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Systematic and palaeoenvironmental investigations of fossil ferns *Cladophlebis* and *Todites* from the Liassic of Hungary

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ABSTRACT. Macrofossil plant remains of the genera *Cladophlebis* Brongniart and *Todites* Seward are very common in the Mecsek Mountains (southern Hungary). They are represented by the following species: *Cladophlebis haiburnensis* (Lindley&Hutton) Brongniart, *C. denticulata* (Brongniart) Fontaine, *C. roesserti* (Schenk) Saporta, *Todites goeppertianus* (Münster) Krasser, and *T. princeps* (Presl) Gothan. The taxonomical investigation of these genera was preceded by the study of their morphological variability within both taxa. The present paper gives taxonomical description and palaeoecology of the fossil taxa from Hungary.

KEY WORDS: *Cladophlebis*, *Todites*, Early Jurassic, Hungary

INTRODUCTION

In the Early Jurassic (Hettangian), four families of ferns were represented in the Hungarian locality Mecsek Mts.: Osmundaceae, Matoniaceae, Dipteridaceae and Dicksoniaceae. Each of these families are represented by one or two species and this is the general tendency observed on the fossil flora from the Mecsek Mts. Fragments of *Cladophlebis* and *Todites* fronds from the family Osmundaceae, are very frequent. During the investigations of the material, some difficulties occurred in species identification, therefore different morphological features were analysed in connection with intraspecific variability, which is usual in ferns (Bodor & Barbacka 2008). As a result of the hitherto studies (Bodor & Barbacka op.cit.), four morphological types of fronds were distinguished which correspond to four species: *Cladophlebis haiburnensis* (Lindley&Hutton) Brongniart, *C. denticulata* (Brogniart) Fontaine, *Todites goeppertianus* (Münster) Krasser, and *T. princeps* (Presl) Gothan. Recently, we distinguished one more species in new collected material, i.e. *C. roesserti* (Schenk) Saporta. We conclued that many characteristics which are usually used for species determination of these two genera are highly variable.

This study aims to present the description of Hungarian taxa of Jurassic ferns and to give some knowledge on the palaeoenvironment.

MATERIAL

The plant fossils were collected in the years 1989–2004 from the Lower Jurassic deposits in the Mecsek Mts, including 108 specimens of the genus *Cladophlebis* Brongniart and 83 specimens of *Todites* Seward. The specimens were preserved in siltstone, shaly siltstone, fine detritic siderite and carbonate sandstone (see also Bodor & Barbacka 2008). The frond fragments are preserved as impressions; small amounts of coalified organic material are occasionally observed. Most of the fragments have details well visible, particularly those preserved in siltstone. The material is stored in the palaeobotanical collection of the Hungarian Natural History Museum, Budapest.

SYSTEMATIC DESCRIPTION

Order Filicales

Family Osmundaceae

Genus ***Todites*** Seward 1900

Todites princeps (Presl in Sternberg 1838) Gothan 1914

Pl. 1, figs. 1–5.

Selected synonyms

1838 *Sphenopteris princeps* Presl in Sternberg, 2, 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. 7, figs 3, 4.
1926 *Todites princeps* (Presl) Gothan; Harris, p. 26, pl. 12, fig. 5, text-fig. 2A–E.
1931 *Todites princeps* (Presl) Gothan; Harris, p. 35, pl. 11, figs 1, 2, 4, 9, pl. 12, fig. 3, text-figs 8, 9.
1940 *Todites princeps* (Presl) Gothan; Oishi, p. 196.
1958 *Todites princeps* (Presl) Gothan; Kräusel, p. 69, pl. 3, figs 6, 7.
1961 *Todites princes* (Presl.) Gothan; Harris, p. 93, text figs 30, 31.
1964 *Todites princeps* (Presl) Gothan; Kilpper, p. 44, pl. 8, figs 6–9, text-fig. 22.
1978 *Todites princeps* (Presl) Gothan; Schweitzer, p. 31, pl. 1 figs 3–5, pl. 2, figs 1–6, pl. 3 figs 1–7, text-figs 10–18.
1997 *Todites princeps* (Presl) Gothan; Schweitzer et al., p. 160, text-fig. 24A.

M a t e r i a l. The material consists of 14 fragments preserved in fine grained and coarse grained siltstone. Most of them are fragments of bipinnate leaves or separated pinnae of sterile and fertile fronds. The biggest fragments are usually 5–7 cm long. The details of pinnules are well visible.

S p e c i m e n s: BP 94.187.1, 94.190.1–192.1, 94.194.1, 94. 685.1–688.1, 94.690.1–692.1, 94.710.1–711.1.

D e s c r i p t i o n. Sterile and fertile fronds are of the same morphological type. Fronds are bipinnate in an anadromic way. The rachis is 1.5–4.5 mm wide and smooth. Pinnae reach more than 60 mm in length (no complete pinnae were preserved). The rachis of pinnae is slender, 0.5–0.8 mm wide. Pinnules are alternate or opposite, and arise on the rachis at about 90°, their size slightly decreases towards the top of the pinna. The neighbouring pinnules are crowded or lying in about 1.0–1.5 mm distance from each other.

Pinnules can be classified into three groups according to their shape. The first type is oblong, 10–15 mm long and about 4 mm wide. The apex is rounded, margins crenate or slightly lobed (Pl. 1, fig. 1). The second type is oval, 4– 5 mm long and 2 mm wide. The apex is rounded, margins almost entire (Pl. 1, figs 2, 5). Pinnules of the third type are about 10 mm long, 1.5–2.5 mm wide, narrowing towards the apex. Margins are deeply dissected – almost to the pinna rachis, lobes are rounded and separate (Pl. 1, fig. 4). Venation is fine, sphenopterid type, often bifurcate, the lamina is thin.

Sporangia were observed on the lower surface of pinnules of the second and third type; they are circular and crowded. The details of their structure are not preserved.

D i s c u s s i o n. *Todites princeps* (Presl) Gothan is a well recognizable species because of its morphological characteristics (see references in the list of synonyms). Although the shape of pinnules is varied, in general this diversity fits into defined frames. According to Harris (1931, 1961) the shape of pinnules might depend on their position in the frond. Harris (op. cit.) noticed that sporangia are attributed rather to less dissected pinnules, but did not differentiate defined sterile and fertile morphotypes.

In the fossil plant community from the Mecsek Mts, this species is not very common. In the time from 1989 to 2004 only 14 specimens with frond fragments were collected, other remains like rhizomes were not found at all.

Todites goeppertianus (Münster in Göppert 1846) Krasser 1922

Pl. 1, figs 6–9, Pl. 2, figs 1–4.

Selected synonyms

1846 *Neuropteris goeppertiana* Münster in Göppert, p. 104, pl. 8, 9, figs 8–10.
1867 *Acrostichites goeppertianus* (Münster) Schenk, p. 44, pl. 5, fig. 5, pl. 7, fig. 2.
1878 *Acrostichites goeppertianus* (Münster) Nathorst, p. 43, pl. 1, figs 7, 8a.
1892 *Todea williamsonis* (Brongniart) Schenk; Raciborski, p. 1, pl. 2, fig. 15.
1894 *Cladophlebis solida* Raciborski, p. 79, pl. 24, figs 10–13.

