raciborski 1894 and *Cladophlebis whitbiensis* Brongniart 1849.

**Occurrence in Mesozoic floras.** Germany, Late Triassic–Early Jurassic (Schenk 1867), France, Jurassic (Saporta 1873), Sweden, Late Triassic–Jurassic (Nathorst 1878, Antevs 1919, Johansson 1922), Greenland, Early Jurassic (Harris 1926), Hungary, Early Jurassic (Barbacka & Bodor 2008), Antarctica,

Late Jurassic–Early Cretaceous (Gee 1989). In the Polish Mesozoic it occurred in Late Triassic sediments from the Tatra Mts (Raciborski 1890).

Family: OSMUNDACEAE  
Berchtold and J.S. Presl 1820

Genus: *Osmundopsis*  
Raciborski 1894 emend. Harris 1961

Type species: *Osmundopsis sturii*  
Raciborski 1894 emend. Harris 1961

*Osmundopsis sturii*  
(Raciborski 1894) Harris 1961

Pl. 5, figs 5, 6

- 1890 *Osmunda* sp. Raciborski, p. 2, pl. 1, figs 1–5.
- 1892 *Polysorites* Raciborski, p. 10.
- 1894 *Osmunda sturii* Raciborski, p. 19, pl. 6, figs 7, 9–16, pl. 11, fig. 7b.
- 1894 *Osmunda* sp.: Raciborski, p. 21, pl. 6, fig. 8.
- 1910 *Osmundites sturii* Seward, p. 123.
- 1931 *Osmundopsis sturii* (Raciborski) Harris, p. 48.
- 1961 *Osmundopsis sturii* (Raciborski) Harris, p. 99, text-figs 32A–D.
- 1964 *Osmundopsis* cf. *plectophora* Harris: Kilpper, p. 42, pl. 7, figs 1–4, pl. 8, figs 1, 2.
- 1970 *Osmundopsis* sp.: Alavi & Barale, p. 244, pl. III, fig. 1.
- 1977 *Osmundopsis sturii* (Raciborski) Harris, p. 4.
- 1996 *Osmundopsis sturii* (Raciborski) Harris: Van Konijnenburg-van Cittert, p. 722, text-fig. 1, pl. 2, fig. 2–4, pl. 3, figs 1–3, pl. 4, figs 2–5.
- 1997 *Osmundopsis sturii* (Raciborski) Harris: Schweitzer et al., p. 169, text-fig. 28D, pl. 18, figs 1–8.

**Material.** 8 fragments of fertile fronds: ZNG PAN A-III-12\13 (Pl. VI, fig. 9), 14, 15, 16–19, 100, all from Grojec.

**Description.** Pinna fragments of fertile fronds reaching 35 mm in length and 11 mm in width. Pinna rachis less than 1 mm wide, usually smooth. Pinnules consist of numerous sporangia (Pl. 5 fig. 5). Pinnules attached alternately or subalternately, 1–8 mm long, 1–3 mm wide, pinnules near pinna base slightly longer and broader, pinnules arise from axis at 70–85° angle. Sporangia usually oblong or obovate, ca 20 sporangia per pinnule (Pl. 5, fig. 6), 0.7 mm long, 0.3 mm wide, arranged on whole pinnule surface.

**Discussion.** *Osmundopsis sturii* is a well-defined species. Details of the pinnules such

as shape and size, the angle of arising from the rachis, and the typical size and shape of sporangia allow assignment of these specimens to this species.

Raciborski (1894) described three taxa of *Osmunda* from Grojec based on sporangia size. *Osmundopsis sturii* has the largest sporangia; those of *O. microcarpa* Raciborski 1894 and *Osmunda* sp. are slightly smaller. In situ spores were not found in the specimens.

Harris (1961) created the fossil genus *Osmundopsis*, including all *Osmunda* taxa described by Raciborski. Later, Kilpper (1964) proposed to refer them to *Todites* or *Todea*, but Harris's (1977) detailed studies confirmed his own point of view. Harris (1977) expressed doubt about the taxonomical value of differences in sporangia size between *O. sturii* and *O. microcarpa*. In his opinion, smaller sporangia might represent a juvenile form improperly developed, or may have come from the upper part of the fronds. Unfortunately, in the present study I did not find specimens of *Osmunda microcarpa*, so it is not possible to confirm the range of sporangia variability in *Osmundopsis*.

So far only fertile fronds of *Osmundopsis sturii* are known, but some authors (e.g. Raciborski 1894, Van Konijnenburg-van Cittert 1978, 1996, Van Konijnenburg-van Cittert & Morgans 1999) noted the occurrence of *O. sturii* and sterile fronds of *Cladophlebis denticulata* with relatively small pinnules together in some localities. This may suggest that the two forms represent one species.

*Osmundopsis sturii* resembles *O. microcarpa*, *O. prigorovskii* Kryshtofovitch et Prynada 1933, *O. prynadae* Delle 1967, *O. plectophora* Harris 1931, and *O. hillii* Van Konijnenburg-van Cittert 1996. Smaller sporangia size in *Osmundopsis microcarpa*, *O. prigorovskii* and *O. prynadae* (Raciborski 1894, Harris 1961, 1977, Van Konijnenburg-van Cittert 1996) are the most distinguishing features between these taxa and *O. sturii* from Grojec. *Osmundopsis plectophora* are tripinnate, the pinnules are long (up to 20 mm), the sori contain no more than 12 sporangia, and sporangia size is 0.8 × 0.5 mm (Harris 1931, Harris 1961), while *O. sturii* has smaller pinnules (up to 8 mm) and smaller sori, with more sporangia. Pinnules of *O. hillii* are attached more distantly, the sporangia are smaller (0.5 × 0.3 mm), and the sori contain only 8 sporangia (Van Konijnenburg-van

Cittert 1996); only the pinnule size corresponds with *O. sturii* from Grojec.

**Occurrence in Mesozoic floras.** This species occurred in Greenland, Early Jurassic (Harris 1931), Romania, Early Jurassic (Popa 1997), Abkhazia, Middle Jurassic (Kryshlofovich & Prynada 1933), the United Kingdom, Middle Jurassic (Harris 1961), and Iran, Early Jurassic (Kilpper 1964, Schweitzer et al. 1997). Wang (2002) assigned frond fragments of cf. *Osmundopsis sturii* (Wu 1991) from the Middle Jurassic of China to *Todites* (possibly *T. williamsonii*). From the Polish Mesozoic *O. sturii* was noted only from Grojec, Middle Jurassic (Raciborski 1894).

#### Genus: *Todites* Seward 1900

Type species: *Todites williamsonii* Brongniart 1828 emend. Seward 1900

***Todites williamsonii***  
Brongniart 1828 emend. Seward 1900

Pl. 6, figs 1–6, Figs 5H, I

#### Selected synonyms.

- 1828 *Pecopteris williamsonis* Brongniart, p. 57.
- 1829 *Pecopteris recentior* Phillips, pl. 8, fig. 15.
- 1829 *Pecopteris curtata* Phillips, p. 148, pl. 8, fig. 12.
- 1829 *Pecopteris hastate* Phillips, p. 148, pl. 8, fig. 17.
- 1829 *Pecopteris williamsonis* Brongniart: Phillips, pl. 10, fig. 7.
- 1892 *Todea williamsonis* (Brongniart) Schenk: Raciborski, p. 1, pl. 2, fig. 15 (fragment of fertile frond).
- 1894 *Cladophlebis whitbiensis* Brongniart: Raciborski, p. 73, pl. 21, figs 8, 9 (non pl. 20, fig. 23, pl. 21, figs 1, 2 fragments of sterile fronds).
- 1894 *Cladophlebis solida* Raciborski, p. 79, pl. 24, figs 10–13 (fragments of sterile fronds).
- 1894 *Todea williamsonis* (Brongniart) Schenk: Raciborski, p. 16, pl. 6, figs 17–20, pl. 7, fig. 9.
- 1900 *Todites williamsonii* (Brongniart) Seward, p. 87, pl. 14, figs 2, 5, 7; pl. 15, figs 1–3; pl. 21, fig. 6; text-fig. 12.
- 1961 *Todites williamsonii* (Brongniart) Seward: Harris, p. 87, text-fig. 29 (with synonyms).
- 1997 *Todites williamsonii* (Brongniart) Seward: Schweitzer et al., p. 165, pl. 15, fig. 6; pl. 1g, figs 1–6; pl. 17, figs 1–5; text-fig. 25A (with synonyms).
- 2016 *Todites williamsonii* (Brongniart) Seward: Tian et al., fig. 1C.

