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Taxonomy and palaeoecology of the Early Jurassic macroflora from Odrowąż, central Poland

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ABSTRACT:

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The locality of Odrowąż is an Early Jurassic section in central Poland, with a taxonomically relatively poor flora. The available material is composed of both macro- and microremains. The macroremains, represented by 720 specimens (491 suitable for study), consist mainly of leaves, shoots, rhizomes, as well as male and female cones and fragments of other fructifications. Sphenophytes, pteridophytes, pteridosperms, bennettites, cycads, ginkgophytes, conifers are represented by single taxa, only ferns are more diverse. The material is dominated by the conifer *Hirmeriella muensteri* (Schenk) Jung and the benettite *Pterophyllum alinae* Barbacka sp. nov. Taxonomically, the ferns are the most diverse group (five species belonging to five genera). Most of the plants show adaptations to wet conditions, which corresponds well to the proposed sedimentary environment, a river plain. The complete material shows, however, that the floral remains originated from a wider area situated along the river and on its banks.

One new genus, *Odrolepis*, three new species, *Odrolepis liassica*, *Pterophyllum alinae*, *Paracycas minuta*, and one new forma, *Todites princeps*, forma *trilobata*, are described. Some forms are left in open nomenclature.

Key words: Early Jurassic; Poland; Macroflora; Taxonomy; Palaeoecology.

INTRODUCTION

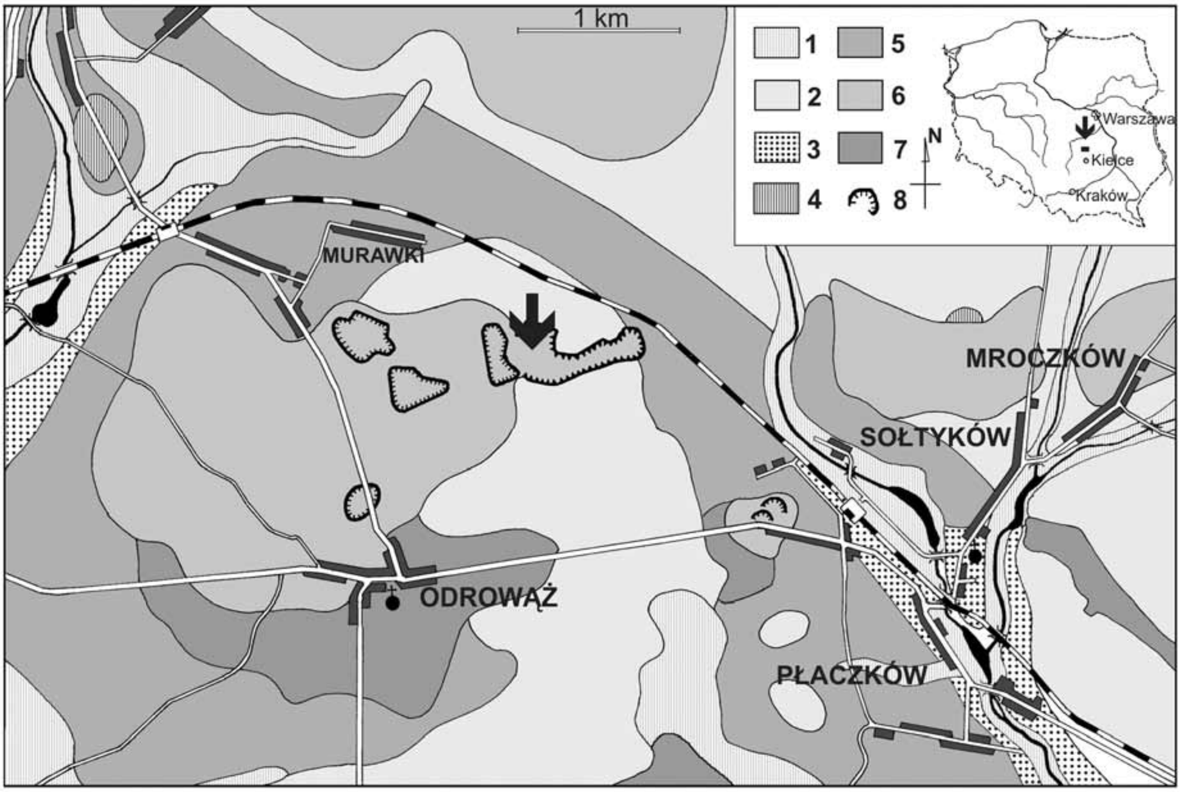
The Early Jurassic (Hettangian) plants from the northern Mesozoic margin of the Holy Cross Mountains (central Poland) have been studied for many years. The first reports were published by Raciborski (1891, 1892). Subsequently, Makarewiczówna (1928) described a flora from the neighbourhood of the town of Ostrowiec. From the beginning of the 1990s, studies of the plant material from the newly discovered locality in Odrowąż (also known as Sołtyków) were continued by Reymanówna (1991a, b, 1992). This material is relatively poorly preserved and, consequently, the investigations covered only a few and best preserved species (Wcisło-Luraniec 1992a, b; Barbacka *et al*. 2007). Because the cuticle of the material was generally not suitable for preparation, most of the determinations, mainly only to generic level, were based on macromorphology. Wcisło-Luraniec (1991) compiled a taxonomic list of the macroflora, which became the basis for a hypothetic reconstruction of the vegetation. The list of taxa from Odrowąż was compared to the main elements of selected European Early Jurassic floras and defined as typical for the European province (Wcisło-Luraniec 1992a). Ziaja (2006) published a palynological analysis of the sediments, and of pollen *in situ*, in which 63 taxa of fossil pollen grains and spores from Odrowąż were recognized. The major plant groups of the microflora correspond to plant groups represented in the macroflora.

Recent revision of the material revealed the presence of formerly unrecognized and/or new taxa: *Odrolepis liassica* Barbacka and Ziaja gen. et sp. nov., *Goepertella microlobus* (Schenk) Oishi and Yamasita, *Todites princeps* forma *trilobata* Barbacka sp. nov., *Paracycas minuta* Barbacka sp. nov., *Pterophyllum alinae* Barbacka sp. nov., and *Piroconites kuespertii* Gothan. In some cases, the generic determinations were changed: *Neocalamites lehmannianus* Halle, *Pachypteris lanceolata* Brongniart, *Otozamites brevifolius* Braun, *Podozamites* sp., and *Podozamites* cf. *schenkii*.

LOCALITY, MATERIAL AND METHODS

The material comes from the clay-pit near Odrowąż (Sołtyków), situated c. 25 km north of Kielce in the Mesozoic margin of the Holy Cross Mountains, central Poland (Text-fig. 1). The geology and stratigraphy of the area was presented in a series of regional studies by Karaszewski (1962), Karaszewski and Kopik (1970), Pieńkowski (1983, 2004), and Pieńkowski and Gierliński (1987). According to Pieńkowski (2004), the Odrowąż succession represents the Zagaje Formation, composed of sandstones, claystones, siltstones, siderite spherolites and siderites, with coal intercalations, and is dated as Early Hettangian. This age was also confirmed by megaspores (Marcinkiewicz 1957; Marcinkiewicz *et al*. 1960) and microspores (Ziaja 2006), especially by the presence of an index species, *Aratrisporites minimus* Schulz.