1919 *Todites williamsoni* Antevs, p. 20, pl. figs 20–22.
1922 *Todites goeppertiana* (Münster) Kryshtofovich; Krasser, p. 355.
1926 *Todites* cf. *williamsoni* (Brongniart) Seward; Harris, p. 55, text-fig. 2F.
1931 *Todites goeppertianus* (Münster) Krasser; Harris, p. 31, pl. 11, figs 3, 8, text-fig. 7.
1940 *Todites goeppertianus* (Münster) Krasser; Oishi, p. 194, pl. 3, figs 1, 1a.
1950 *Todites goeppertianus* (Münster) Krasser; Lundblad, p. 18, pl.2, figs 8–11.
1961 *Todites roesserti* (Presl) Kryshtofovich; Nagy, p. 617, pl. 2, fig. 4, pls 3, 4.
2005 *Todites* cf. *goeppertianus* (Münster) Krasser; Wang et al., p. 830, fig. 5(2, 3).

Material. Sixty nine specimens of sterile (50) and fertile (19) fronds of different size were preserved mainly in siltstone and fine grained detritic limestone. The remains are mostly large (50–190 mm long), often bipinnate fragments (two specimens up to 16 branches) or fragments of separated pinnae. The details of pinnules are well visible, but the structure of sporangia is not preserved.

Specimens: BP 89.179.1, 89.224.1, 89.251.1–266.1, 89.347.1, 94.187.1, 94.190.1, 94.192.1, 94.194.1, 94.222.1– 224.1, 94.226.1–227.1, 94.437.1, 94.440.1, 94.444.1, 94.450.1, 94.517.1, 94.617.1–634.1, 94.685.1–688.1, 94.690.1–692.1, 94.710.1–711.1, 94.798.1, 96.338.1, 96.345.1, 98.224.1, 98.762.1–763.1, 98.1003.1, 2000.1168.1, 2005.644.1, 2005.949.1, 2006.681.1–683.1, 2007.155.1, 2007.175.1, 2007.908.1– 909.1.

Description. Fronds are bipinnate and large. The sterile and fertile leaves represent different morphotypes. The sterile morphotype has a primary rachis up to 20 mm wide, smooth; the pinna rachises are 1.5–3.0 mm wide. Pinnae arise from the primary rachis at about 45°. Pinnules are opposite, close to each other, but not overlapping. They are straight or falcate. Their length ranges from 5 to 10 mm (extremely 2.5 and 12.0 mm), width 2.5–6.0 mm (extremely 1 mm), the ratio of length/width is 1.6–2.2. Their bases are broad, sometimes acroscopically slightly extended, and they are usually in contact with each other, with entire margins, apex subacute or rounded. Venation is of neuropterid type, the secondary veins fork once.

Fertile fronds are also of large size. Their primary rachis is similar to those of sterile fronds, and reaches 20 mm in length; pinna rachises are up to 3 mm in width. Typical pinnules are 5–8 mm long and 3.0–4.5 mm wide, often falcate, the length/width ratio 1.6–2.5. They are attached to the rachis with their broad base. The distance between neighbouring pinnules ranges from 1.5–4.0 mm. Margins of the pinnules are entire with rounded apex. Venation of neuropterid type is similar to those of sterile pinnules.

Sporangia occur on the lower side of pinnules, they cover the whole surface or are distributed between veins. They are round and about 0.25–0.3 mm in diameter. Spores (prepared *in situ*) are trilete, about 40 μ in diameter.

Discussion. Both sterile and fertile type of fronds were described by Harris (1931) and Lundblad (1950) as belonging to the same species and the remains of investigated material entirely correspond with these descriptions.

The species *Todites goeppertianus* (Münster) Krasser differs from other species of this genus by its characteristic neuropterid venation, in contrast to the pecopterid venation typical for fronds of other *Todites* species. This venation is the only distinctive mark which separates *T. goeppertianus* (Münster) Krasser from the very similar *T. roesserti* (Presl) Kryshtofovich (Gothan 1914, Kräusel 1958), *T. scoresbyensis* Harris (Harris 1931, Frenquelli 1947), or *T. leei* Wu (Wu 1991). Other morphological features are similar to these species, including features like number and size of fronds and pinnules, shape of pinnules (length/width ratio), shape of base and apex, bifurcations of the secondary veins and their number at the margin, angles of secondary veins, and vein density (see also Bodor & Barbacka 2008).

Todites goeppertianus (Münster) Krasser occurs on all stone slabs itself, unaccompanied by the remains of other taxa. Fertile and sterile fragments occur together sporadically.

Genus ***Cladophlebis*** Brongniart 1849

Cladophlebis denticulata (Brongniart 1828) Fontaine 1889

Pl. 2, figs. 5–9. Selected synonyms

1828 *Pecopteris denticulata* Brongniart, p. 301, pl 98, figs 1, 2.
1828 *Pecopteris phillipsi* Brongniart, p. 304, pl. 109, fig. 1.
1876 *Cladophlebis denticulata* (Brongniart) Nathorst, p. 19.
1889 *Cladophlebis denticulata* (Brongniart) Fontaine, p. 71 pl. 7 figs 7, 7a.

1894 *Cladophlebis denticulata* Brongniart; Raciborski, p. 224, pl. 22, figs 3, 4.
1894 *Cladophlebis* cf. *nebbensis* Brongniart, p. 227, pl. 22, figs 5, 6.
1905 *Cladophlebis denticulata* (Brongniart) Nathorst; Ward, p. 68, pl. 11, figs 1–7.
1911 *Cladophlebis denticulata* Brongniart; Thomas, p. 63, pl. 2, figs 10–12.
1911 *Cladophlebis denticulata* Brongniart; Seward, p. 668, pl. 2, figs 31–36, 38, pl. 6, figs 8, 9, pl. 8, fig. 29.
1913 *Cladophlebis antarctica* Halle, p. 14, pl. 1, figs 15–23, pl. 3, fig. 6.
1913 *Cladophlebis denticulata* Brongniart; Halle, p. 12, pl. 2, figs 7–9, text-fig. 3.
1935 *Cladophlebis denticulata* Brongniart; Oishi & Takahasi, p. 118, pl. 10, fig. 2.
1940 *Cladophlebis denticulata* Brongniart; Oishi, p. 256, pl. 48, fig. 1.
1947 *Cladophlebis denticulata* (Brongniart) Fontain; Frenguelli, p. 17, text-fig. 4.
1947 *Cladophlebis antarctica* Halle; Frenguelli, p. 19, text-fig. 5 a–d (redrawn from Halle 1913)
1959 *Cladophlebis denticulata* Brongniart; Kimura, p. 13, pl. 3, fig. 4; pl. 4, figs 3,6, pl.5, fig.1, pl. 12, fig. 10, text-fig. 8.
1959 *Cladophlebis* sp. A, Kimura, p. 20, pl. 4, fig. 1.
1959 *Cladophlebis* sp. B, Kimura, p. 20, pl. 3, fig. 6.
1959 *Cladophlebis raciborskii* Zeiller; Kimura, p. 19, pl. 3, fig. 5; pl. 5, figs 3, 6.
1961 *Todites denticulatus* (Brongniart) Krasser = *Cladophlebis denticulata* (Brongniart) Fontaine; Harris, p. 78, text-figs 25–27.
1962 *Cladophlebis denticulata* (Brongniart) Fontaine; Kiritchkova, p. 501, pl. 9, figs 5, 10, 11.
1962 *Cladophlebis denticulata* (Brongniart) Fontaine var. *asiatica* Kiritchkova, p. 505, pl. 9, figs 1, 2, 8.
1962 *Cladophlebis raciborskii* Zeiller; Kiritchkova, p. 537, pl. 1, figs 1, 8, pl. 3, figs 1–6, pl. 4, fig. 1.
1962 *Cladophlebis uralica* Prynada; Kiritchkova, p. 525, pl. 1, figs 2, 3–7, pl. 2, figs 1, 2, 5–7, pl. 5, fig. 1.
1964 *Cladophlebis denticulata* (Brongniart) Nathorst; Kilpper, p. 55, pl. 10, figs 8, 10–12; pl. 11, figs 1–6, 11, text-figs. 33–34.
1971 *Cladophlebis denticulata* (Brongniart) Seward; Sharma, p. 62.
1989 *Cladophlebis antarctica* Halle; Gee, p. 166, pl. 2, fig. 15, pl. 3, fig. 23.
1989 *Cladophlebis denticulata* (Brongniart) Fontaine emend. Harris; Gee, p. 166, pl. 2, fig. 14, pl. 3, fig. 25.
1997 *Cladophlebis denticulata* (Brongniart) Fontaine; Popa, pl. 2, fig. 3, text-fig. 31.
1997 *Cladophlebis denticulata* (Brongniart) Nathorst; Schweitzer et al., p. 179, pl. 22, figs 1–4, text-figs 25 C, 28 A–C, 29.
2004 *Cladophlebis denticulata* (Brongniart) Fontaine emend. Harris; Rees & Cleal, p. 26, pl. 6, fig. 4, pl. 7, figs 1, 2, text-fig. 3D.
2004 *Cladophlebis antarctica* Halle; Rees & Cleal, p. 25, pl. 6, fig 2, pl. 7, fig.3, text-fig. 3C
2005 *Todites denticulatus* (Brongniart) Krasser; Wang et al. p. 826, figs. 3(1–7), 4(A–F), 5(1).
2008 *Cladophlebis denticulata* (Brongniart) Nathorst, emend. Harris; Birkenmajer & Ociepa, p. 34, Figs 15, 17 F, G.
2008 *Cladophlebis antarctica* Halle; Birkenmajer & Ociepa, p. 34, figs 15, 17 F, G.