**Material.** 9 sterile frond fragments: ZNG PAN A-III-12\378 (pl. XXIV, fig. 10), 379

(pl. XXIV, fig. 11), 380 (pl. XXIV, fig. 13), 381, GBA/051/0196; 7 fertile frond fragments: ZNG PAN A-III-12\7 (pl. VI, fig. 18), 8.2, 9–10, 136.5, GBA/051/0002, GBA/051/0196, fertile and sterile on the same slab: GBA/051/0196, all from Grojec.

**Description.** Fronds dimorphic, bipinnate in a katadromic way. Fragments of sterile fronds (Pl. 6, figs 3, 4) up to 80 mm long, 20 mm wide. Rachis smooth, 3–4 mm wide. Pinna rachis 1–2 mm wide, arises from main rachis at 40–50° angle. Pinnules sessile, entire, rarely slightly crenate near apex, attached alternately, closely but not overlapping (Pl. 6, figs 3, 4). Distance between midvein of adjacent pinnules ca 3–4 mm. Shape variable from oval to falcate (dominant). Pinnule base contracted, apex subacute or rounded, length 5–8 mm, width 3–4 mm, length/width ratio 1.2 to 2.25. Pinnule venation neuropterid (Figs 5H, I). Midrib does not reach apex, secondary veins arise from midrib at 30–60° angle, divide usually twice, sometimes three times in basal part of pinnules, once in apical part.

Fragments of fertile fronds small, length reaches 32 mm (Pl. 6, figs. 1, 2). Pinna rachis smooth, 2–4 mm wide. Pinnules oppositely attached, entire, oblong and falcate (Pl. 6, figs 1, 2, 5, 6), length 6–11 mm, width 2–3 mm, length/width ratio 2.5 to 4. Pinnule usually contracted (Pl. 6, fig. 1), apex rounded. Venation, similar to that of sterile frond, of neuropterid type. Secondary veins forked once or twice. Sporangia (Pl. 6, figs 1, 2, 5, 6) irregularly distributed on whole lower surface of pinnules, rounded, diameter ca 0.2–0.3 mm. Spores not found.

**Discussion.** *Todites* is known as a genus with high intraspecific variability (e.g. Harris 1931, 1961, Schweitzer et al. 1997, Barbacka & Bodor 2008, Tian et al. 2016). Features used for differentiation of species from this genus are pinnule size, margins, length/width ratio, angle of secondary vein arising, number of secondary veins near pinnule margin, and venation pattern (Harris 1931, 1961, Barbacka & Bodor 2008). These features are similar in several Triassic and Jurassic species such as *Todites goeppertianus* (Münster) Krasser 1922, *T. leei* Wu 1991, *T. scoresbyensis* Harris 1931, and *T. williamsonii*. Katadromic venation is characteristic for all of them, but *T. scoresbyensis* and *T. leei* have pecopterid venation, while in

*Todites goeppertianus* and *T. williamsonii* it is neuropterid (Gothan 1914, Harris 1931, Frequelli 1947, Kräusel 1958, Wu 1991). The material from Grojec is characterised by the neuropterid type of venation and contracted bases of the pinnules, which is specific for *T. williamsonii*, while *T. goeppertianus* has extended bases (Harris 1931). On the basis of these features the specimens from Grojec were assigned to *T. williamsonii* (Brongniart) Seward.

Some authors believed that *T. williamsonii*, *T. goeppertianus*, and *T. whitbiensis* Brongniart 1828 are extremely different forms of the same species – *T. williamsonii* (Brongniart) Harris (Harris 1961, Schweitzer et al. 1997). In a study of spores in situ, however, Van Konijnenburg-van Cittert (1978) concluded that these species are different but closely related.

Raciborski (1894) assigned three morphological forms of frond to three different species. Fertile fronds were described as *Todea williamsonis* (Brongniart) Schenk, sterile ones as *Cladophlebis solida* Raciborski, and a smaller form of *Cladophlebis whitbiensis* Brongniart. Later, Harris (1961) included *T. williamsonis* and *C. whitbiensis* from Grojec in *Todites williamsonii*.

**Occurrence in Mesozoic floras.** *Todites williamsonii* was noted from Sweden, Late Triassic (Dobruskina 1994), Germany, Late Triassic–Early Jurassic (Weber 1968), Greenland, Late Triassic–Early Jurassic (Harris 1926, 1931, 1937), China, Late Triassic–Middle Jurassic (Tian et al. 2016), France, Early Jurassic (Corsin 1973), Serbia, Early Jurassic (Djordjević-Milutinović, 2010), Iran, Late Triassic–Middle Jurassic (Kilpper 1964, Schweitzer et al. 1997), Antarctica, Early–Middle Jurassic (Cantrill & Poole 2012), and the United Kingdom, Middle Jurassic (Harris 1961, Van Konijnenburg-van Cittert 1978). In the Polish Mesozoic it occurred in Grojec (Raciborski 1894) and the Holy Cross Mts. (Raciborski 1892).

#### ***Todites princeps* (Presl in Sternberg 1838)** Gothan 1914

Pl. 7, figs 1–4

- 1838 *Sphenopteris princeps* Presl in Sternberg, p. 126, pl. 59, figs 12, 13.
- 1867 *Acrostichites princeps* Presl: Schenk, p. 46, pl. 7, figs 3, 4, pl. 8, fig. 1.
- 1891 *Todea princeps* (Presl) Raciborski, p. 9, pl. 1, figs 10–13.

- 1894 *Todea princeps* (Presl) Raciborski, p. 18, pl. 6, figs 22–27.
- 1914 *Todites princeps* (Presl) Gothan, p. 95, pl. 17, figs 3, 4.
- 1926 *Todites princeps* (Presl) Gothan: Harris, p. 26, text-figs 2A–E, pl. 12, fig. 5.
- 1931 *Todites princeps* (Presl) Gothan: Harris, p. 35, text-figs 8, 9, pl. 11, figs 1, 2, 4, 9, pl. 12, fig. 3.
- 1940 *Todites princeps* (Presl) Gothan: Oishi, p. 196.
- 1958 *Todites princeps* (Presl) Gothan: Kräusel, p. 69, pl. 3, figs 6, 7.
- 1961 *Todites princeps* (Presl) Gothan: Harris, pp. 93–98, text-figs 30, 31.
- 1964 *Todites princeps* (Presl) Gothan: Kilpper, p. 44, text-fig. 22, pl. 8, figs 6–9.
- 1978 *Todites princeps* (Presl) Gothan: Schweitzer, p. 31, text-figs 10–18, pl. 1, figs 3–5, pl. 2 figs 1–6, pl. 3, figs 1–7.
- 1997 *Todites princeps* (Presl) Gothan: Schweitzer et al., p. 160, text-fig. 24A.
- 2002 *Todites princeps* (Presl) Gothan: Wang, p. 130, pl. 2, fig. 1.
- 2005 *Todites princeps* (Presl) Gothan: Wang et al., p. 834, fig. 8(3).
- 2008 *Todites princeps* (Presl) Gothan: Barbacka and Bodor, p. 134, pl. 1, figs 1–5.
- 2010 *Todites princeps* (Presl) Gothan: Barbacka et al., p. 376, pl. 1, figs 7, 8.

**Material.** 3 fragments of fertile fronds: ZNG PAN A-III-12\11.1 (Pl. VI, fig. 22) – 11.3, 193, all from Grojec.

**Description.** Fronds bipinnate with anadromic branching and venation. Pinnae (Pl. 7, figs 2–4) 17–34 mm long, up to 14 mm wide. Pinna rachis smooth, less than 1 mm wide. Pinnules sessile, oblong with slightly crenate margins (Pl. 7, figs 1, 2), 6–7 mm long, 2–3 mm wide near base, attachment varies from alternate to almost opposite, arises at 70–90° angle from rachis. Pinnule base broad, apex rounded. Pinnules become slightly smaller towards pinna apex, length/width ratio 2.3–3. Pinnule venation of sphenopterid type, where midrib arises from rachis at 55–75° angle; secondary veins numerous, arise from midrib at 45–60° angle.

**Discussion.** The set of morphological features such as the characteristic sphenopterid type of venation and anadromic branching (Harris 1961) place it in *Todites princeps*. Other pinnule details such as shape and size are very variable within this species and are the bases for distinguishing several morphotypes.