Of the collected material, 284 specimens were sufficiently well preserved for further investigation. They were preserved chiefly in grey shale, and represent mainly leaves, cones, cone scales, fragments of stems, rhizomes and fructifications. The organic matter of the remains was strongly coalified, so the cuticle was rarely suitable for preparation. The cuticles were prepared first in hydrofluoric acid and then with the usual method in Schultze's dry solution ($KClO_3 + HNO_3$ and washed in weak ammonia, or 3% KOH^-) and examined under



Text-fig. 1. Map of Odrowąż (Sołtyków) locality after Krajewski (1955), modified (drawing by J.W. Wieser, published with permission of the W. Szafer Institute of Botany, Polish Academy of Sciences, Cracow); The Odrowąż outcrop with the Jurassic flora is indicated by the arrow. 1. Holocene fluvial deposits; 2. Quaternary sands; 3. Pleistocene sands of the accumulation terraces; 4. Pleistocene sands and gravels of a front moraine and eskers; 5. Pleistocene postglacial sands with boulders; 6. Jurassic sandstones, siltstones and mudstones; 7. Triassic siltstones and silts; 8. Old mine excavations a light microscope and a SEM. The cuticle of most specimens cracked into small pieces during maceration, because of a large number of micro-cracks. Observation of the structure of the cuticles was possible only under the fluorescent microscope without maceration. When possible, the cuticle was examined separately but, in some cases, fragments of samples were observed directly on their lithic matrix. For study of the lower side of the cuticle, embedded in the matrix, cuticle pieces were covered with a thin coat of polymerizing glue and then the matrix was removed by fluoric acid. Unfortunately, due to the delicate structure of the cuticle and its bad preservation, pictures taken under fluorescence are of poor quality. Nevertheless they give useful information for identification.

REPOSITORIES

The macrofossils are stored in the in the palaeobotanical collection of the W. Szafer Botanical Institute of the Polish Academy of Sciences in Cracow.

SYSTEMATICS

Sphenophyta
Neocalamites Halle 1908

Neocalamites lehmannianus (Goeppert) Weber, 1968
(Pl. 1, Fig. 1)

1845. *Calamites lehmannianus* Goeppert, p. 143.
1867. *Calamites guembeli* Schenk, p. 10, pl. 1, figs 8–10.
1869. *Schizoneura hoerensis* Schimper, p. 283.
1908. *Neocalamites hoerensis* Schimper; Halle, p. 6, pls 1–2.
1931. *Neocalamites hoerensis* (Schimper) Halle; Harris, p. 22, text-fig. 4.
1961. *Neocalamites hoerensis* (Schimper) Halle; Harris, p. 30, text-fig. 8 (with synonyms).
1968. *Neocalamites lehmannianus* Goeppert; Weber, p. 31, pl. 1, figs 17–23; pl. 2, fig. 24; pl. 3, figs 25–27 (with synonyms).
?1997. *Neocalamites* sp.; Schweitzer *et al.*, p. 148, pl. 10, fig. 4.

MATERIAL: KRAM-P PM 68/7, 16, 20, 35, 215/III, 245, 256, 258, 260-66, 312, 969, 986, 1000, 1001, 1005, 1040-42, 1044-45, 1049-53 (1049, 1050, 1051, 1052 part, 1053 counterpart), 1058, 1060, 1067, 1080, 1090, 1091, 1093, 1100, 1119, 1121, 1123, 1128-30, 1141, 1144, 1156, 1166, 1251, 1267, 1272, 1274. Mostly fragments of compressed stems of various sizes, up to 30 cm long, without leaves; the cuticle not preserved and the organic matter not showing fluorescence. In most cases, the nodes hardly distinguishable.

DESCRIPTION: The stems are 7–28 mm wide, without diaphragm, internodes are more than 45 mm long. The leaf scars are round with central pit, about 0.5–0.75 mm in diameter, 8 scars per cm. The surface of stem is ribbed, the ribs are narrow and well marked, 12–20 per cm. Leaves are unknown.

DISCUSSION: Although the preservation of the stems is rather poor, their general habit and size, and other observed features were sufficient to refer them to *N. lehmannianus*. Their morphology corresponds well to the original German material of the species as described by Weber (1968) [as well as to *N. hoerensis* (Schimper) Halle as given by Harris (1961), and synonymised later by Weber (1968) with *N. lehmannianus*].

Diaphragms
(Pl. 1, Fig. 2)

MATERIAL: KRAM-P PM 68/ 255, 259, 280/I, 973, 1101. Separate diaphragms; one with incomplete leaves.

DESCRIPTION**:** The diaphragms are 20–30 mm in diameter, the leaves (7 leaves per half of diaphragm) are over 40 mm long (the length of broken fragments) and 2 mm wide with almost parallel margins from their bases. The other morphological details and the cuticular structure of the leaves are unknown.

DISCUSSION: These few diaphragms belong, most probably, to *N. lehmannianuss*. The leaves are incomplete and badly preserved, but the diameter of the diaphragm, as well as the width of the leaves (their total length is unknown) are of *N. lehmannianus* type.

? Lycopodiales
Genus *Odrolepis* Barbacka et Ziaja gen. nov.

Odrolepis liassica Barbacka et Ziaja sp. nov.
(Pl. 1, Figs 3–6)

HOLOTYPE: KRAM-P PM 68/119, preserved in mudstone, Pl. 1, Fig. 3F

TYPE LOCALITY AND STRATIGRAPHIC HORIZON: Odrowąż, the Holy Cross Mountains, Poland; Lower Jurassic, Hettangian

DERIVATION OF NAME: The generic name after the locality of Odrowąż; the specific name after the age of the stratum (Liassic).

MATERIAL: KRAM-P PM 68/119 I – II, 130. Three specimens with crowded detached sporophylls; poorly preserved; cuticle not preparable (too strongly coalified) and not reactive to fluorescent light. Many sporophylls with preserved apices, some also with the base, but in most cases only the middle parts remained.

DIAGNOSIS: Wedge-shaped sporophylls, c. 20 mm long, with extended oval base and obtuse or subacute apex. Abaxial surface with well marked midvein running from about 1/4 of length from base and ending at apex. Median groove, 1–1.2 mm wide, with edges parallel to margins of lamina, on adaxial side. No sporangia observed.

DESCRIPTION: The sporophylls are wedge-shaped with an extended, oval base (Pl. 1, Figs 4, 6) and tapering obtuse or subacute apex (Pl. 1, Figs 5, 6). Their total length is 19–20 mm, the width of the lamina near the base is 3.5–5 mm, and the base extends to about 7x3 mm. On the abaxial surface, a prominent vein is visible along the whole lamina, running from about 1/4 distance from the base to apex. On the adaxial side, there is a median groove running along the lamina (except the oval base) reaching the apex, with edges parallel to the margins of the lamina (Pl. 1, Figs 1, 6). The groove is about 1–1.2 mm wide at its base and follows the wedge shape of the scale.

DISCUSSION: Based on morphology, the remains may be interpreted as sporophylls of Lycophyta. Similar structures were described from the Triassic and compared to the strobili of Carboniferous Lycophyta (Grauvogel-Stamm and Duringer 1983). From the Triassic, the following genera were described: *Pleuromeia* Corda, *Lycostrobus* Nathorst (1908), *Cylostrobus* (Walkom) Helby and Martin (1965), *Skilliostrobus* Ash (1979), and *Annalepis* Fliche (1910 = *Lepacyclotes Emmons, 1856; Annalepis is a junior synonym of* *Lepacyclotes*). With their extended, oval base, the scales from Odrowąż resemble closely the Carboniferous genus *Lepidocarpopsis* (Abbot 1963) or *Lepidostrobophyllum*. It differs from *Cylostrobus* (Helby and Martin 1965), *Pleuromeia* (Dobruskina 1974; Wang and Wang 1982) or *Skilliostrobus* (Ash 1979) in the shape of the scales.