M a t e r i a l. Fifty-six specimens of sterile frond fragments preserved in siltstone were collected. There are several bipinnate fragments, not larger than 112 mm, and separate pinnae reaching about 70 mm. The details of pinnules are well visible.

S p e c i m e n s: BP 94.438.1, 94.450.1, 94.704.1, 96.75.1, 96.317.1, 96.333.1, 96.389.1, 96.390.1, 96.395.2, 96.397.1, 96.403.2, 96.992.1, 96.999.1, 98.1050.1–1051.1, 98.1075.1, 98.1177.1, 2004.97.1, 2004.366.1, 2004.966.1–967.1, 2004.969.1, 2004.971.1–973.1, 2004.976.1–979.1, 2004.1040.1, 2004.1001.1–1004.1, 2004.1006.1–1007.1 2004.1013.1–1016.1, 2004.1021.1, 2004.982.1, 2004.983.1, 2004.986.1, 2004.987.1–988.1, 2004.994.1–995.1, 2004.999.1, 2004.1200.1, 2005.840.1–843.1, 2005.863.1.

D e s c r i p t i o n. Fronds are bipinnate. The rachis is 1–3 mm wide, rarely 4 mm, ridged alongside or smooth. Pinnae are opposite, alternate or subalternate. The angle of arising pinnae in larger specimen is 27°–65° (Pl. 2, figs 5–9). The angle often slightly decreases towards the top of the frond. Pinnules are opposite, semi-alternate (Plate 2, fig. 5) or alternate, elongated (ratio length/width is 1.5–4.6), often falcate (Pl. 2, fig. 8). Their length ranges from 7 to 28 mm and the width from 3 to 9 mm.

Venation is distinct; the midrib reaches to the top of the pinnule; secondary veins divide once or twice (Pl. 2, figs 5, 8, 9). In many cases, the division is restricted to the basal part of pinnules, but can also be visible along the whole length of pinnules, on one (acroscopical or basal) or both sides of the midrib.

The number of secondary veins varies from 4 to 14 on one half of the pinnule, most specimens have 5 or 11–12 veins (Pl. 2, figs 5–9). The vein density at the pinnule margin is 3–9/cm, (mostly 5–6/cm). The angle of arising veins ranges between 25° and 64° (mostly at 51°). The margins of pinnules are in most cases dentate, but partly dentate (especially in the apical part of the pinnule) or entire margins are not rare. The apex is acute or subacute,

Table1. Comparison of pinnules of species most similar to *Cladophlebis denticulata* (Brongniart) Fontaine (data from the Mecsek Mts.), according to data from literature: *C denticulata* (Brongniart) Fontaine var. *asiatica* Kiritchkova, *C. antarctica* Halle (Halle 1913, Gee 1989, Rees & Cleal 2004), *C. raciborskii* Zeiller (Kiritchkova 1962), *C. uralica* Prynada (Kiritchkova 1962)

Species / Feature	*Cladophlebis denticulata*	*Cladophlebis denticulata* var. *asiatica*	*Cladophlebis antarctica*	*Cladophlebis raciborskii*	*Cladophlebis uralica*
Arrangement of pinnules	opposite to alternate	opposite to semialternate	almost opposite alternate to subopposite	almost opposite to alternate	alternate
Base of pinnule	not extended or slightly extended acroscopically	–	not widened, slightly expanded, acroscopically or slightly contracted basiscopically	slightly extended or not	slightly extended or not
Pinnule apex	acute or subacute	rounded	pointed, acute	acuminated, acute	acute
Margin of pinnule	entire – dentate towards apex	entire	slightly dentate, entire, serrate at the apex	dentate, serrate at the upper half	crenate
Length of pinnule (mm)	7–28	9 –13	5.5–35	17–20 (31)	20–30
Width of pinnule (mm)	3–9	3–5	3–5 basal width 2.5–7.5	5–8	4–6
Ratio length/width of pinnule	1.5–4.6	–	2.9–4.7	4	5
Width of the rachis (mm)	1–4	–	2–4.5	4–5, extremely 7	1.5–2
Number of secondary veins at the margin of pinnule	4–14	5–7	10–20 (most often 10–16)	8–13	10–15
Vein density/cm	3–9	–	10–20	–	
Angle of arising secondary veins	25–64°	–	40–46°	–	
Bifurcation of the secondary veins of the pinnule	once or twice	once	once, twice only at the base of pinnule	twice	twice

its base as wide as the pinnule or slightly extended acroscopically.

D i s c u s s i o n. *Cladophlebis denticulata* (Brongniart) Fontaine is a very common species in the Early Jurassic and well distinguishable due to its elongated pinnules with dentate margins, acute or subacute apices, and rachis ridge. The Hungarian specimens were found in a large number, enough to show the variability within this species. The most variable characteristics are the shape and size of pinnules, their venation patterns, and in certain cases the margins. The genus *Cladophlebis* contains numerous species distinguished on morphological differences. *Cladophlebis denticulata* (Brongniart) Fontaine is morphologically closest to three species: *C. antarctica* Halle, *C. raciborskii* Zeiller, and *C. uralica* Prynada. Differences between those three species, including additionally *C. denticulata* (Brongniart) Fontaine var. *asiatica* Kiritchkova (Kiritchkova 1962) are very slight and all those forms may represent morphological differentiation of the same species (see Tab. 1). This is a matter of rather subjective point of view regarding systematics. Halle (1913) regarded *C. antarctica* Halle as belonging to the "group *denticulata*", and Kiritchkova (1962) was of the opinion that it is better to "separate distinct smaller species than to keep "one large collective species". However, in this case there will be numerous form species with very similar, sometimes almost the same morphology. It causes a problem with the determination of a new material, which may show slight differences from forms described, and again justify creating new species. In our opinion such similar forms as mentioned above should be considered as one species with differences that are the result of natural intraspecific diversity.