Raciborski (1894) described two taxa belonging to *Todea*: *Todea williamsonis* Brongniart 1828 (=*Todites williamsonii*) and *Todea princeps* (Presl) Raciborski 1890 (=*Todites*

*princeps*). Pinnules with slightly crenate margins have been described from Afghanistan and Iran (Schweitzer 1978, Schweitzer et al. 1997), China (Wang et al. 2005) and Japan (Oishi 1932, 1940); their morphological features correspond to the material from the Grojec clays. Specimens described from Germany (Gothan 1914), the United Kingdom (Harris 1961), and Poland (Barbacka et al. 2010) are characterised by having somewhat dissected pinnules. *Todites princeps* from the Triassic and Jurassic of Greenland and the Middle Jurassic of Yorkshire is represented by two morphotypes and a series of transitional forms (Harris 1926, 1931, 1961), which differ mainly by their pinnule margin and the degree of pinnule division. Three morphotypes (1, 2, 3) are known from Lower Jurassic strata of Hungary (Barbacka & Bodor 2008, Bodor & Barbacka 2008). The differences between these forms relate to the size, shape, and margin of pinnules. The material from Grojec is similar in the size and margin of the pinnules to morphotype 2 from Hungary.

**Occurrence in Mesozoic floras.** *Todites princeps* is known from Germany, Late Triassic–Early Jurassic (Schenk 1867, Gothan 1914, Kräusel 1958, Weber 1968, Achilles 1981, Gregor & Hauptmann 1998); Greenland, Late Triassic–Early Jurassic (Harris 1926, 1931, 1937), Iran, Late Triassic–Middle Jurassic (Kilpper 1964, Schweitzer 1978, Schweitzer et al. 1997), China, Late Triassic–Middle Jurassic (e.g. Wu 1991, Wang 2002, Wang et al. 2005, Sun et al. 2010), France, Early Jurassic (Corsin, 1973), Hungary, Early Jurassic (Barbacka 2011, Barbacka & Bodor 2008, Bodor & Barbacka 2008, 2012), and the United Kingdom, Middle Jurassic (Harris 1961). In the Polish Mesozoic this species was previously noted only from the Early Jurassic of the Holy Cross Mts area (Raciborski 1891, Makarewiczówna 1928, Pacyna 2013, Barbacka et al. 2014b). Barbacka et al. (2010) described two taxa of *Todites* from Odrowąż: *T. princeps* and *Todites princeps forma trilobata*.

## GENERAL REMARKS

The material of osmundaceous ferns from Grojec shows high variability of morphological features such as pinnule shape and size, vein number and density, angle of departing veins,

and angle of bifurcation (Table 2). Some other characteristics (e.g. dichotomy, pinnule base, apex and margin) are less variable, but generally the occurrence of different shapes even in the same frond is common, especially within the genus *Cladophlebis*. The high morphological variation of these features, along with additional characters such as the presence of hair traces, “roughness” of the lamina, pinnules that are “wrinkled and bent”, and “fuzzier” lamina (Table 1), led Raciborski (1894) to distinguish 15 different taxa of *Cladophlebis*. Studies of the variability of some morphological features such as the presence of hair traces and the thickness of lamina indicated that they can be caused by environmental conditions or the state of preservation (e.g. Caponetti 1972, Kvaček & Walther 1978, Metcalfe 1979, Chaloner & Creber 1990, Osborn & Taylor 1990, Barbacka & Van Konijnenburg-van Cittert 1998) and should not be treated as taxonomically significant features (e.g. Ward 1905, Thomas 1911, Rees & Cleal 2004, Barbacka & Bodor 2008, Bodor & Barbacka 2008).

My current study confirmed that the number of *Cladophlebis* species proposed by Raciborski (1894) should be reduced (Table 3), because some features (e.g. presence or absence of hair traces, thickness of lamina) are unstable and cannot be used to create new species (e.g. *Cladophlebis solida*, *C. subalata*) or forms (e.g. *C. recentior* var. *dubia*, *Cladophlebis whitbiensis* var. *crispata*). In my opinion, one specimen of *Cladophlebis denticulata*, all specimens of *Cladophlebis* cf. *nebbensis*, *C. insignis*, *Cladophlebis* sp. a forma *Cl. recentioris* Phillips, as well as part of the specimens of *C. recentior* and *C. subalata* described by Raciborski (1894) belong to one species, *Cladophlebis denticulata* (Brongniart) Fontaine. All the material described by Raciborski as *Thinnfeldia haiburnensis*, *Cladophlebis* sp., *C. huttoniana*, *C. recentior* var. *dubia*, *C. tchihatchewii* Schmal. *similis*, *C. whitbiensis* var. *crispata*, and several specimens ascribed by him to *C. recentior* can be assigned to *Cladophlebis haiburnensis*. Part of the specimens described as *Cladophlebis subalata* and *C. whitbiensis* are assigned here to *Cladophlebis roessertii* (Schenk) Saporta.

On the other hand, some exceptional characters such as the presence of a basal lobe in pinnules of *C. aurita*, together with other morphological features (e.g. pinnule shape and margin, venation type) confirm this species.

**Table 3.** Comparison of the results of previous work (Raciborski 1894) with the results of this study

Current study	Raciborski's study (1894)
<i>Cladophlebis aurita</i>	<i>Cladophlebis aurita</i>
<i>Cladophlebis bartonecii</i>	<i>Cladophlebis bartonecii</i> , <i>Cladophlebis recentior</i> (specimens with entire margin and twice-forked secondary veins), <i>Cladophlebis subalata</i> (specimens with longer and narrower pinnules and twice-forked secondary veins), <i>Cladophlebis whitbiensis</i> (specimens with larger pinnules and pecopterid venation)
<i>Cladophlebis denticulata</i>	<i>Cladophlebis denticulata</i> , <i>Cladophlebis bartonecii</i> (specimens with wider and dentate pinnules), <i>Cladophlebis cf. nebbensis</i> , <i>Cladophlebis insignis</i> , <i>Cladophlebis recentior</i> (specimens with dentate pinnule margin and once-forked secondary veins), <i>Cladophlebis</i> sp. (an forma <i>Cl. recentioris</i> ), <i>Cladophlebis subalata</i> (specimens with larger and wider pinnules and once-forked secondary veins)
<i>Cladophlebis haiburnensis</i>	<i>Thinnfeldia haiburnensis</i> , <i>Cladophlebis bartonecii</i> (specimens with wider pinnules and twice-forked secondary veins), <i>Cladophlebis huttoniana</i> , <i>Cladophlebis</i> sp. indet., <i>Cladophlebis recentior</i> (specimens with falcate pinnules and extended bases), <i>Cladophlebis recentior</i> var. <i>dubia</i> , <i>Cladophlebis tchihatchewi similis</i> , <i>Cladophlebis whitbiensis</i> var. <i>crispata</i>
<i>Cladophlebis roessertii</i>	<i>Cladophlebis subalata</i> (specimens with smaller, triangular pinnules), <i>Cladophlebis whitbiensis</i> (specimens with triangular pinnules and pecopterid venation)
<i>Osmundopsis sturii</i>	<i>Osmunda sturii</i> , <i>Osmunda</i> sp.
<i>Todites williamsonii</i>	<i>Cladophlebis whitbiensis</i> (specimens with shorter pinnules and nuropterid venation), <i>Cladophlebis solida</i> , <i>Todea williamsonis</i>
<i>Todites princeps</i>	<i>Todea princeps</i>

*Cladophlebis bartonecii* is the second species of Raciborski (1894) that can be retained. The set of morphological characteristics, especially the combination of pinnule shape (narrow and long, often falcate, narrow bases, length/width ratio), and venation patterns (frequent bifurcation, angle of dichotomy and arising of secondary veins) is quite unique.

Raciborski (1894) also distinguished one species of *Osmundopsis* (originally described by him as *Osmunda*) and two species of *Todites* (originally described by him as *Todea*). The differences between these genera are all well recognised and focus on different aspects of morphology such as the type of pinnule base and apex, pinnule shape, length/width ratio, venation patterns, and the presence and distribution of sporangia.

The material described by Raciborski (1894) as *Osmunda sturii* and *Todea princeps* showed the typical morphological features for these species and needs only to be assigned to the previously proposed new combinations *Osmundopsis sturii* (Raciborski) Harris and *Todites princeps* (Presl) Gothan. Specimens assigned by him to *Todea williamsonis*, *Cladophlebis whitbiensis* and *C. solida* are characterised by katadromic branching, neuropterid venation and other

typical features for sterile and fertile fronds of *Todites williamsonii* (Brongniart) Seward.

The current study has shown that although some morphological features can be highly variable they can still be used as diagnostic features if used in combination. In order to understand whether the various features are diagnostic, it is necessary to examine a large number of specimens in order to observe transitional forms and the variability of features. The use of a large sample will make species separations more reliable.