Odrolepis resembles *Annalepis*, a monospecific genus reported from France (Fliche 1910), characterized by wedge-shaped sporophylls with an extended base (the apex is unknown) and median groove. The only species of *Annalepis* is *A. zeilleri*, described by Grauvogel-Stamm and Duringer, 1983 (with added emended generic diagnosis), based on 80 well-preserved sporophylls with base and apex. According to their emended diagnosis, the apex of the sporophyll is dome-shaped with an acute tip. The lamina tapers towards the base, which is slightly falcate and has a clearly visible attachment mark. Some of the sporophylls show wings along the margins. The same type of *A. zeilleri* scales was described by Kelber and Hansch (1995).

Although in shape and presence of a median groove, the material from Odrowąż resembles *Annalepis*, it does not agree with the main diagnostic features of that genus in that the base of the scale is extended and rounded, the lamina is relatively narrow and the apex tapers to almost acute.

Usually, such sporophylls have sporangia placed at the base and not along the lamina as in *A. zeilleri*. Unfortunately, we do not have any sporangium in the material studied. This might be caused by bad preservation or an unripe stage of the sporophylls.

The sporophylls from Odrowąż are of the same size as, and correspond to the smallest scales of *A. zeilleri* from France. The French specimens have a type of wing along the lamina, which has not been observed in any of the specimens from Odrowąż.

All of the Mesozoic genera, *Lycostrobus*, *Cyclostrobus*, *Skilliostrobus* and *Annalepis*, have the same type of microspores, *Aratrisporites* (Grauvogel-Stamm and Duringer 1983), identical to spores occurring in sediments from Odrowąż, where *Aratrisporites minimus* Schulz (1967) was found in a great number (Ziaja 2006). This proves that *Odrolepis* belongs to the same group of sporophylls.

Osmundaceae
Todites Seward 1900
Todites princeps (Presl) Gothan 1914
(Pl. 1, Figs 7–8)

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, fig. 10–13.

1894. *Todea princeps;* (Presl) Raciborski, p. 18, pl. 6, fig. 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.
1958. *Todites princeps* (Presl) Gothan; Kräusel, p. 69, pl.3, figs 6–7.
1961. *Todites princeps* (Presl) Gothan; Harris, p. 93, text-fig. 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.
2008. *Todites princeps* (Presl) Gothan; Barbacka and Bodor, pl. 1, figs 1–5.

MATERIAL: KRAM-P PM 68/131, 135, 139, 156, 203/II, 383/I, 384/I-II, 385/I, 1089. Several fragments of sterile pinnate fronds, with the largest fragment 30 mm long. Preservation rather poor; details of venation mostly invisible.

DESCRIPTION: The pinnae are part of the sterile, at least bipinnate fronds. The rachis is 0.5 mm wide; pinnules are opposite to alternate (Pl. 1, Figs 9 and 10). Their size ranges from 3x1.5 mm at the apex of the pinna to 15x3–4.5 mm towards its middle part. The distance between the neighbouring pinnules (the middle part of their bases) is 2–4 mm, smaller at the pinna apex. The pinnule base is considerably contracted. The margins of the pinnules are crenate at the pinna apex to lobed, from slight to deep (almost to the midrib). The apex tapers, ending in a single small lobe (Pl. 1, Figs 7–8). The midrib is well marked; the secondary veins are invisible because of poor preservation.

DISCUSSION**:** Although preservation of the material is quite poor and details of venation are invisible, the shape of pinnae and pinnules is so characteristic that the specimens may safely be placed in *Todites princeps*. Based on the shape of the pinnules, especially their lobed margins, the material from Odrowąż most closely resembles the specimens described from Germany (Gothan 1914), Greenland (Harris 1926, 1931) and Yorkshire (Harris 1961). Specimens from Iran and Afghanistan (Schweitzer 1978; Schweitzer *et al*. 1997), as well as from Poland (Raciborski 1891, 1894), have their pinnules less lobed, with entire margins. Kilpper (1964) presented fronds with both forms of pinnules: lobed, and with almost entire margins. Especially the fragment on his pl. 8, fig. 7 is identical with the Odrowąż specimens. Pinnules with intermediate forms were also illustrated by Harris (1926, 1931, 1961). In comparison with the Hungarian specimens, the material from Odrowąż agrees with morphotype 3 from Hungary (Barbacka and Bodor 2008).

Todites princeps, forma *trilobata* Barbacka et Ziaja, forma nov., named for the three-lobed apex of the pinnae
(Pl. 1, Figs 9–10; Pl. 2, Figs 1–2)

MATERIAL: KRAM-P PM 68/123-24, 137-38, 151, 1075, 1084, 1097, 1133, 1158. Several sterile pinnae and a frond fragment up to 60 mm long. Preservation quite poor; details of morphology clearly visible on some specimens.

DESCRIPTION: Preserved fragments of sterile pinnae have a slender rachis, 1 mm wide. The branches are opposite, up to 30 mm long and 8 mm wide at the basis, sparsely placed (distance between the neighbouring pinnae is about 6 mm). Pinnules at the basis alternate catadromically, towards the top they become opposite. They are oval, with an obtuse apex, max 5 mm long and 3 mm wide (Pl. 1, Figs 9–10; Pl. 2, Fig. 1). Their base is wide, decreases slightly at the acroscopic margin. The margins are irregularly crenate to double-toothed. The top pinnules are usually wedge-shaped, dissected into 3 lobes, of which the central one also shows also three lobes at the apex (Pl. 1, Fig. 10). Venation is sphenopteridal (Pl. 2, Fig. 2), the midrib is not prominent, secondary veins sparse, dichotomically branching in both catadromic and anadromic order in different pinnules.

DISCUSSION: From the basic form of *Todites princeps*, forma *trilobata* differs in the shape and margins of pinnules, particularly in their apical part. Usually, it tapers gradually and the last pinnules at the apex of the pinnae are very small and simple. The pinnule venation in *T. princeps* is anadromic, and mixed anadromic and catadromic in forma *trilobata*. Such mixed type of branching is quite common in various species of *Coniopteris*. The general morphology of the new form resembles closely *Todites princeps* of Harris (1931, text-fig. 8).

Matoniaceae
Phlebopteris Brongniart 1836
Phlebopteris angustiloba (Presl) Hirmer and Hörhammer 1936
(Pl. 2, Fig. 3)

1867. *Gutbiera angustiloba* Presl; Schenk, p. 64, pl. 18, figs 5–10.
1867. *Andriania baruthina* Braun; Schenk, p. 87, pl. 21, figs 1–6.
1891. *Laccopteris angustiloba* Presl; Raciborski, p. 15, pl. 2, figs 6–9.
1892. *Laccopteris angustiloba* Presl; Raciborski, pl. 2, fig. 22.
1931. *Laccopteris angustiloba* (Presl) Raciborski; Harris, p. 74, pl. 14, figs 6–17, text-fig. 26.
1936. *Phlebopteris angustiloba;* (Presl) Hirmer and Hörhammer, p. 26, pl. 6, text-fig. 5:3.
1950. *Phlebopteris angustiloba* (Presl) Hirmer and Hörhammer; Lundblad, p. 23, pl. 2, fig 14; pl. 3, figs 1–5 pl. 13, fig. 2; text-fig. 4.
1963. *Phlebopteris angustiloba* (Presl) Hirmer and Hörhammer; Reymanówna, p. 10, figs 1, 4–5, text-fig. 1A–E.
1993. *Phlebopteris angustiloba* (Presl) Hirmer and Hoerhammer; van Konijnenburg-van Cittert, p. 241.