Very close similarity between *Cladophlebis denticulata* (Brongniart) Fontaine and *C. antarctica* Halle was noticed by Halle (1913) when he created the second species. Later, both species were described and discussed by Gee (1989), Rees and Cleal (2004), and Birkenmejer and Ociepa (2008). The authors left these species separate, but Rees and Cleal (2004) suggested that *C. antarctica* Halle and *C. denticulata* (Brongniart) Fontaine might be conspecific. Because they did not have sufficient material for such revision, they suggested a fusion of species with emended diagnosis. However, the emended diagnosis given earlier by Harris (1961) seems to be adequate. The differences between *C. denticulata* (Brongniart) Fontaine and *C. antarctica*

Halle presented in Table 1 fit into the range given by Harris (op.cit.) and observed also in the Hungarian material. The only features that seemed to have a taxonomical value (among others Halle 1913, Gee 1989, Ociepa & Birkenmayer 2008), the number (or density) of secondary veins and their bifurcations in the investigated material also show intermediate forms. There are pinnules with a single division of secondary veins, double division at the base of pinnules or double division on one or both sides of the midrib along the pinnule.

Table 1 also contains data of several other species that resemble *Cladophlebis denticulata* (Brongniart) Fontaine to a high degree. The specimens described by Kimura (1959) and Kiritchkova (1962) as *C. raciborskii* Zeiller as well as *C. uralica* Prynada and the *C. denticulata* (Brongniart) Fontaine var. *asiatica* Kiritchkova (Kiritchkova 1962) fit also into the range of features observed in *C. denticulata*. The entire margin in *C. denticulata* var. *asiatica* corresponds with entire pinnules of *C. denticulata* from Hungary (the entire and serrate margins occur even within the same fronds). The difference between *C. raciborskii* and *C. uralica* was discussed by Kiritchkova (1962), who contrasted the alternate pinnae in *C. uralica* with the opposite pinnae in *C. raciborskii.* In the light of our previous study on taxonomical and non taxonomical features in *Cladophlebis* and *Todites* (Bodor & Barbacka 2008), this feature does not seems to have a truly taxonomical value as it highly varies in Hungarian material. The above remarks refer to specimens described by Kimura (1959) and Kiritchkova (1962), but for so far they can not refer to the all taxa. We do not have access to the specific diagnosis of *C. uralica* Prynada and *C. raciborskii* Zeiller, nor to original specimens, so that we can only suggest a critical revision of this material. It is worth noticing that all discussed forms usually occur in the same localities with *C. denticulata* (Brongniart) Fontaine, and their easily identifiable morphology may be the result of environmental circumstances.

Cladophlebis haiburnensis (Lindley & Hutton 1836) Brongniart 1849

Pl. 2, figs. 10–13.

Selected synonyms

1836 *Pecopteris haiburnensis* Lindley & Hutton, p. 97, pl. 187.

1849 *Cladophlebis haiburnensis* (Lindley & Hutton) Brongniart, p. 105.

1894 *Thinnfeldia haiburnensis* (Lindley & Hutton) Raciborski, p. 67, pl. 20, figs 3–6.

1905 *Cladophlebis haiburnensis* (Lindley & Hutton) Brongniart; Ward, p. 71, pl. 11, figs 8– 10.

1911 *Cladophlebis haiburnensis* Lindley & Hutton; Thomas, p. 65, pl. 3, figs 4–6a.

1922 *Cladophlebis haiburnensis* (Lindley & Hutton) Brongniart; Yabe, p. 16, pl. 2, fig. 9.

1940 *Cladophlebis haiburnensis* (Lindley & Hutton) Brongniart; Oishi, p. 266.

1947 *Cladophlebis haiburnensis* (Lindley & Hutton) Brongniart; Frenguelli, p. 30, text-fig. 18.

1959 *Cladophlebis haiburnensis* (Lindley & Hutton) Brongniart; Kimura, p. 16, pl. 4, fig. 8, pl. 6, figs 3, 5, 7, text-fig. 10.

1961 *Cladophlebis haiburnensis* (Lindley & Hutton) Brongniart; Harris, p. 187, text-fig. 69.

1962 *Cladophlebis haiburnensis* (Lindley & Hutton) Brongniart; Kiritchkova, p. 507, pl. 4, figs. 2–3, pl. 13, figs 2–7, pl. 14, figs 4, 6.

1964 *Cladophlebis haiburnensis* (Lindley & Hutton) Brongniart; Kilpper, p. 62, pl. 15, fig. 13, text-fig. 32.

1997 *Cladophlebis haiburnensis* (Lindley & Hutton) Brongniart; Kostina & Doludenko, p. 181, text-fig. 2.

1997 *Cladophlebis haiburnensis* var. *ingens* (Harris) Kilpper; Popa, text-figs 32, 33.

Material. *Cladophlebis haiburnensis* (Lindley & Hutton) Brongniart is represented by 35 sterile specimens. They are fragments of bipinnate fronds or pieces of separated pinnae preserved in siltstone, foliated siltstone and fine grained detritic limestone. The size of fragments does not exceed 90 mm.

Specimens: BP 89.186.1, 89.194.1, 94.213.1, 94.229.1, 94.435.1–436.1, 94.450.1, 94.637.1, 96.346.1, 96.383.1, 96.385.1–388.1, 96.345.1, 96.409.1, 96.979.1–982.1, 96.989.1–990.1, 96.993.1, 96.997.1, 98.1073.1–1074.1, 2004.118.1, 2004.975.1, 2004.980.1, 2004.989.1–991.1, 2004.1000.1, 2004.1019.1, 2005.844.1.

Description. The frond is bipinnate. The main rachis is slender, up to 2.5 mm wide, and smooth (Pl. 2, fig. 10). The primary rachises are about 1.0–1.5 mm wide, opposite, not crowded. Pinnules are alternate or opposite (Pl. 2, figs 11, 12), 6–18 mm long, 3–8 mm wide (in an extremely large specimen 25 x 10 mm). They are lanceolate (length/width ratio 2–3), straight or falcate, depending on position along the frond. The margins are entire, with subacute apex. Pinnules are attached to the rachis with the whole basis, which may be acroscopically extended (Pl. 2, figs 10–13). Adjacent pinnules are in contact with each other or the distance between them is about 1 mm. Venation is of

Table 2. Comparison of pinnules of species most similar to *Cladophlebis haiburnensis* (Lindleay & Hutton) Brongniart (data from the Mecsek Mts.) according to data from literature: *C. harrisii* van Cittert (van Cittert 1966), *C. nebbensis* (Brongniart) Nathorst (Nathorst 1876, Yokoyama 1905, Oishi 1940, Johansson 1922, Frenquelli 1947), *C. aktashensis* Turutanova-Ketova (Harris 1961), *C. svedbergii* Frenquelli (Frenquelli 1947, Harris 1931), and *Todites recurvatus* Harris (Harris 1931)