## PALAEOECOLOGY OF GROJEC OSMUNDALES

The flora assemblage of Grojec is dominated by ferns, which constitute 79% of all plant remains; Osmundales (with *Cladophlebis* species) is the most common group (see Fig. 1). It is widely believed that osmundaceous ferns preferred usually wet habitats in the immediate vicinity of riverbanks, lake shores, and marshes in temperate, subtropical, and tropical areas (e.g. Vakhrameev 1991, Deng 2002, Wang 2002, Van Konijnenburg-van Cittert 2002). These ferns formed the understorey of

forests growing in swampy areas (Abbink et al. 2004, Van Konijnenburg-van Cittert 2008).

The fragments are represented by fragile and delicate compound fern fronds, suggesting autochthonous or paraautochthonous origin. Since transport was minimal, I suggest that the co-occurrence of plants on the same stone slab reflects their common occurrence at the site.

Four *Cladophlebis* species (*C. denticulata*, *C. haiburnensis*, *C. roessertii*, *C. bartonecii*) show similar wide spectra of co-occurring taxa (Fig. 6). They are accompanied mainly by other ferns such as *Eboracia lobifolia*, *Klukia exilis*, *Coniopteris cf. murrayana*, *C. hymenophylloides*, and *Gleichenia rostafinskii*. They might also have co-occurred with the cycad *Ctenis potockii* and the seed fern *Pachypterus rhomboidalis*. *Cladophlebis bartonecii* co-occurs with the bennettite *Pterophyllum subaequale*; *C. roessertii* co-occurs with the ferns *Hausmannia cracoviensis* and *Matoniidium goeppertiae*; and *C. denticulata* co-occurs with *Osmundopsis sturii*, *Dictyophyllum cf. rugosum*, and *Gonatosorus natherstii*. Self-occurrence within these species is highest for *Cladophlebis*

*haiburnensis* (ca 54%), followed by *C. denticulata* (ca 30%), *C. bartonecii* (38%), and *C. roessertii* (ca 40%). In Grojec, generally it seems that *Cladophlebis* formed mixed communities of more than one species of the same genus.

*C. roessertii*, however, was not found co-occurring with *C. haiburnensis*, suggesting that they did not grow at the same sites. Species of the genus *Cladophlebis* also formed communities with sphenophytes and other ferns (Table 4) that probably grew on periodically flooded areas near riverbanks and lake shores, or with cycads, seed ferns, and ferns that might occupy the edges of marshes.

*Osmundopsis sturii* occurs only with *Eboracia lobifolia*, *Coniopteris hymenophylloides*, and *Cladophlebis denticulata* (Fig. 7).

The composition of species co-occurring with *Todites princeps* (Fig. 8) suggests that they were a part of communities growing in drier habitats, with sphenophytes (*Neocalamites lehmannianus*, *N. grojencensis*) and other ferns such as *Gleichenia rostafinskii* and *Coniopteris cf. murrayana*. *Todites williamsonii* shows a slightly wider spectrum of co-occurring taxa

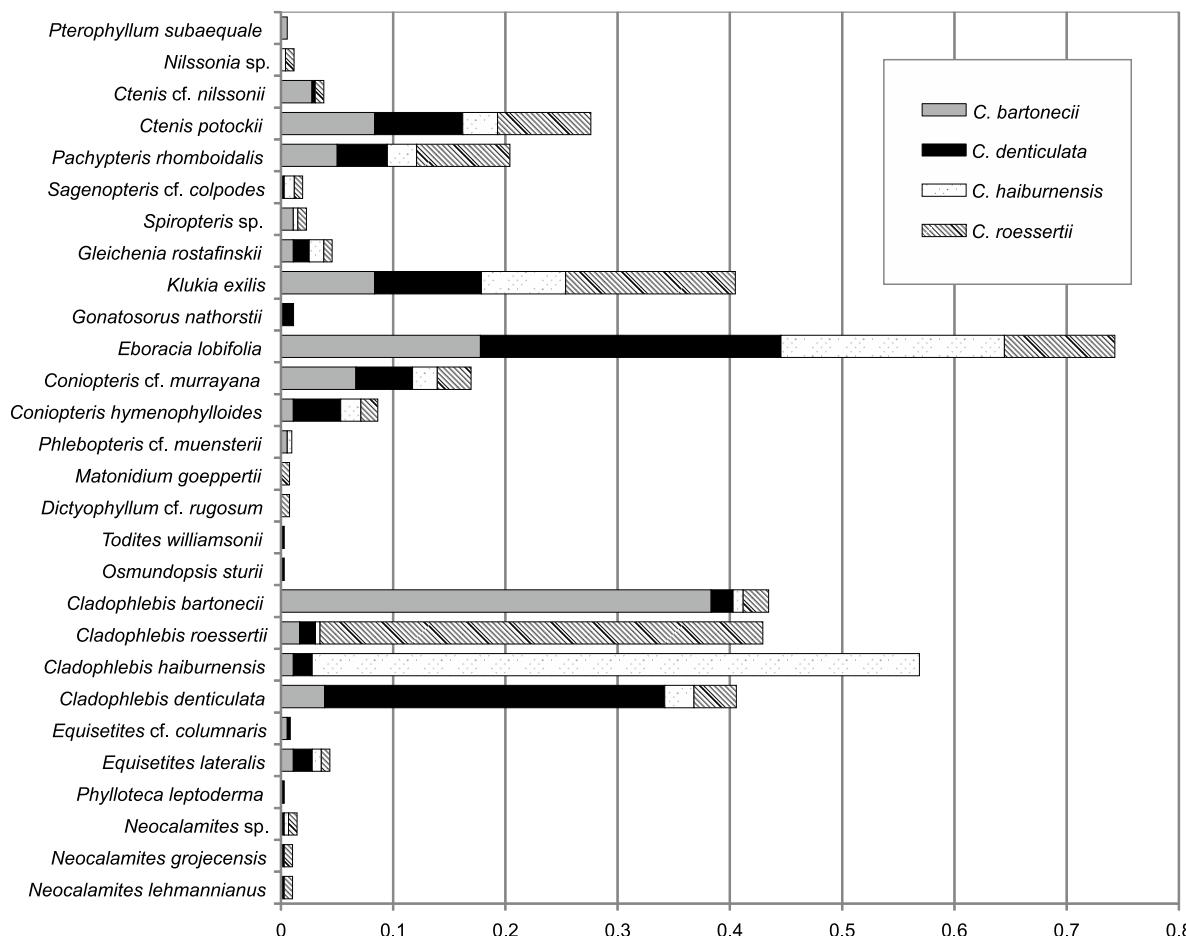


Fig. 6. Co-occurrence of *Cladophlebis* species with other plants in the flora of the Grojec clays

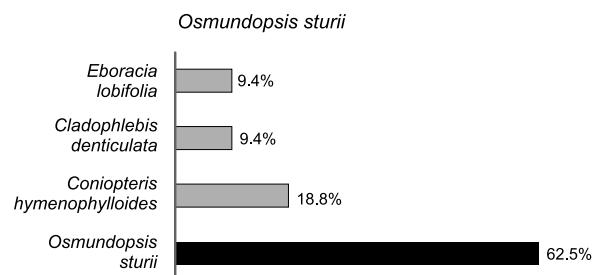
**Table 4.** Co-occurrence of osmundaceous ferns with other plants in the flora of Grojec (+ co-occurrence, – lack of co-occurrence)

	<i>Cladophlebis denticulata</i>	<i>Cladophlebis haiburnensis</i>	<i>Cladophlebis roessertii</i>	<i>Cladophlebis bartoneci</i>	<i>Osmundopsis sturii</i>	<i>Todites williamsonii</i>	<i>Todites princeps</i>
<i>Neocalamites lehmannianus</i>	+	–	+	–	–	–	–
<i>Neocalamites grojencensis</i>	+	–	+	–	–	–	–
<i>Neocalamites</i> sp.	+	+	+	–	–	–	–
“ <i>Phyllocoel leptoderma</i> ”	+	–	–	–	–	–	–
<i>Equisetites lateralis</i>	+	+	+	+	–	–	–
<i>Equisetites</i> cf. <i>columnaris</i>	+	–	–	+	–	–	–
<i>Cladophlebis denticulata</i>		+	+	+	+	+	–
<i>Cladophlebis haiburnensis</i>	+		–	+	–	–	–
<i>Cladophlebis roessertii</i>	+	+		+	–	–	–
<i>Cladophlebis bartoneci</i>	+	+	+		–	–	–
<i>Osmundopsis sturii</i>	+	–	–	–		–	–
<i>Todites williamsonii</i>	+	–	–	–	–		–
<i>Todites princeps</i>	–	–	–	–	–	–	
<i>Dictyophyllum</i> cf. <i>rugosum</i>	–	–	–	+	–	–	–
<i>Hausmannia cracoviensis</i>	–	–	–	+	–	–	–
<i>Matoniidium goeppertii</i>	–	+	+	+	–	–	–
<i>Coniopteris hymenophylloides</i>	+	+	+	+	+	–	–
<i>Coniopteris</i> cf. <i>murrayana</i>	+	+	+	+	–	–	+
<i>Eboracia lobifolia</i>	+	+	+	+	+	+	–
<i>Gonatosorus nathorstii</i>	+	–	–	–	–	–	–
<i>Klukia exilis</i>	+	+	+	+	–	+	–
<i>Gleichenia rostafinskii</i>	+	+	+	+	–	–	+
<i>Spiropteris</i> sp.	–	+	+	+	–	–	–
<i>Sagenopteris</i> cf. <i>colpodes</i>	+	+	+	–	–	–	–
<i>Pachypterus rhomboidalis</i>	+	+	+	+	–	–	–
<i>Ctenis potockii</i>	+	+	+	+	–	+	–
<i>Ctenis</i> cf. <i>nilssonii</i>	+		+	+	–	–	–
<i>Nilssonia</i> sp.	–	+	+	–	–	–	–
<i>Pterophyllum subequale</i>	–	–	–	+	–	–	–