MATERIAL: KRAM-P PM 68/23,133, 155, 209/I, 221/I, 978, 1013, 1015, 1038, 1039, 1042, 1046, 1057, 1059, 1061, 1077, 1096. Several separated, small fragments of pinnules, 4–20 mm long; the details of venation hardly visible.

DESCRIPTION: The fragments of fertile pinnules are 1.5 mm wide. The margins are entire, the midrib is deeply depressed, about 0.4 mm wide. On both sides along the midrib the lamina is divided into highly convex fields containing sori, about 0.5 mm in diameter. The structure of the sori and sporangia is unknown.

DISCUSSION: Although the fragments are very small, they undoubtedly belong to *P. angustiloba*. The proportions of the pinnule fragments as well as the presence and distribution of sporangia are typical for this species.

Dipteridaceae
Goeppertella Oishi and Yamasita 1936
Goeppertella microloba (Shenk) Oishi and Yamasita 1936
(Pl. 2, Figs 4–5)

1867. *Woodwardites microlobus*; Schenk, p. 68, pl. 13, fig. 11–13.
1892. *Woodwardites microlobus* Schenk; Raciborski, p. 3, pl. 2, fig. 17.
1919. *Woodwardites microlobus* Schenk; Antevs, p. 14, pl. 1, figs 5–6a.
1936. *Goepertella microlobus;* (Schenk) Oishi and Yamasita, p. 146.
1946. *Goepertella microlobus* (Schenk) Oishi and Yamasita; Harris, p. 23, text-fig. 9 A–G.
2009. *Goepertella microloba* (Schenk) Oishi and Yamasita; Schweitzer *et al*., p. 52, pl. 18, figs 2–3, text-fig. 15.

MATERIAL: KRAM-P PM 68/24-25 (part and counterpart), 71/ I, 1007, 1008-09 (part and counterpart), 1016-18, 1026, 1028, 1047, 1050, 1095. Several small fragments of sterile pinnae, with the largest 11 mm long, and others 4, 5 and 10 mm. Details of morphology clearly visible.

DESCRIPTION: The pinnae are 3–7 mm wide, opposite to alternate segments are incised fully or partly, to the rachis, up to 4/5 of their total length. The segments are 1.5 to 3.5 mm long and 1–2 mm wide at the base. Their margins are entire, the apex is subacute or acute. The midrib is well-marked, the veins are visible as deeply sunken lines between convex, nearly oval meshes up to 1 mm long (Pl. 2, Fig. 5).

DISCUSSION: The small size, the shape of pinnules and the characteristic convex meshes clearly distinguish this species from other taxa.

Thaumatopteris Goeppert 1841
Thaumatopteris brauniana Popp 1863
(Pl. 2, Fig. 6)

1863 *Thaumatopteris brauniana*; Popp, p. 409.
1978 *Thaumatopteris brauniana* Popp; Schweitzer, p. 36, pl. 4, figs 5–9; pl. 5, figs 1–7; pl. 6, figs 1–3; text-figs 20, 23, 24, 26–28, 30–31; and additional synonymy.

MATERIAL: KRAM-P PM 68/30, 72, 83, 140. Very small fragments of sterile pinnules, with lengths 4, 5, 8 and 12 mm respectively.

DESCRIPTION: The preserved fragments are very short and come from the middle part of the pinnules. Their width ranges from 1 to 3 mm. Their margins are parallel and characteristically crenate, the midrib is readily distinguishable and the lateral veins form irregular meshes.

DISCUSSION: Although very small in size, the pinnule fragments have a morphology typical of fronds of *Thaumatopteris schenkii*. Schweitzer (1978) discussed the genus *Thaumatopteris* in detail and revised some of its species. As a result, he proved that *T. schenkii* falls into the variability range of *T. brauniana* and, consequently, should be placed into its synonymy.

Rhizomes/stems
(Pl. 2, Fig. 7)

MATERIAL: KRAM-P PM 67/941–57, 959–60, 68/13–14, 158, 192/I, 961–62, 992, 1002, 1033, 1055, 1122, 1143, 1208, 1215, 1217, 1220–21. Besides leaves, rhizomes/stems are richly represented (36 specimens), these being the longest remains (up to 230 mm) next to the *Neocalamites* fragments, with which they are commonly associated.

DESCRIPTION: The fragments of rhizomes/stems are long, in some cases branched, 10–20 mm wide; the diameters of broken fragments are 28–37 mm. Their surfaces are covered by dense scales, which are either drop-shaped, or have an oval or rhomboid base and a protruded narrowing apex. They are about 7–8 mm long and 3–5 mm wide, with an imbricate arrangement.

DISCUSSION: This type of stem/rhizome is characteristic of Pteridophytes. The specimens studied correspond well to those described by Schweitzer (1978) as the stem of *Todites princeps*. The size of the remains and the shapes of scales covering their surfaces are very similar. They also resemble the rhizome fragments illustrated by Schenk (1867), some associated with leaves of *T. princeps* (pl. 7, figs 4, 5), and others found separately (pl. 35, fig. 1).

Fern rhizomes were also described by Nathorst (1878a), under the name *Rhizomopteris schenki*, and connected with leaves of the genus *Dictyophyllum*; and by Seward (1911), under the name *R. gunni*, with preserved anatomy, and connected questionably with *Hausmannia*. The smooth surface and the lack of scales distinguishes both these species from the Odrowąż rhizomes.

Ferns are rare in Odrowąż and all of the specimens found are strongly fragmented. In contrast, rhizomes are quite common (36 specimens), with their number being more than 50% of all the preserved fern specimens (total number of fern remains is 45) and significantly more common than *T. princeps* (together with the forma trilobata 20 specimens). They are preserved in much larger fragments than the fronds. This may be explained by the more delicate structure of the fronds than that of the rhizomes, and by the fact that rhizomes usually grow underground and are not exposed to damage, as against fronds which are susceptible to necrobiosis and transport. It is also possible that the preserved rhizome fragments belong to more than one genus.

Pteridospermopsida
Corystospermales

Pachypteris Brongniart 1828
Pachypteris lanceolata Brongniart 1828
(Pl. 2, Figs 8–13; Pl. 3, Fig. 1)

1828. *Pachypteris lanceolata*; Brongniart, p. 167, pl. 45, fig. 1.
1836. *Pachypteris lanceolata* Brongniart; Goeppert, p. 179, pl. 1, fig. 4.
1900. *Pachypteris lanceolata* Brongniart; Seward, p. 171, text-figs 27–28.
1913. *Pachypteris lanceolata* Brongniart; Halle, p. 39.
1914. *Pachypteris lanceolata* Brongniart; Antevs, p. 62, pl. 1, fig. 1.
1954. *Pachypteris lanceolata* Brongniart; Thomas, p. 316, text-figs 1–3.
1955. *Pachypteris lanceolata* Brongniart; Thomas and Bose, p. 542.
1964. *Pachypteris lanceolata* Brongniart; Harris, p. 137, pl. 5, figs 1–5; pl.7, fig. 6; text-figs 55–58.
1999. *Pachypteris lanceolata* Brongniart; van Konijnenburg-van Cittert and Morgans, p. 65, pl. 7, fig. 4.
1969. *Pachypteris lanceolata* Brongniart; Doludenko and Svanidze, p. 20, pl. 9, figs 1–7; pl. 10 figs 1–4, pl. 11 figs 1–5, pl. 12 figs 1–5, pl. 13 figs 1–5, pl. 14 figs 1–5.
1976. *Pachypteris lanceolata* Brongniart; Barnard and Miller, p. 41, pl. 1-10-13, pl. 2–1 text-figs 3 A–H, 4 A–E.