Species / Feature	*Cladophlebis. haiburnensis*	*Cladophlebis harrisii*	*Cladophlebis nebbensis*	*Cladophlebis aktashensis*	*Cladophlebis svedbergii*	*Todites recurvatus* (sterile)
Base of pinnule	acroscopically extended	always united	slightly extended	contracted or wide as pinnule	acroscopically extended	wide as pinnule
Pinnule apex	subacute	obtuse	rounded or subacute	obtusely angular, rounded or acute	acute or subacute	subacute
Margin of pinnule	entire	entire	entire	entire	entire	entire, at the apex small teeth
Length of pinnule (mm)	6–18, extreme 25	10–15	15	25, extreme 34	7–9	20
Width of pinnule (mm)	3–8, extreme 10	2–4	7–9	7, extreme 10	4–5	8
Ratio length/width of pinnule	2–3	3–5	about 2	about 3	> 2	2,5
Width of the pinna rachis (mm)	2.5	2	5	up to 10 mm	4	6
Number of secondary veins at the margin	4–11	no data	no data	no data	4–6	no data
Vein density number/cm	7–28	no data	no data	18–24	no data	18
Angle of arising secondary veins	16–64°	40°	35–45°	about 70°	45°	35°
Bifurcation of the secondary veins of the pinnule	once or twice	none or once	once or twice	usually twice	usually once	once, near the base twice

pecopterid type, with straight midvein and secondary veins forked once or twice. The number of veins ranges from 4 to 11 on one half of pinnule, 6–10 is common, but in most cases there are 8. The vein density ranges between 7 and 28 veins/cm. The angle of arising secondary veins varies between 16° and 64°.

Discussion. *Cladophlebis haiburnensis* (Lindley & Hutton) Brongniart together with *C. denticulata* (Brongniart) Fontaine are the most widespread species of this genus in lower Mesozoic floras. They both often occur in the same localities (Raciborski 1894, Ward 1905, Thomas 1911, Frenquelli 1947, Kimura 1959, Harris 1961, Kiritchkova 1962, Kilpper 1964).

Similarly to *Cladophlebis denticulata*, C. *haiburnensis* is highly variable in its morphology. Investigation of Hungarian material regarding diversity, taxonomical and nontaxonomical features proved that these species are significantly different (Bodor & Barbacka 2008). Morphologically *C. haiburnensis* (Lindley & Hutton) Brongniart is very close to *C. nebbensis* Brongniart, *C. svedbergii* Frenquelli, *C. aktashensis* Turutanova-Ketova, and *C. harrisii* van Konijnenburg-van Cittert. Table 2 shows the comparison of these species. Based on the data presented, the differences between particular species do not seem to be really significant in many cases. They mainly concentrate on divisions of veins and on size of pinnules – the rest of the features fit into the range of diversity (compare also Bodor & Barbacka 2008). With these remarks we would merely like to suggest that in the future some species of *Cladophlebis*, and also generally of ferns, would need re-examination and revision.

Cladophlebis roesserti
(Schenk) Saporta 1873

Pl. 2, fig. 14.

1867 *Asplenites roesserti* Schenk, p. 49, pl. 7, fig. 7; pl. 10, figs 1–4.
1873 *Cladophlebis roesserti* (Schenk) Saporta, p. 301, pl. 31, fig.4.
1878 *Cladophlebis* (*nebbensis* var.) *roesserti* Presl; Nathorst, p. 42, pl.2, figs 1–3.
1919 *Cladophlebis roesserti* Presl; Antevs, p. 18, pl. 2, fig. 1, text-fig. 2.
1922 *Cladophlebis roesserti* (Presl) Saporta; Johansson, p. 18, pl. 5, figs 4–9.
1926 *Cladophlebis roesserti* (Schenk) Saporta; Harris, p. 57, text-fig. 3 A–D.
1989 *Cladophlebis* sp., Gee, p. 169, pl. 2, fig. 20.

M a t e r i a l. Sixteen specimens were collected during one field trip. They originate from some large slabs of siltstone. There are bipinnate fragments of sterile fronds, as well as separated pinnae. The biggest fragment reaches 80 mm in length. Details of the pinnules are well visible.

S p e c i m e n s: BP 2004.12.1, 2004.118.1, 2004.981.1, 2004.984.1–985.1, 2004.992.1–993.1, 2004.996.1–998.1, 2004.1005.1, 2004.1008.1, 2004.1011.1–1012.1, 2004.1198.1, 2005.839.1.

D e s c r i p t i o n. Fronds are slender and probably bipinnate. A well preserved bipinnate fragment, 55 mm long, contains 7 branches (Pl. 2, fig. 14). The rachis is 1.5 mm wide, rachis of the pinna is 0.5–0.8 mm in width. Pinnae are opposite, the distance between neighbouring pinnae is 15 mm or more. Pinnules are opposite, triangular with acute apex and relatively wide base, or rarely rectangular with rounded apex. The adjacent bases are in contact with each other. The largest pinnules (one specimen) are 18 x 6 mm (at the base of the pinna), commonly 6–7 x 3–4 mm. Margins are entire. Pinnules are falcate near the pinna apex, straight towards the base, arising to the rachis at a straight angle. Venation is of pecopterid type, secondary veins are forked mostly once, occasionally twice. The number of veins at the margin of pinnule is usually 5–11, mostly 7–9. The vein density is 8–13 veins/cm.

D i s c u s s i o n. This group of specimens shows a quite uniform unit among *Cladophlebis* with clear and hardly variable features. The slender form of frond with small triangular pinnules with entire margins makes these fragments different from both other species occurring in the same locality and indicates their best resemblance with *C. roesserti* (Schenk) Saporta. Also, the specimen described by Gee (1989) as *Cladophlebis* sp. represents the same morphological type.

PALAEOENVIRONMENTAL REMARKS

During the Hettangian the locality of the Mecsek Mts. was a delta plain, with a more or less closed lagoon system to the sea shore, and numerous islands with a system of lakes along the branches of the river. According to Némedi-Varga (1998) the coal deposits can be typically split into three main sections:

1. The lowermost section, Rhaetian (having no importance regarding plant remains).

2. The middle section (Hettangian) contains the thickest coal beds and the most plant remains. This section is divided into five levels:

2.1. Limnic, with thin coal beds, dominant siltstones and shales, subordinate sandstones;

2.2. Limnic, with dominant sandstones, subordinate siltstones, without coal beds;

2.3. Limnic, with thick coal beds, dominant siltstones, shales, sandstones in some areas, and tufite layer (volcanic activity).

2.4. Limnic-paralic transitional level. Dominant siltstones – sandstones, without coal beds, containing tufite layer with phyllopods (*Howellites princetonensis* Bock var. *minor* Nagy) indicating freshwater environments.

2.5. Paralic transitional level with coal beds of medium thickness; dominant siltstones and shales.

3. The uppermost section (Lower Sinemurian) is of paralic type, characterized by thin coal beds that are not suitable for the coal production. In the southern part of the basin, the facies is heteropical, marine, coastal, with grey calcareous siltstones, fine- and coarse grained sandstones and fine grained marls.

The plant remains originate from the coal mines, where they were found among the coal layers.

The representatives of Osmundaceae in the Mecsek Mts. are preserved in four types of stones: 1. siltstone; 2. foliated siltstone - both of these types represent fluvial or brackish enclosed bay sediments – 71.5% of all specimens and 7.3%, respectively; 3. fine grained detritic siderite that represents delta sediments – 3.3%, and 4. fine grained detritic limestone of limnic origin – 17.9%.