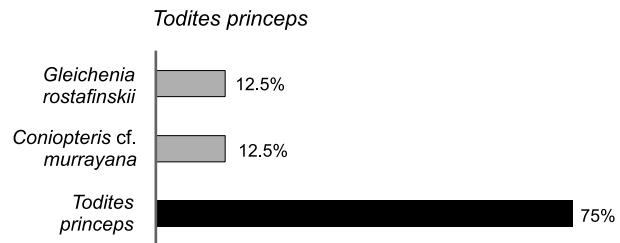
(Fig. 9), including some fern species (*E. lobifolia*, *C. denticulata*, *K. exilis*) and the cycad *Ctenis potockii*. Both *T. princeps* and *T. williamsonii* show high self-occurrence, 75% and 55% respectively (Fig. 8, 9).

Previous studies of Mesozoic plant communities have confirmed that *Cladophlebis denticulata* grew in subtropical and tropical areas (e.g. Vakhrameev 1991, Van Konijnenburg-van Cittert 2002). More detailed analyses of Jurassic floras from China, Romania, and the United Kingdom revealed that these plants formed communities within the genus in areas of higher moisture near rivers and lakes, but sometimes even in brackish conditions (Harris 1961, Barbacka & Bodor 2008, Popa & Meller 2009, Sun

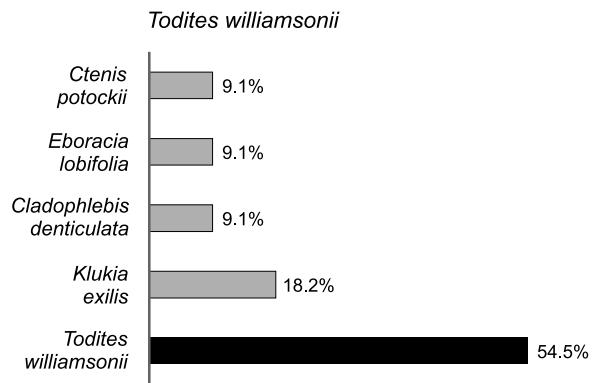
et al. 2010, Barbacka 2011). They were also present in drier habitats (i.e. Early Jurassic of Hungary, Upper Jurassic of Sutherland, Scotland), indicating a wider range of environmental tolerance (Van Konijnenburg-van Cittert & Van der Burgh 1996, Barbacka 2011). Some similar preferences have been observed in *C. haiburnensis*, especially their occurrence in wet habitats of lake shores, riverbanks, and marshes of subtropical and tropical areas (e.g. Harris 1931, Vakhrameev 1991, Popa 1997). Barbacka (2011) concluded that *C. haiburnensis*, like *C. denticulata*, could grow in drier habitats but that the most optimal conditions for these species were in moderately humid, only periodically flooded areas. The presence of *Cladophlebis roessertii* is connected with two types of area: moist habitats



**Fig. 7.** Co-occurrence of *Osmundopsis sturii* with other plants in the flora of the Grojec clays (black bar – self-occurrence value)



**Fig. 8.** Co-occurrence of *Todites princeps* with other plants in the flora of the Grojec clays (black bar – self-occurrence value)



**Fig. 9.** Co-occurrence of *Todites williamsonii* with other plants in the flora of the Grojec clays (black bar – self-occurrence value)

at lake shores and riverbanks, or river influxes with brackish conditions (Harris 1926, Gee 1989, Barbacka & Bodor 2011). Overflow areas and margins of swamps are postulated as typical for *Osmundopsis sturii* by numerous authors (Harris 1931, 1961, Krystofovich & Prynada 1933, Van Konijnenburg-van Cittert 1996, Popa & Meller 2009).

*Todites* has been associated with wet habitats within floodplains, deltas, marshes, riverbanks, and lake shores (Krassilov 1973, Van Konijnenburg-van Cittert 2002, Abbink et al. 2004). Wang (2002) suggested that these are herbaceous and hydrophytic ferns growing in warm and wet habitats, but some authors noted their tolerance of semi-dry conditions (Batten 1974, Hesselbo et al. 2003, Barbacka 2011). According to Harris (1961) and Schweitzer (1978), *Todites princeps* could be an epiphytic plant, but Barbacka (2011) inferred from the composition of the Hungarian Early Jurassic flora that its morphological features may reflect adaption to the relatively dry conditions (even periodically dry; Weber 1968) in non-flooded areas in relatively narrow ecological niches. In the Early Jurassic flora from China and Poland, however, *T. princeps* occurred in humid habitats in the vicinity of lakes and rivers (Wang 2002, Wang et al. 2005, Barbacka et al. 2010).

## CONCLUSIONS

The re-examined osmundaceous material consists of three collections: 185 specimens collected by Stur and published in German (Stur 1888), 377 specimens collected by Raciborski and published in Polish (Raciborski 1894), and 32 unpublished specimens stored in the Jagiellonian University, collected by Raciborski. As a result of this re-examination of material published by Raciborski (1894), 13 taxa of *Cladophlebis* described by Raciborski are reassigned to the three species *C. roessertii*, *C. haiburnensis*, and *C. denticulata*, based on the observed variability of morphological features. Two species created by Raciborski (1894), *C. aurita* and *C. bartonecii*, are confirmed. The extant generic names for *Osmunda sturii*, *Todea williamsonis*, and *Todea princeps* are changed to *Osmundopsis* and *Todites* respectively.

Osmundaceous ferns in Grojec most probably grew in the close vicinity of waterbodies,

near freshwaters, such as on riverbanks and lake banks. These sites were periodically flooded and were characterised by higher moisture. Moreover, the low degree of frond fragmentation suggests relatively undisturbed and stable conditions, and short transport to the sedimentary basin.

The most numerous species of *Cladophlebis* in the Grojec flora – *C. denticulata*, *C. haiburnensis*, *C. roessertii*, and *C. bartonecii* – show similar, comparatively wide spectra of co-occurring taxa among which other ferns dominated, but cycads and seed ferns were also present. Only one of these species, *C. bartonecii*, co-occurred with bennettites. Both species of *Todites* showed high self-occurrence, but *T. princeps* apparently could overgrow drier habitats with sphenophytes. Interestingly, *Osmundopsis sturii* co-occurred with only one species of *Cladophlebis*, *C. denticulata*; this makes plausible the suggestion that the taxon erected as *C. denticulata* actually consists of sterile fronds of *O. sturii*. Generally the composition of Grojec osmundaceous ferns indicates that *Cladophlebis* formed mixed communities with other species from the genus, but *C. roessertii* was not found co-occurring with *C. haiburnensis*.