MATERIAL: KRAM-P PM 68/2, 6, 8, 1082-1083 (part and counterpart), 1060. Few leaf fragments with pinnules, with a well preserved cuticle. The largest fragment c. 8.5 cm long with the apical part of the leaf; the others, from the middle part, 2–5 cm long.

DESCRIPTION: The fragments are pinnate; pinnules are not crowded, from 10 × 3 to 19 × 5 mm, the rachis is 1.5–2 mm wide. Fully developed pinnules are lanceolate with a subacute apex, small ones are ovate with a rounded apex (Pl. 2, Fig. 8). The base is generally slightly constricted and decurrent. The midrib is weakly indicated, with thin, arched lateral veins. Some separated pinnae have lobed margins. The lobes are c. 3 mm long and 1.5 mm wide (Pl. 2, Fig. 9).

The cuticle is moderately thick, the upper cuticle being thicker than the lower. On both cuticles the cell outlines are strongly marked; the cells are irregularly polygonal with thick and straight cell walls. The leaves are amphistomatic, with sporadic stomata on the upper cuticle. On the lower cuticle, the stomata are numerous, but not crowded; they are randomly orientated, scattered over the whole surface but tending to avoid the midrib. A typical stoma has about 6 small subsidiary cells situated around the stomatal pit (Pl. 2, Fig. 11). The encircling cells are not specialized. Guard cells are weakly cutinised, and commonly destroyed.

Numerous trichome bases occur on the lower cuticle, mainly near the margins (Pl. 3, Fig. 1). They consist of a distinct irregular thickening surrounded by 5–8 irregular cells, with a small pit in the centre (Pl. 2, Figs 12–13).

DISCUSSION: In the shape and arrangement of the pinnules, the material studied closely resembles the forms illustrated by Brongniart (1828). The large and lobed forms described and illustrated by Harris (1964) are also very similar.

P. lanceolata is close to *Pachypteris rhomboidalis*, especially forms with large and entire pinnae. The difference, as discussed by Harris (1964, p. 140), is slight and concerns mainly the larger leaves with more robust pinnae in the latter and some details in the structure and distribution of stomata. It seems that *P. lanceolata* has narrower pinnae, which tend to be lobed, which is not usual in *P. rhomboidalis* (however, a lobed form of *P. rhomboidalis* was illustrated by Weber 1968). Although it is not excluded that these two taxa may be conspecific, it was the presence of lobed pinnae in our material that inclined us to identify it as *P. lanceolata*. On the other hand, the trichome bases have not been mentioned in this species so far. The same type of trichome base was observed in *Komlopteris nordenskioeldii* and *Pachypteris banatica* from Hungary (Barbacka 1994a, 1994b), as well as in *P. rhomboidalis* from Germany (van Konijnenburg-van Cittert pers.com.). They were not found in all leaves, and their frequency was different in different specimens, which suggests that the presence of this type of trichome was caused or influenced by external conditions.

A similar type of trichome occurs in the Recent angiosperm *Gonocaryum* from the family Icacinaceae (Hejnowicz 1980), which lives in a tropical climate along riverbanks in frequently flooded soil (Wilkinson 1979a). In this family, this type of trichome functions as a hydatode enabling the exudation of superfluous water.

The environment in which the *Komlopteris* grew is inferred to have been marsh, close to water basins. *Pachypteris lanceolata* in Odrowąż might perhaps have lived in similar wet conditions.

Cycadopsida
Bennettitales
Otozamites Braun in Muenster 1843
Otozamites brevifolius Braun in Muenster 1843
(Pl. 3, Figs 2–8)

1843. *Otozamites brevifolius*; Braun in Muenster, p. 29, pl. 13, figs 13–15.
1867. *Otopteris bucklandi*; Schenk, p. 139, pl. 31, figs 2–3; pl. 33, figs 2-3; pl. 34, figs 1–7.
1914. *Otozamites brevifolius* Braun; Gothan, p. 136, pl. 28, fig. 1.
1968. *Otozamites brevifolius* Braun; Weber, p. 57, pl. 12, figs 121–125.
1992. *Otozamites brevifolius* Braun; Kirchner, p. 31, pl. 7, figs 1–4.

MATERIAL: KRAM-P PM 68/1, 4, 71/I – II (part and counterpart), 284, 1094. One large apical leaf fragment (about 110 mm long), and four separated pinnae, with preserved cuticle.

DESCRIPTION: The leaf fragment is pinnate, at the widest point c. 120 mm wide (pinnae on one side are not completely preserved). The rachis is slender (1–2 mm), the pinnae are oblong and alternate. The longest pinnule (probably from the middle part of the leaf) is 34 mm long and 5 mm wide. Their bases show typical auricles which increase the width of pinnae by 1 mm. They are separated by a space of 1 mm in the middle part of the leaf, becoming denser towards the apex, where they may overlap the opposite pinnula base (Pl. 3, Fig. 4). Veins are radiate, sometimes singly forked. Margins are entire, apex subacute (Pl. 3, Figs 2–3).

The leaf is hypostomatic. The upper cuticle shows almost square or rectangular cells with well marked sinusoid cell walls. On the lower cuticle, most cells are nearly square, virtually each one possesses a tall and thin central papilla. Cells are elongated at the pinna margin and papilla-free (Pl. 3, Fig. 5). The stomata are arranged in bands 1–2 stomata wide, separated by non-stomatal rows 3 cells wide. The stomata are dense, separated from each other by one to two cells, orientated transversely to the veins (Pl. 3, Fig. 6). Thickly cutinised guard cells are protected by prominent papillae. The lower cuticle also shows numerous trichome bases in both the stomatal and non-stomatal rows, commonly situated in the neighbourhood of the stomata. On the inner side of the cuticle, they have the appearance of a collapsed spherical body about 30 µm in diameter (Pl. 3, Fig. 8, 9).

A single row of dark oval hole-like structures was observed under the fluorescent microscope along the margins of the upper cuticle (Pl. 3, Fig. 7). They were restricted to the area of one cell, being as long as a cell. In SEM the holes were not visible, which suggests that they are not openings but instead are very thin membranes on the periclinal cell walls.

DISCUSSION: The leaf morphology and cuticle structure correspond to those features in *Otozamites brev-*

ifolius from Germany (Kirchner 1992). Particularly characteristic are the dense papillae as well as the presence, density and structure of the trichomes. Spherical, one-cell secretory trichomes of a similar type are found in leaves of recent angiosperms, e.g. *Phaseolus*, by which they secrete water or mineral salts (Hejnowicz 1980). Their presence in *O. brevifolius* may suggest its adaptation to a very wet environment, or to redundant minerals in the soil that were excreted through the leaf. This type of trichome was rarely described in Mesozoic plants, partly because of preservation, or an inaccurate image in a light microscope. Among bennettites it is the only known species in which such trichomes were observed.