These sediments indicate a tendency of cyclic changes that took place in this area over a long time, the formation of strata with coal layers involved about 5 million years (Némedi-Varga 1998). The fact that they contain Osmundaceae remains proves that they grew in a close neighbourhood of water basins near fresh water (lake bank, riverbank) or possibly also in a brackish environment near the sea coast. The environment close to water basins must have been relatively undisturbed what is suggested by the small degree of frond fragmentation (Figs 1–5. It appears that generally fragments of fronds longer than 30 mm are

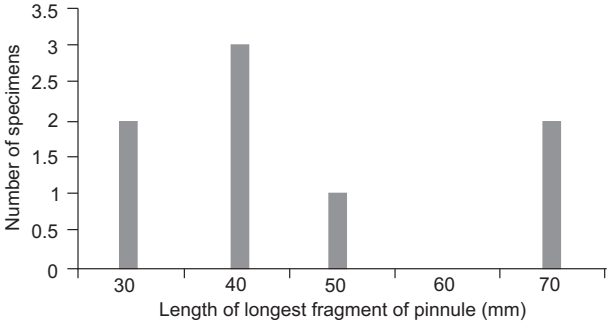

Fig. 1. Lenght distribution of *Todites princeps* (Presl) Schenk fragments of pinnule

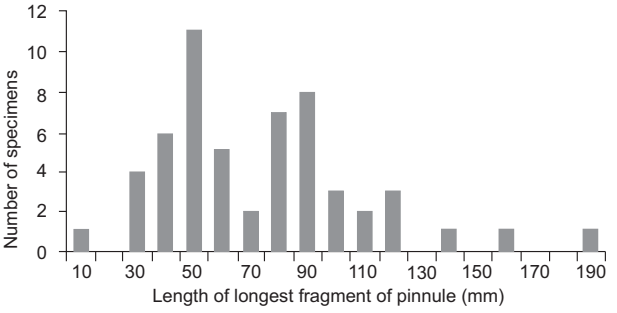

Fig. 2. Lenght distribution of *Todites goeppertianus* (Münster) Krasser fragments of pinnule

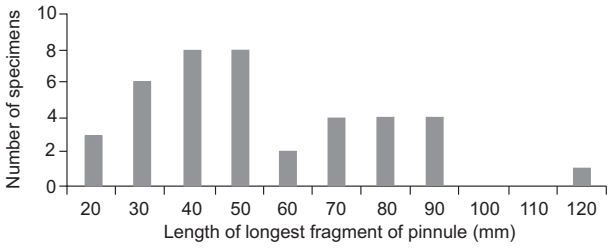

Fig. 3. Lenght distribution of *Cladophlebis denticulate* (Brongniart) Fontaine fragments of pinnule

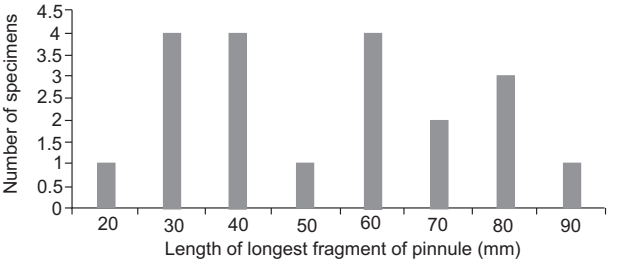

Fig. 4. Lenght distribution of *Cladophlebis haiburnensis* (Lindley & Hutton) Brongniart fragments of pinnule

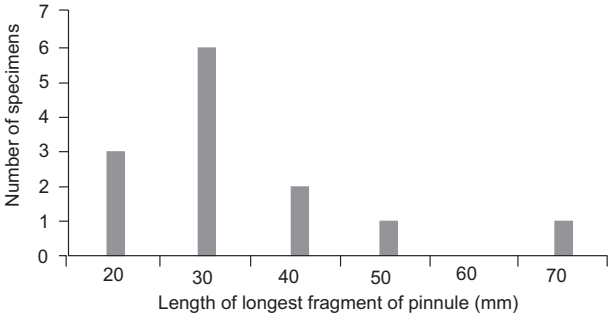

Fig. 5. Lenght distribution of *Cladophlebis roesserti* (Schenk) Saporta fragments of pinnule

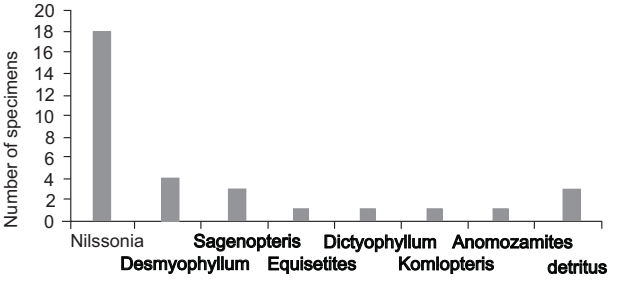

Fig. 6. Co-occurrence of fronds of *Cladophlebis denticulata* (Brongniart Fontaine) with leaf remains of other genera

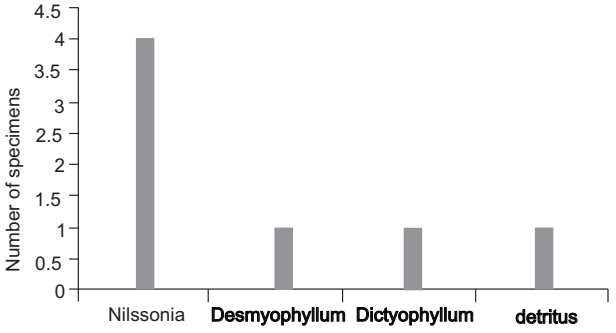

Fig. 7. Co-occurrence of fronds of *Cladophlebis haiburnensis* (Lindlea & Hutton) Brongniart with leaf remains of other genera

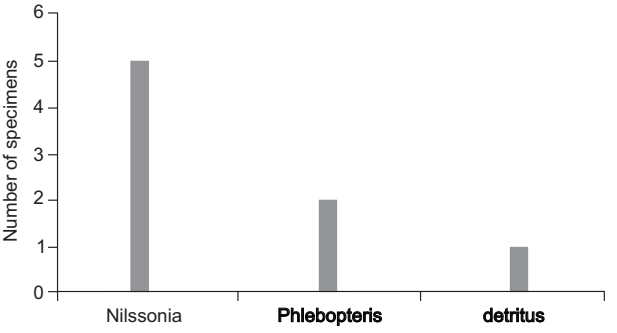

Fig. 8. Co-occurrence of fronds of *Cladophlebis roesserti* (Swchenk) Saporta with leaf remains of other genera

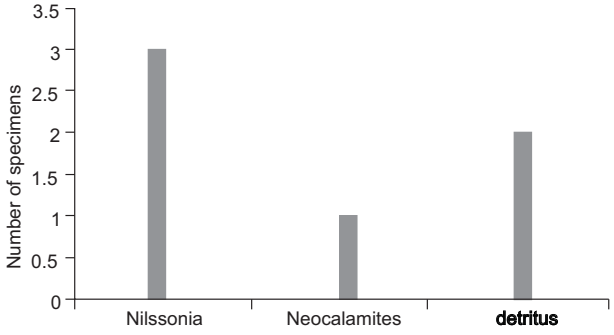

Fig. 9. Co-occurrence of fronds of *Todites goeppertianus* (Münster) Krasser with leaf remains of other genera

not rare. The length of most specimens ranges from 30–80 mm, except species *Todites princeps* (Presl) Gothan and *Cladophlebis roesserti* (Schenk) Saporta with smaller fronds (20–70). Most of the largest fragments represent *T. goeppertianus* (up to 190 mm). Considering that fossil remains are very well preserved, we conclude that the ferns were growing near the sedimentation place.