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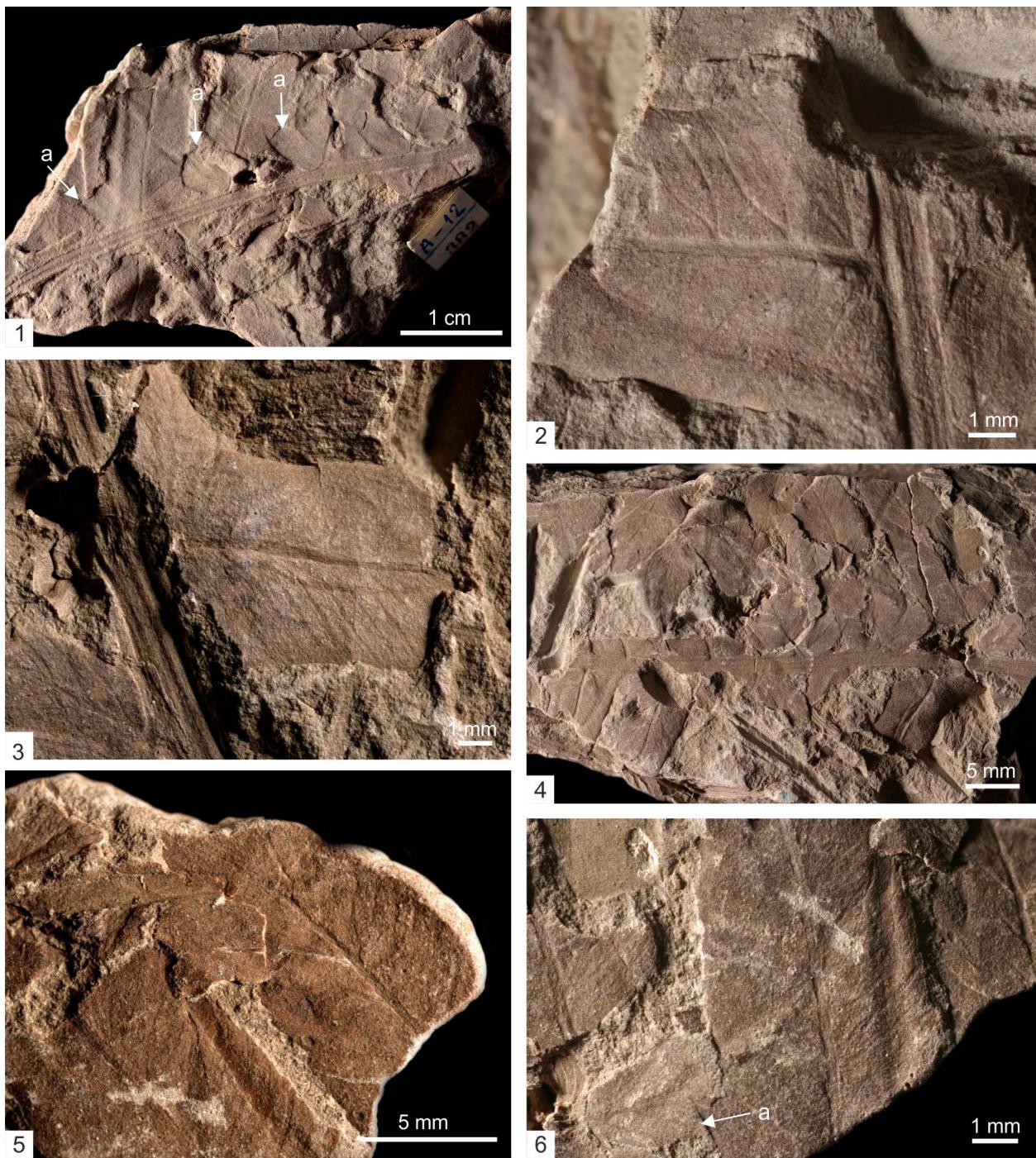
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## PLATES

### Plate 1

#### 1–6. *Cladophlebis aurita* Raciborski 1894

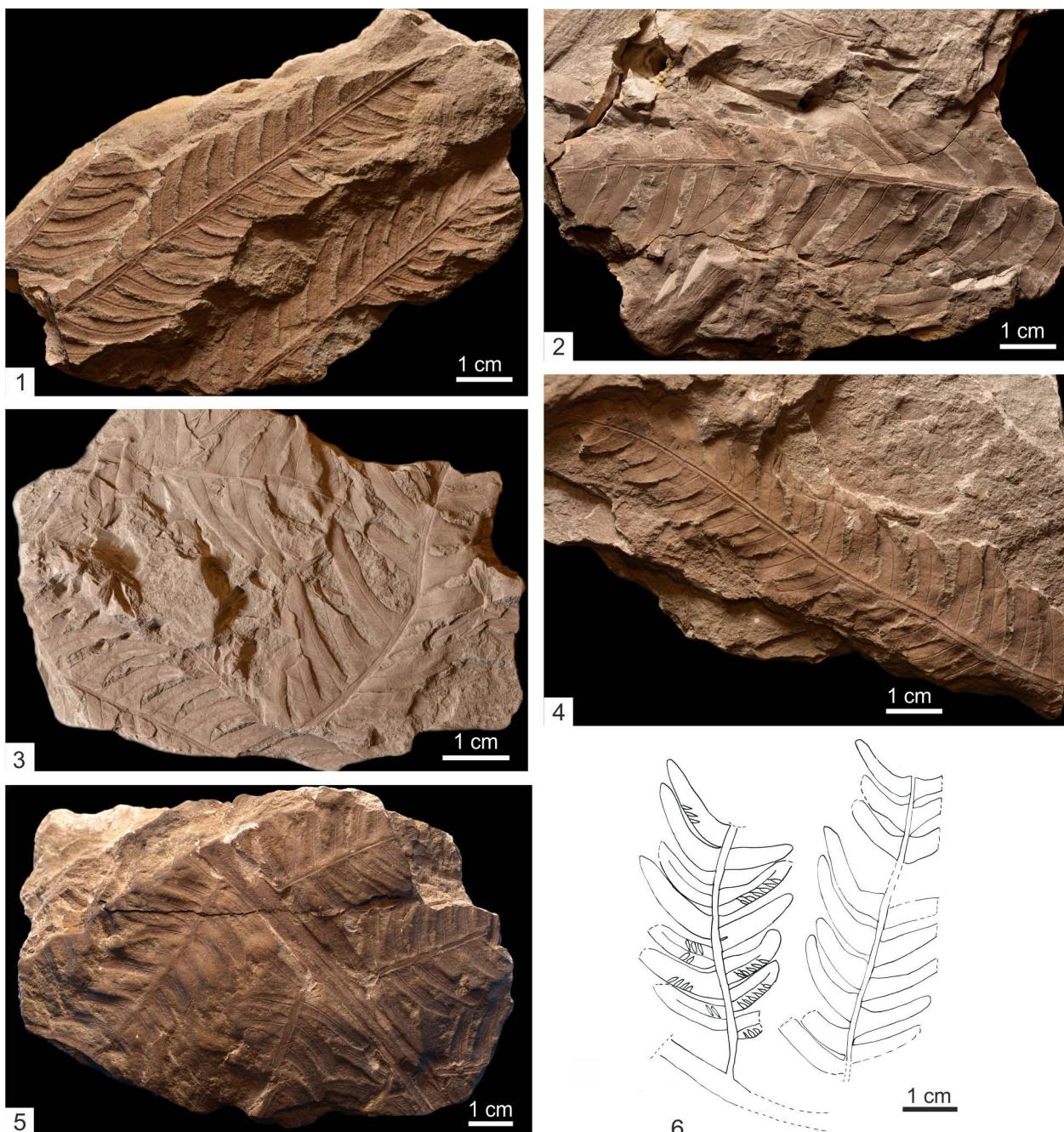
1. Fragment of sterile frond, ZNG PAN A-III-12\382, illustrated by Raciborski in pl. XX, fig. 24; a – auricle
2. Holotype, details of pinnule venation, ZNG PAN A-III-12\383
3. Holotype, details of pinnule venation, ZNG PAN A-III-12\383
4. Holotype, fragment of sterile frond, ZNG PAN A-III-12\383, illustrated by Raciborski in pl. XX, figs 25–26
- 5, 6. Holotype, details of pinnule venation and venation of auricle, ZNG PAN A-III-12\383



## Plate 2

1–6. *Cladophlebis bartonecii* Raciborski 1894

- 1–5. Fragments of sterile fronds, 1 – ZNG PAN A-III-12\389, 2 – ZNG PAN A-III-12\390,  
3 – ZNG PAN A-III-12\391, 4 – ZNG PAN A-III-12\392, 5 – ZNG PAN A- III-12\399  
6. Drawing of specimen ZNG PAN A-III-12\396, with schematic venation pattern marked