The oval structures observed on the upper cuticle at the margins of the pinnae resemble secretory cells of present-day angiosperms. In Recent plants, secretion takes place through the membrane. Such types of cells may secrete water, dissolved salts, polysaccharides, or poisons. In *Otozamites brevifolius*, the location of such cells at the leaf margins on the upper surface suggests that the secreted substances might have had a protective or attractive purpose (Metcalfe 1979).

Pterophyllum Brongniart 1824
Pterophyllum alinae Barbacka sp.nov.
(Pl. 3, Figs 10–12; Pl. 4, Figs 1–4)

?1928. *Pterophyllum polonicum*; Makarewiczówna, p. 20, pl. 1, figs 3–5.

HOLOTYPE: KRAM-P PM 68/1088 (Pl. 3, Fig. 10), preserved in grey mudstone.

TYPE LOCALITY AND STRATIGRAPHIC HORIZON: Odrowąż, the Holy Cross Mountains, Poland; Lower Jurassic, Hettangian.

DERIVATION OF NAME: From the first name of Alina Makarewiczówna, Polish palaeobotanist.

MATERIAL: KRAM-P PM 68/39/I-II, 81, 84, 92/I-V, 95/I-IV, 102/I-II, 103, 104, 115/I-II, 142/I-III, 164/I-V, 174/I-V, 192/I, 198, 201/I-II, 203/II, 205/I-II, 206/I-II, 210/I-III, 212- 214/I-II, 223, 225, 242-244, 248, 250, 252, 253, 267-273, 275/I, 280/I-IV, 282, 284, 286, 294/III, 295/I-II, 299/I-II, 301/VI, 301/VII, 301/IX, 302/I-II, 302/VII, 308, 346, 941, 942, 944, 948, 953, 961, 966, 967, 973, 974, 996, 999, 1000, 1002, 1031, 1052, 1053, 1056, 1066, 1067, 1078, 1080, 1081, 1087, 1088, 1097, 1104, 1107, 1111, 1113, 1121, 1129, 1155, 1207, 1214, 1224, 1229, 1232, 5950. Hundreds of separated pinnae on numerous specimens, commonly randomly crowded on slabs. Most pinnae of almost equal size. No pinnae attached to the rachis. All pinnae broken at the basis and usually with preserved apex. The cuticle poorly preserved, with micro-cracks, coalified to a high degree, not suitable for preparation (observable only in a fluorescent microscope).

DIAGNOSIS: Pinnae 8–10 times as long as wide, with parallel margins and thin, 6–12 parallel veins. Apex of pinna subacute or acute, sometimes slightly bent acroscopically. Leaf hypostomatic. Cell walls thin and straight. Upper cuticle with small elongated-rectangular cells in longitudinal rows. On the lower cuticle, veins indicated by elongated cells. Stomata large, dense, between the veins in 1–3 regular rows, orientated transversely to the veins. Guard cells large, semicircular.

DESCRIPTION: The pinnae are elongated; their preserved length is c. 8–10 times their width. Usually, the fragments are 10–40 mm long and 2–3.5 mm wide, in a few cases 4 mm. Their margins are almost parallel along the entire length, tapering to a subacute or acute apex. The pinnae are sometimes slightly bent acroscopically. The veins are very weakly visible and thin, 6–12 /pinna, and parallel (Pl. 3, Figs 11–12).

The leaf is hypostomatic. The cuticle is thin, the cell walls are thin and straight. On the upper cuticle, the cells are uniform, elongated-rectangular, narrow. The veins are not indicated, the cells on the entire surface form longitudinal rows (Pl. 4, Fig. 3). On the lower cuticle, the veins are marked by elongated cells, 4–10 times as long as wide. The stomata are situated between the veins in 1–3 regular rows. The rows of stomata are separated by one, rarely two rows of narrow, elongated cells (Pl. 4, Fig. 1). They are syndetocheilic, large (57–70 µm), orientated transversely to the veins. The guard cells are large, semicircular (Pl. 4, Fig. 4). Stomata commonly separated from each other by their nearly rectangular subsidiary cells, or a few (1–3) ordinary, nearly square cells lie between them. In some cases, cells on the lower cuticle are irregular in shape and orientation (Pl. 4, Fig. 2).

DISCUSSION: Identification and description of the new species is based on separate pinnae, which occur in large numbers in the Odrowąż section; neither pinnae attached to rachis nor fragments of rachis were found. The pinnae were first incorrectly classified as *Podozamites* sp. 2 (Wcisło-Luraniec 1991). Examination of its cuticle in a fluorescent microscope showed clearly the bennettitalean character of the stomata.

Considering that among hundreds of pinnae none has the base preserved and they broke from the rachis along the whole width, it is inferred that the pinnae did not possess a tapering base, but were attached by their whole width to the rachis. In the other case, pinnae with a constricted base could be more easily detached from the rachis and the base would be preserved. This is the first reason to classify our material as *Pterophyllum* and not *Zamites*, which has very similar pinnae but its base is "contracted and attached by all area in middle of basal margin" (Harris 1969). The other argument is the structure of the cuticle which shows straight cell walls and transversal orientation of the stomata, whereas in *Zamites*, the cell walls are usually sinusoid and the stomata are not orientated so regularly.

In addition, the specimens from Odrowąż have a cuticle structure with very regular cells and a particular arrangement of the stomata, which differs from those of any existing species. In consequence, a new species, *P. alinae* is proposed.

Based on macromorphology, the pinnules from Odrowąż may be conspecific with *P. polonicum*, as described by Makarewiczówna from the region of Ostrowiec (Makarewiczówna 1928). The distance between both localities does not exclude this supposition. However, Reymanówna (1963) included *P. polonicum* in *P. subaequale* described from Grojec near Cracow (Middle Jurassic). Unfortunately, even though Makarewiczówna's material was stored in three different places (Cracow, Warsaw and Vilnius), no specimen has remained. The only data were found in the literature and the species was established on macromorphology. The size and length/width ratio, as well as the shape of apex of the material from Ostrowiec correspond to those of the pinnules from Odrowąż, while Reymanówna's material was considerably smaller. However, as the original material of *P. polonicum* is missing, we cannot include our specimens in that species, hence the new specific name *P. alinae*.

Cycadales
Paracycas Harris 1964
Paracycas minuta Barbacka sp. nov.
(Pl. 4, Figs 5–7)

HOLOTYPE: KRAM-PPM 68/293 (Pl. 4, fig. 5), preserved in grey mudstone.

TYPE LOCALITY AND STRATIGRAPHIC HORIZON: Odrowąż, the Holy Cross Mountains, Poland; Lower Jurassic, Hettangian.

DERIVATION OF NAME: After the fine, thin pinnae.

MATERIAL: KRAM-P PM 68/293. One leaf fragment, poorly preserved. Its preservation is poor, having a lot of micro-cracks, so that the cuticle breaks during maceration into microscopic pieces. The cuticle structure can be observed only under a fluorescent microscope.

DIAGNOSIS: Leaf pinnate, pinnae narrow (less than 1 mm), opposite or subopposite, arising at almost right angles to the relatively broad rachis, attached by the whole bases. Bases slightly extended, almost in contact with each other. Pinnae with prominent midrib, parallel, entire margins and subacute apex. Leaf hypostomatic. Cells on upper surface elongated-rectangular, narrow, in longitudinal rows. On lower surface, cells irregular, elongated above midrib, stomata with prominent papillae on subsidiary cells.