The co-occurrence of *Todites* and *Cladophlebis* with other plants species is shown in Figures 6–9. The the percentage of samples that are not accompanied by any other species is following: *C. denticulata* – 54.5%, *C. haiburnensis* – 85.7%, *C. roesserti* – 60%, *T. goeppertianus* – 91.5%, *T. princeps* – 100%. As it appears from these data and Figures 6–9, the particular species formed rather monospecific thickets, and if they occurred with other plants, they were usually from the genus *Nilssonia* Brongniart. The species of *Nilssonia* found in the Mecsek Mts. like *N. obtusa* (Nathorst) Harris, *N. polymorpha* Schenk,and *N. revoluta* Harris, are all characteristic for wet conditions (Barbacka 2001).

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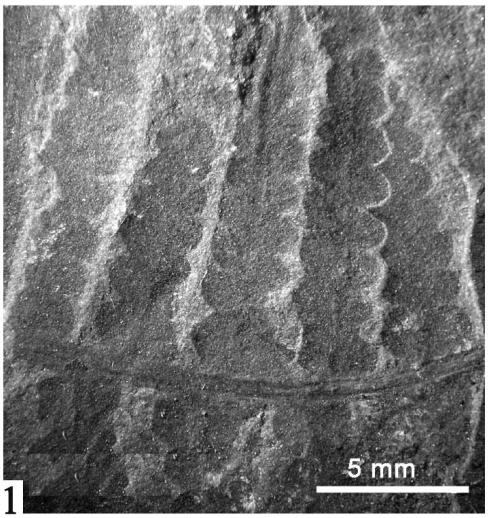
PLATES

Plate 1

1–5. *Todites princeps* (Presl) Gothan
1. pinnules of type 1 (BP 2008.422.1)
2, 5. pinnules of type 2 (BP 94.690.1, 2008.424.1)
3. details of venation (BP 94.685.1)
4. pinnules of type 3 (BP 2008.423.1)
6–9. *Todites goeppertianus* (Münster) Krasser
6. sterile frond (BP 89.224.1)
7–8. details of sterile pinnules (BP 89.257.1, 89.256.1)
9. fertile frond (BP 94.622.1)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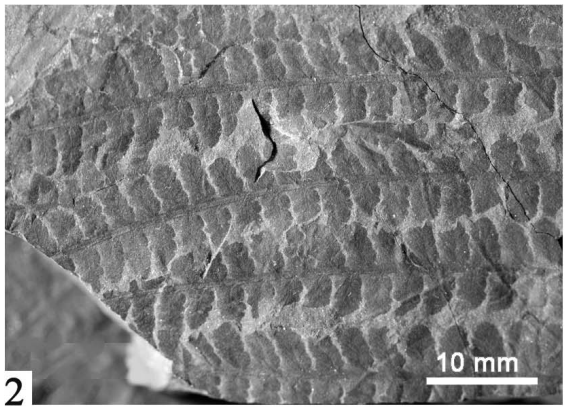
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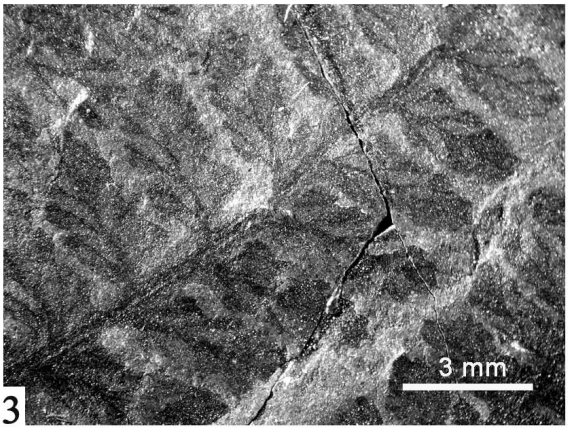
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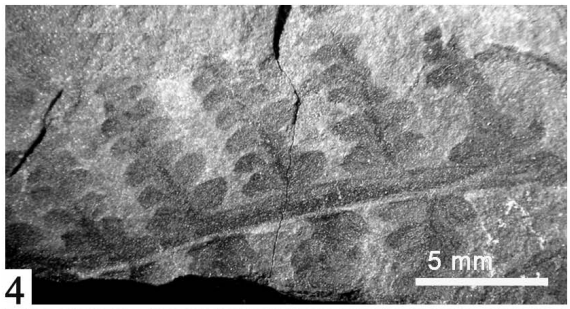
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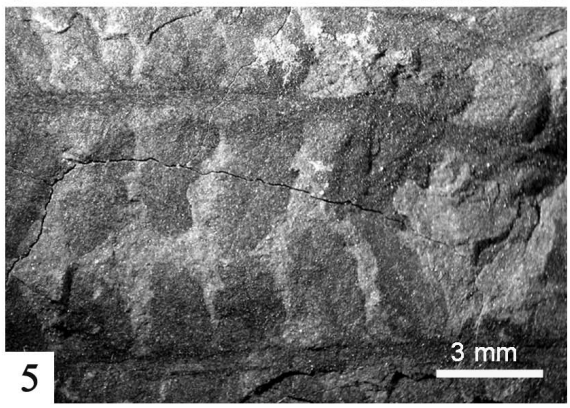
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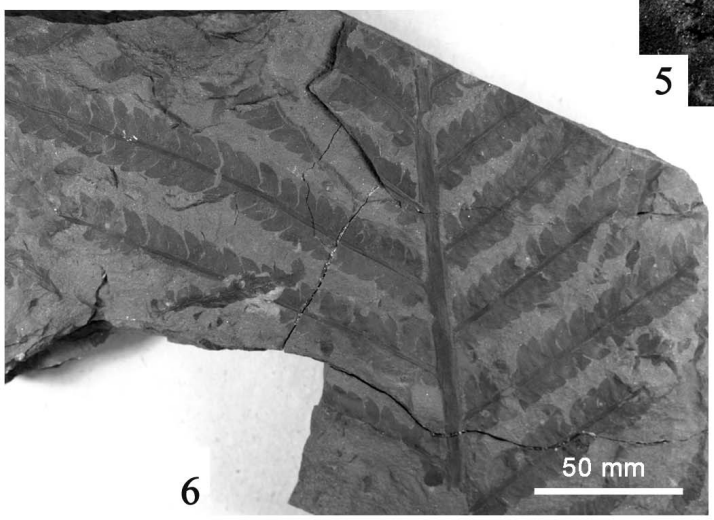
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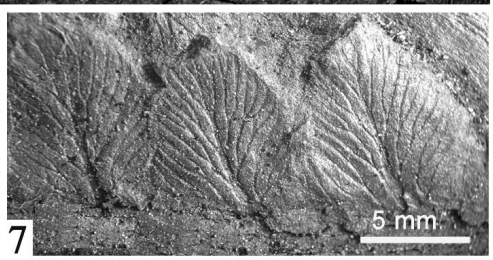
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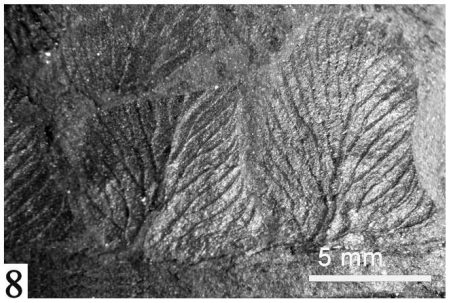
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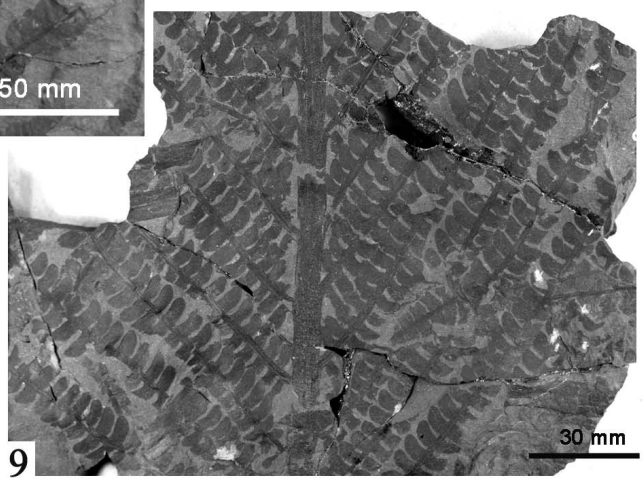
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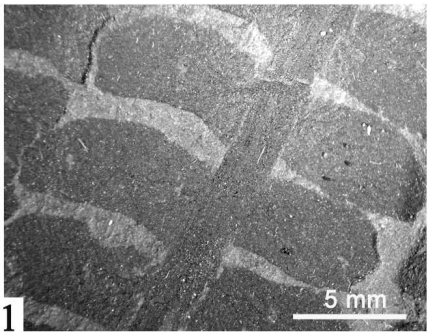
Plate 2