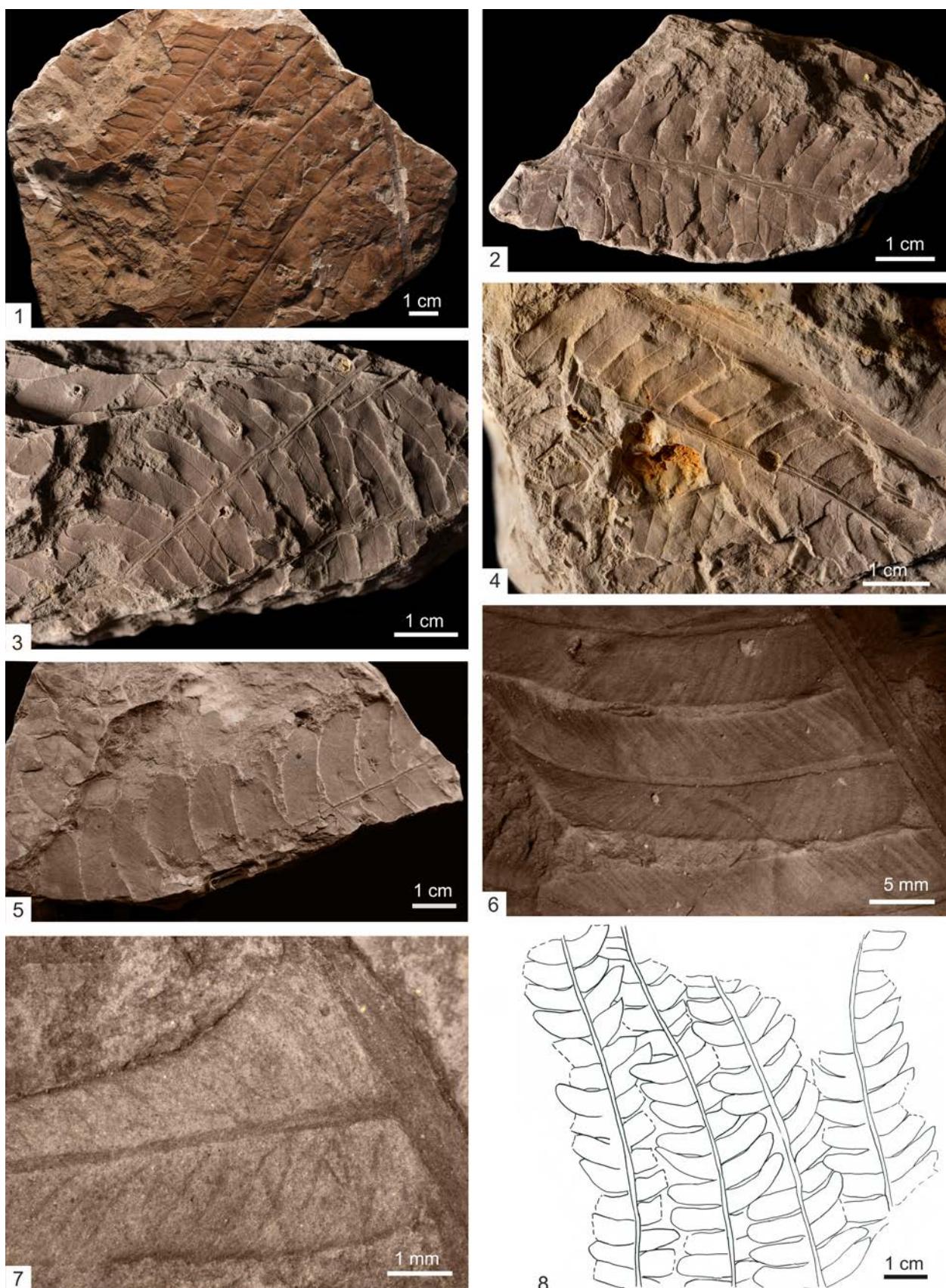
## Plate 3

1–8. *Cladophlebis denticulata* (Brongniart 1828) Fontaine 1889

1–5, 8. Fragments of pinnae, 1, 8 – ZNG PAN A-III-12\349, 2 – ZNG PAN A-III-12\372,  
3 – ZNG PAN A-III-12\372.1, 4 – KRA-PALEO 105/60/2, 5 – ZNG PAN A-III-12\362

6. Details of pinnule venation, GBA/051/0140

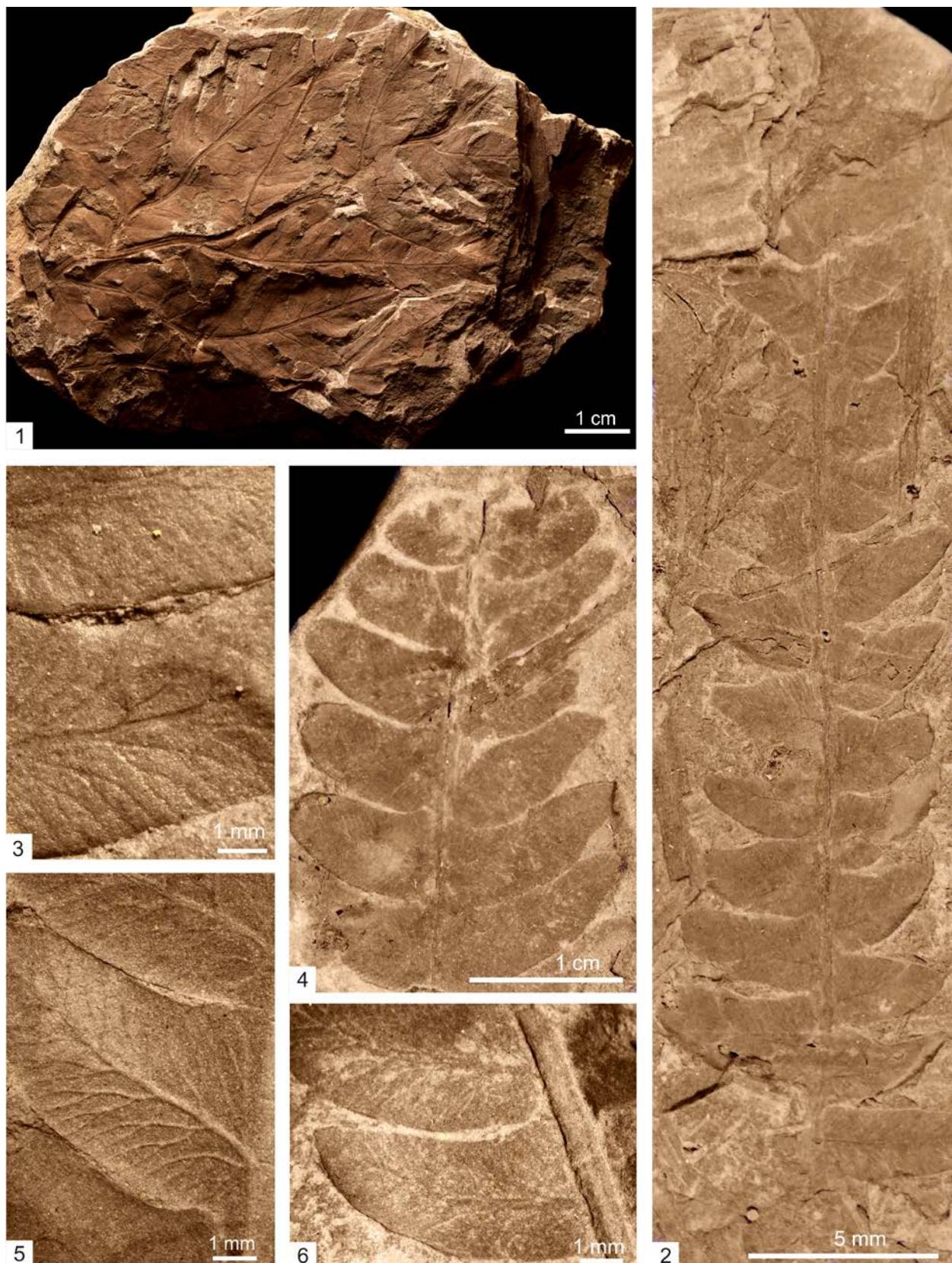
7. Details of pinnule venation, ZNG PAN A-III-12\391



## Plate 4

1–5. *Cladophlebis haiburnensis* (Lindley et Hutton 1836) Brongniart 1849

1. Fragment of sterile frond, ZNG PAN A-III-12\385
2. Fragment of pinnae, GBA/051/0116
3. Fragment of pinnae, GBA/051/0107
- 4, 5. Details of pinnule venation, 5 – ZNG PAN A-III-12\338, 6 – ZNG PAN A-III-12\336