DESCRIPTION: The leaf is pinnate, with narrow pinnae. Pinnae arise at almost right angles to the rachis, which is 2 mm wide. They are opposite or subopposite, 0.9 mm wide; the distance between neighbouring pinnae is 0.5 mm. Their margins are parallel, entire, apex subacute. The pinnae are attached to the rachis by their whole bases, which are slightly expanded; the neighbouring bases are almost in contact with each other. In each pinna there is only a prominent midrib, no other veins (Pl. 4, Fig. 5).

The leaf is hypostomatic, with a very delicate cuticle. The cell walls are straight and thin. On the upper surface, the cells are nearly rectangular, but long and narrow. Their length/width ratio is 5–10. They are arranged in regular, longitudinal rows (Pl. 4, Fig. 6). On the lower surface, the cells are more irregular than on the upper one; above the midrib they are elongated. Stomata are present in the area between the midrib and margins, their exact distribution and orientation is unknown. The guard cells are surrounded by 5–9 subsidiary cells with prominent papillae (Pl. 4, Fig. 7).

DISCUSSION: The macromorphology of the specimen constrains its determination to a quite narrow range of possible taxa. The genus *Cycadites* is a form genus, which groups leaves with narrow segments arising from the rachis at almost right angle and having a single vein. It was established by Sternberg (1825) but appeared to be heterogeneous, as proved by Harris (1964), who removed some species and proposed for them a new genus, *Paracycas*, characterized by a single vein and haploheilic stomata characteristic of cycads. *Cycadites cteis* Harris (1952) became the type species of the new taxon. Another genus removed from *Cycadites* was *Pseudocycas* (Nathorst 1907), created for leaves with syndetocheilic stomata typical of bennettites.

The morphogenus *Cycadites* remained for the specimens with unknown cuticle structure.

The specimen from Odrowąż most resembles some bennettites like *Pterophyllum cycadites* Harris (1969) and two species of *Pseudocycas*: *P. lesleyae* Watson & Sincock and *P. saportae* (Seward) Holden (Watson and Sincock 1992), as well as the cycad *Paracycas cteis* Harris (Harris 1964). However, apart from the size difference, the pinna bases of *P. lesleyae* are rounded as typical of bennettites, whereas the epidermal cells of *P. saportae* have sinusoid cell walls. The specimen from Odrowąż most resembles *Pterophyllum cycadites* and *Paracycas cteis* in its macromorphology (including its size), but *P. cycadites* has a bennettitalean cuticle with sinusoid cell walls and syndetocheilic stomata.

The genus *Paracycas* contains so far four species: *P. cteis* Harris from Yorkshire, England (Harris 1964), as well as *P. georgiepillsoni* Watson and Cusack, *P. wysesiorum* Watson and Cusack, and *P. aureservoir* Watson and Cusack from the English Wealden (2005). At first the specimen from Odrowąż was classified as *P. cteis*. However, that species differs significantly from the material from Odrowąż in irregularly polygonal cells on the upper cuticle, whereas our species has rectangular and elongated cells with a regular arrangement. In cycads, the structure of the upper cuticle has taxonomic value (also in comparison with recent species, Greguss 1968). In addition, the stomata have hollow papillae, whereas in the material from Yorkshire the subsidiary cells form ingrowths only. The size of the papillae itself might be caused by the environment but, taken together with the cell arrangement, allows for a new species to be established.

?Gnetales
Piroconites Gothan 1914
Piroconites kuespertii Gothan 1914
(Pl. 4, Figs 8–11)

1914. *Piroconites kuespertii*; Gothan, p. 130, pl. 28, fig. 4, text-fig. 4.
1992. *Piroconites kuespertii* Gothan emend van Konijnenburg-van Cittert, p. 253, pl. 1, figs 2–4, pl. 2, figs 1–4.
1992. *Piroconites kuespertii* Gothan; Kirchner, p. 34, pl. 8, fig. 4–6, text-fig. 5.

MATERIAL: KRAM-P PM 68/232/I, 233 (part and counterpart). One fragment of microsporophyll (with counterpart). The organic matter strongly coalified, unsuitable for preparation. The cuticle structure hardly observable in the fluorescent microscope.

DESCRIPTION: The specimen is 15×7 mm large, probably representing the middle part of a microsporophyll. The shape of the entire microsporophyll is unknown; the fragment probably represents its adaxial side (Pl. 4, Fig. 8). The triangular synangia are c. 1.2 mm across and have a prominent triradiate mark (sides of pollen sacs grown together into synangia). Some of them (especially near the margin of the fragment) are overlapped by neighbouring synangia (Pl. 4, Fig. 9). The cross-section of the compressed synangia shows some layers of cuticle (Pl. 4, Fig. 10). The cuticle is very thin, small fragments show straight and arched rows of elongated cells, or large rectangular cells. The cell walls are straight and very thin (Pl. 4, Fig. 11).

DISCUSSION: The specimen is referred to *P. kuespertii*, albeit it is incomplete. The fragment has neither the base nor the apex or margins. The bract remains were not found. However, the morphology of the synangia and of the microspores, *Ephedripites tortuosus* Mädler, is very characteristic. The genus *Piroconites* was established for two species, *P. kuespertii* and *P. froschii* (Gothan 1914). Van Konijnenburg-van Cittert (1992) suggested, however, that the difference between both species (obtuse and acute apex respectively) reflects the variability of a single species, and that consequently both species should be synonymised. Because the Odrowąż specimen is small and fragmentary, the traditional concept is followed herein and, based on its size, shape and the arrangement of synangia, it was placed in *P. kuespertii*.

The systematic position of this microsporophyll was discussed by several authors. Based on morphology, Schuster (1911) attributed it to the Williamsoniaceae, and Gothan (1914) compared it to *Bennettites morierei*, but without a thorough discussion. Based on microspore structure (palynological analysis), Bolkhovitina (1961) suggested its relationship with the Schizaeaceae because of the striate *in situ* pollen grains, Schulz (1967) placed the affinity of dispersed *Ephedripites tortuosus* in Ephedraceae or ?Schizeaceae, and Balme (1995) in Ginkgopsida (Peltaspermales, Gnetales). Van Konijnenburg-van Cittert (1992) described the microsporophyll *P. kuespertii* and microspores *in situ* which are comparable to dispersed *Ephedripites tortuosus* from the Liassic of Germany. Ziaja (2006) previously described *Ephedripites tortuosus* dispersed in sediment from Odrowąż.

Unfortunately, we did not find any leaves of *Desmiophyllum gothani*, which are probably connected with *Piroconites* (van Konijnenburg-van Cittert 1992).

Ginkgoaceae
Schmeissneria Kirchner and van Konijnenburg-van Cittert 1994

Schmeissneria microstachys (Presl) Kirchner and van Konijnenburg-van Cittert 1994
(Pl. 5, Fig. 1)

1992b. *Stachyopitys preslii* Schenk; Wcisło-Luraniec, p. 248, pl. 1, figs 1–4; text-figs 1–2.

1994. *Schmeissneria microstachys*; Kirchner and van Konijnenburg-van Cittert, with synonyms, p. 199, pl. I, fig. 1, text-fig. 1.

MATERIAL: KRAM-P PM 68/1226-27

REMARKS: The specimens from Odrowąż were referred by Wcisło-Luraniec (1992) to *Stachyopitys preslii*, as female fructification of Ginkgoales. However, Kirchner and van Konijnenburg-van Cittert (1994) reclassified this material to the new genus *Schmeissneria* (*S. microstachys*), which was proposed for the female cones of this type, while the genus *Stachyopitys* was retained for male cones.