1–4. *Todites goeppertianus* (Münster) Krasser, fertile frond
1. detail of pinnules (BP 94.622.1)
2, 4. distribution of sporangia (BP 89.263.1)
3. spore *in situ*
5–9. *Cladophlebis denticulata* (Brongniart) Fontaine
5. BP 2005.840.1.
6. details of the margin (BP 2004.969.1, teeth indicated by arrows)
7. BP 2004.1040.1
8–9. Details of varied venation – once or twice furcating (BP 2004.1040.1)
10–13. *Cladophlebis haiburnensis* (Lindley & Hutton) Brongniart
10. BP 98.1073.1.
11. BP 89.194.1.
12–13. Details of pinnules (BP 89.252.1, 2005.842)
14. *Cladophlebis roesserti* (Schenk) Saporta (BP 2004.1002.1)



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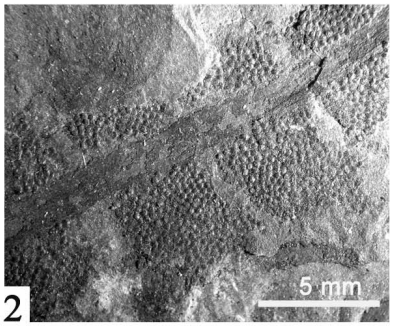

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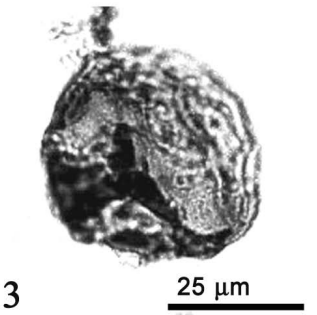

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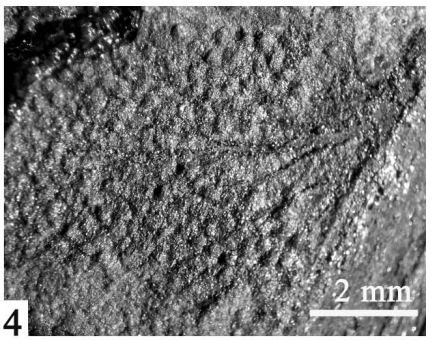

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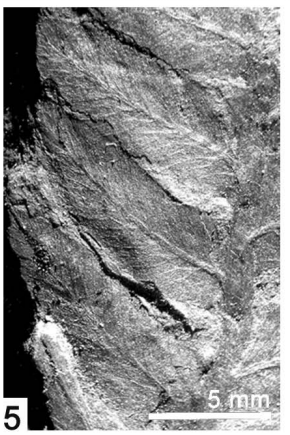

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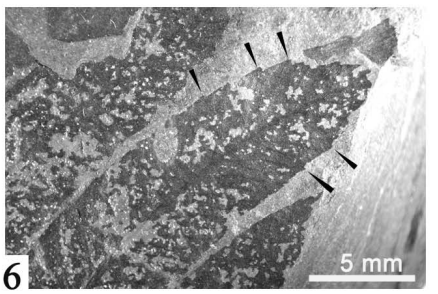

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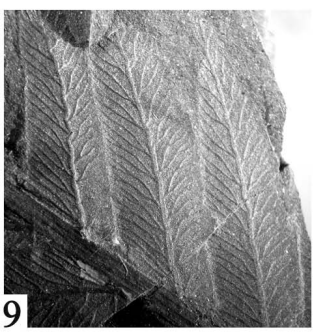
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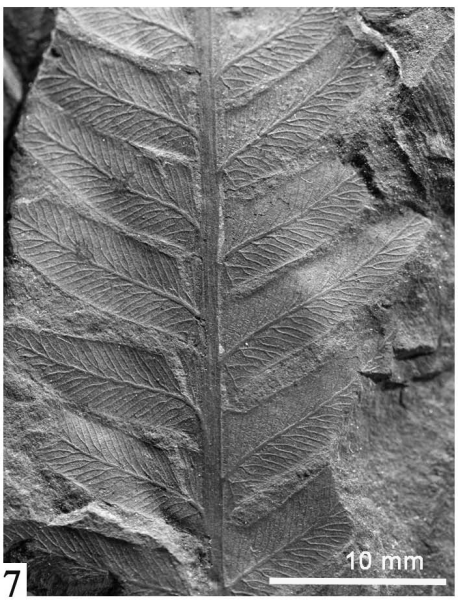

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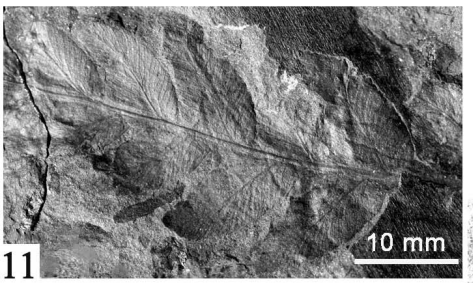

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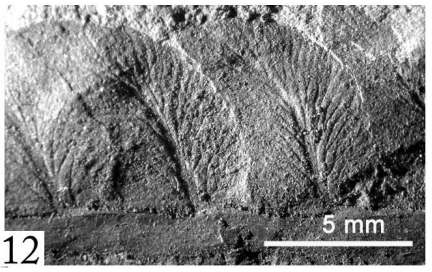

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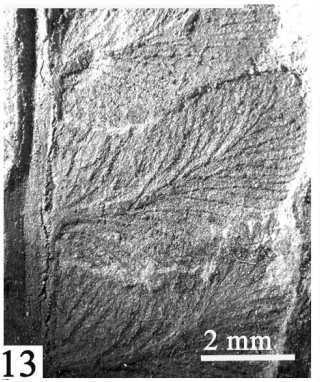

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