## Plate 5

1–3. *Cladophlebis roessertii* (Schenk 1867) Saporta 1873

1. Fragment of sterile frond, ZNG PAN A-III-12\324

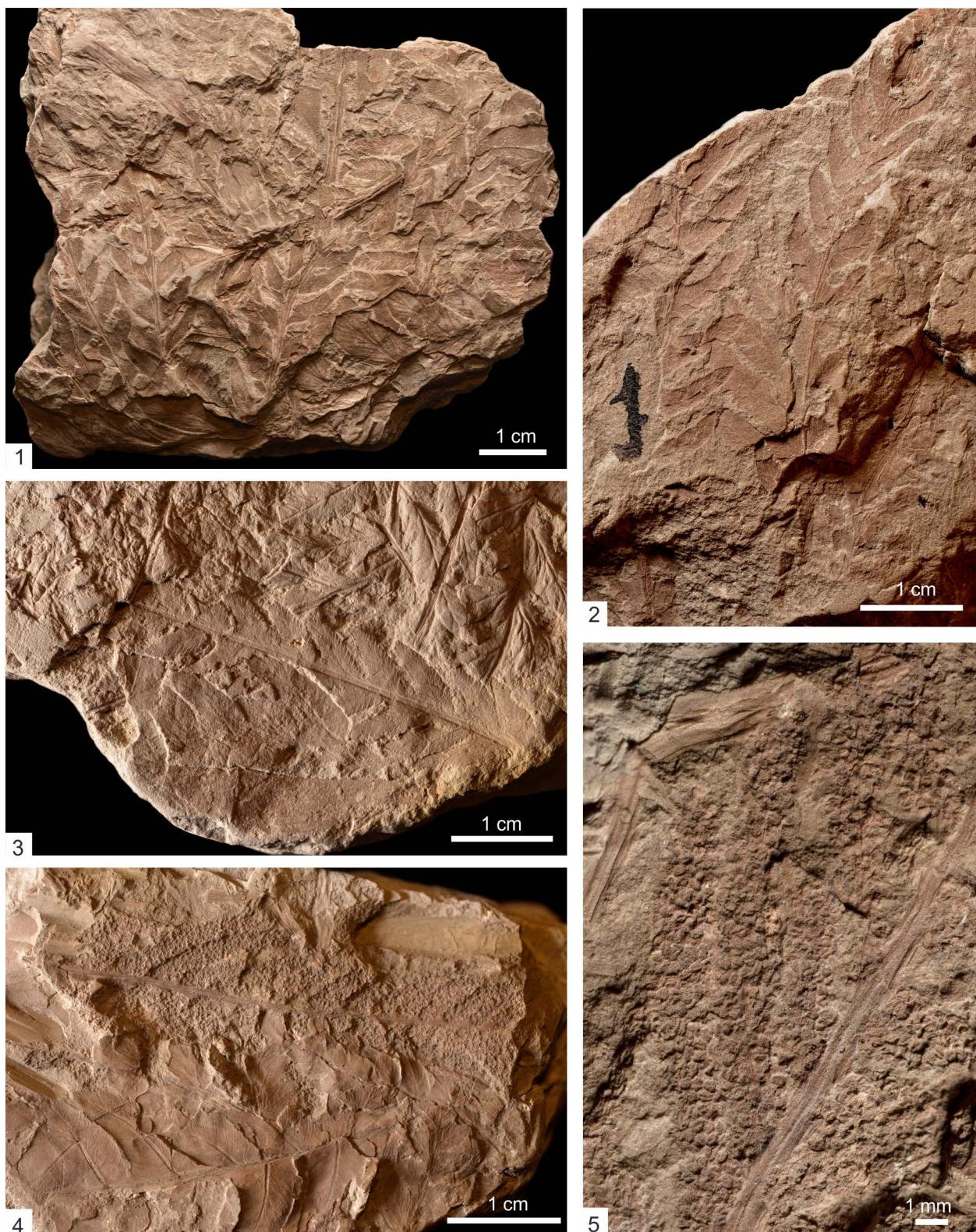
2, 3. Fragments of pinnae,

2. ZNG PAN A-III-12\430,

3. KRA-PALeO 105/60/1

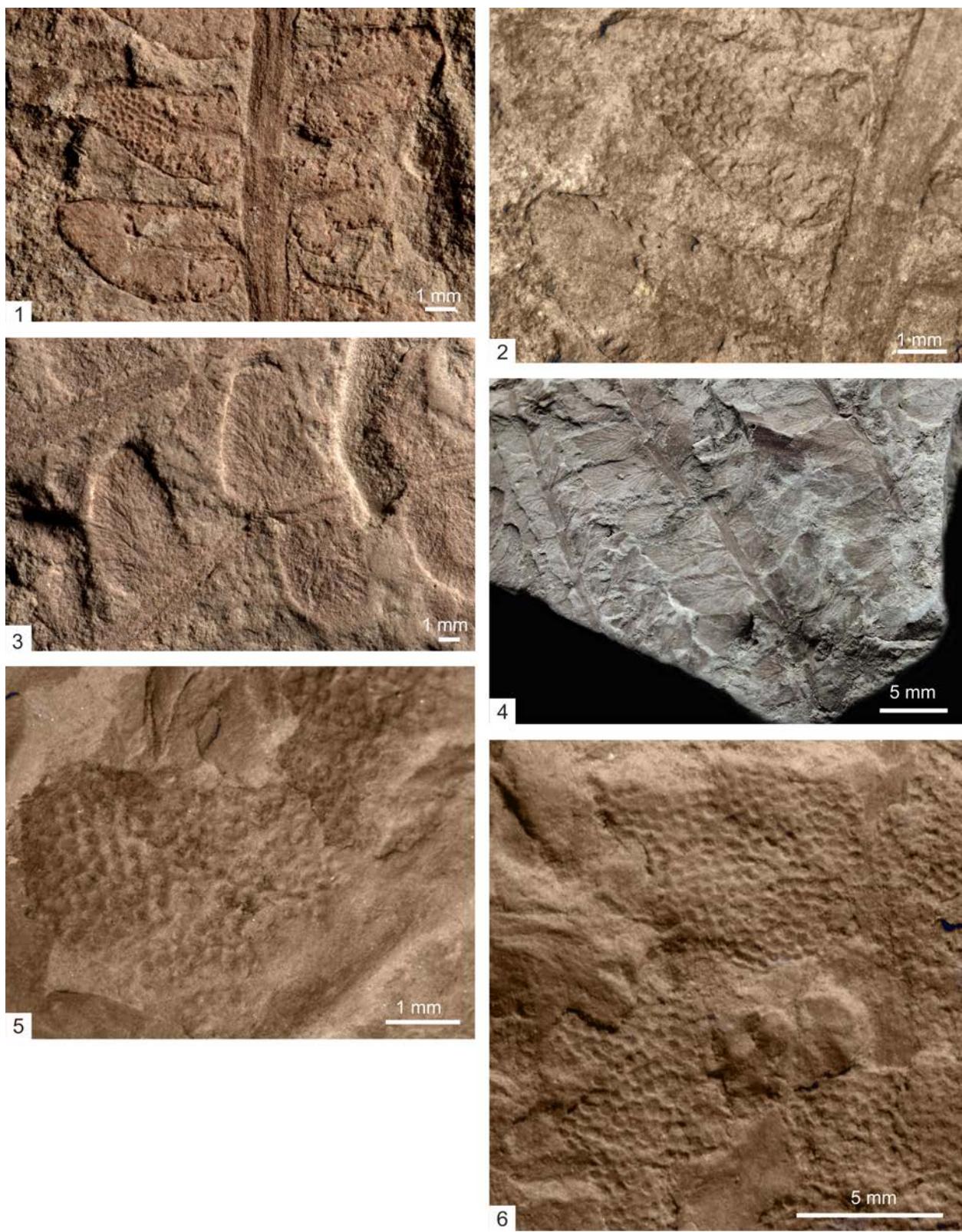
4. *Cladophlebis denticulata* (Brongniart 1828) Fontaine 1889 and *Osmundopsis sturii* (Raciborski 1894)  
Harris 1961, ZNG PAN A-III-12\13

5. *Osmundopsis sturii* details of pinnule morphology and distribution of sporangia, ZNG PAN A-III-12\13



## Plate 6

- 1–6. *Todites williamsonii* (Brongniart 1828) Seward 1900
1. Fragment of fertile pinnae, ZNG PAN A-III-12\7
  2. Details of fertile pinnule morphology, ZNG PAN A-III-12\7
  3. Details of sterile pinnule morphology, ZNG PAN A-III-12\8.2
  4. Fragment of sterile pinnae, ZNG PAN A-III-12\380
  - 5, 6. Details of pinnules with sporangia, GBA/051/0196



## Plate 7

1–4. *Todites princeps* (Presl in Sternberg 1838) Gothan 1914

1. Details of fertile pinnules, ZNG PAN A-III-12\11.2
2. Drawing of shape of fertile pinnule, ZNG PAN A-III-12\11.1, illustrated by Raciborski in pl. VI, fig. 22
- 3, 4. Fragments of fertile pinnae,  
3 – ZNG PAN A-III-12\11.1, illustrated by Raciborski in pl. VI, fig. 22,  
4 – ZNG PAN A-III-12\11.2