Coniferales
Podocarpaceae
Podozamites Braun 1843
Podozamites cf. *schenkii* Heer 1876
(Pl. 5, fig. 2)

MATERIAL: KRAM-P PM 68/141. One small fragment (up to 50 mm) of a leafy schoot with 6 leaves. Leaves incomplete, only one apex preserved. Preservation poor, venation not visible. The cuticle not suitable for preparation, not showing fluorescence.

DESCRIPTION: The rachis is very slender, 1 mm wide, with spirally arranged leaves. The preserved remains of leaves attached are up to 35 mm long and 1–2 mm wide. The distance between adjacent leaves is about 4–7 mm. The leaf bases taper gradually, the margins are nearly parallel along their entire length, tapering only near the apex. The apex is acute where preserved. The leaf substance is very thin and the veins are invisible.

DISCUSSION: Since the cuticle is unknown, the specimen was identified by study of its macromorphology. It closely resembles *P. schenkii* from Greenland described by Harris (1926), as well as some slender forms from Yorkshire, England (Harris 1935), which he did not classify at species level. He grouped all narrow-leaved *Podozamites* remains in the group of *P. schenkii–P. agardhianus*, and divided them into 4 types according to their size and the shape of their leaves. The Odrowąż specimen corresponds to his type 4, compared by Harris to *P. schenkii* from Greenland. It also agrees with *P. schenkii* described by Weber (1968, pl. 14, figs 143–144), and those described by Schweitzer and Kirchner (1996, pl. 2, fig. 6, 7; pl. 3, fig 1–3, text-fig. 3).

On the basis of the cuticular structure, *P. schenkii* was not transferred to the genus *Lindleycladus*. The species *P. schenkii* was mentioned by Kirchner (1992) as probably connected with the female cone scale species *Swedenborgia cryptomerides*, which resembles the specimens of *Swedenborgia* sp. found in Odrowąż.

Podozamites sp.
(Pl. 5, Figs 3–6)

MATERIAL: KRAM-P PM 68/109, 1079. Two separate, poorly preserved leaves, the thin cuticle broke into microscopic pieces (during preparation), so observation of its structure was possible only under a fluorescent microscope.

DESCRIPTION: The leaves are lanceolate, 30–35 mm long and 4–5 mm wide, in the widest, middle part of the leaf. The leaf base is contracted, the apex is subacute, the veins converge towards the apex and are hardly visible (Pl. 5, Figs 1–2). The leaf is hypostomatic. On the upper cuticle, the cells are large and irregular, with straight and thin cell walls (Pl. 5, Fig. 5). On the lower cuticle, areas with stomata are separated by wide non-stomatal areas (Pl. 5, Fig. 4). In stomatal areas, the stomata form 3–4 files separated by single rows of rectangular epidermal cells. The stomatal pit is large and rectangular. Two of the 4–6 subsidiary cells have a polar position, the others are situated at the sides of the stomatal pit. The guard cells are very weakly cutinised. The areas without stomata show similar cells to those on the upper cuticle.

DISCUSSION: The morphology of the leaves corresponds to two genera: *Podozamites* Braun (1843) and *Lindleycladus* Harris (1979). The genus *Lindleycladus* was separated by Harris (1979) from the genus *Podozamites* for those leaves in which stomata are orientated longitudinally and placed in longitudinal files, whereas in *Podozamites* they are distributed more irregularly and orientated more or less perpendicularly. In *Lindleycladus*, the leaves are arranged helically (Harris 1979), whereas in *Podozamites* they are arranged helically or distichously (Harris 1935). Unfortunately, the material from Odrowąż does not show these features clearly, so its identification is difficult. Although the cuticle was investigated under the fluorescent microscope, the guard cells were not preserved (only dark holes), so that their orientation is unknown. We can only say that their distribution is quite regular, which is rather a feature of *Lindleycladus* (Harris 1979), but not excluded in *Podozamites* (Harris 1935). The leaves were found separately and therefore their arrangement cannot be determined.

Since *Lindleycladus* is known only from the Middle Jurassic, and *Podozamites* was common in the Lower Jurassic (Liassic), we decided to classify our material as *Podozamites*.

The cuticle of our specimens corresponds most to *P. distans* (Presl) Braun and *P. stewartensis* Harris (Harris 1935). They have rectangular cells arranged in regular rows and a similar structure and distribution of the stomata (Harris 1935, text-fig. 37A, G, respectively). Other species of *Podozamites* have more irregular cells and the stomata do not form such defined rows.

In Poland, some species of *Podozamites* were described from the northern part of the Holy Cross Mountains: *P. lanceolatus* (Lindley) Schimper, *P. stobieckii* Raciborski, (Raciborski 1891, 1892) and from Ostrowiec: *P. distans* Presl, *P. angustifolius* Eichwald, *P. gramineus* Heer and *P. stobieckii* Raciborski (Makarewiczówna 1928). Especially similar to the specimen from Odrowąż is *P. distans* reported by Makarewiczówna (1928, pl. IV, fig. 1), in which the author included *P. lanceolatus* as described by Raciborski (1891, 1892). Unfortunately, comparison with this material is impossible because the specimens are missing.

Swedenborgia Nathorst 1876
Swedenborgia sp.
(Pl. 5, Figs 7–8)

1876. *Swedenborgia cryptomerides* Nathorst, p. 66, pl. 16, figs 6–12.
1935. *Swedenborgia cryptomerides* Harris, p. 108, pl. 18, figs 8, 10-18, 21, 22; pl. 19, figs 5–8, 20–22.
1959. *Swedenborgia cryptomerides* Kräusel, p. 127, pl. 4, figs 20–21, pl. 5, figs 26–27, pl. 6, figs 34–35, text-fig. 7.
1992. *Swedenborgia cryptomerides* Nathorst; Kirchner, p. 44, pl. 11, figs 1, 2.
1992. *Swedenborgia* sp.; M. Reymanówna, p. 308, pl. I, fig. 4.

MATERIAL: KRAM-P PM 68/146, 146/II, 215/II, 221, 274/I, 274/II, 276/I. Seven fragments (one of them with counterpart) of detached macrosporophylls with partly preserved cuticle. The cuticle coalified to a high degree, not suitable for preparation, hardly recognisable under a fluorescent microscope.

DESCRIPTION: The macrosporophylls from Odrowąż are visible from their lower surface (the surface without seeds). They are about 13–15 mm long, and their terminal end is divided palmately into 5 lobes. The stalk of the scale is 6 mm long (the preserved part) and 1.5 mm wide. The lobes are 3 mm long and 1 mm wide, slightly extended in the middle part and narrowing towards the apex. The apex is subacute. The structure of the cuticle is unknown due to its very poor preservation.

DISCUSSION: Several (about 14) species of *Swedenborgia* have been described so far. Four species are known from Europe and Greenland: *S. cryptomerides* (Greenland, Liassic – Harris 1935; Sweden, Rhaetic – Nathorst 1876; Liassic – Antevs 1919; Germany, Liassic – Kräusel 1959), S. major (Greenland, Liassic – Harris 1935), *S. minor* (Greenland, Liassic – Harris 1935), *S. benkertii* (Germany, Triassic/Liassic boundary – Weber 1968). Species described from Asia are also of Triassic (Norian–Rhaetian) and early Early Jurassic age (Grauvogel-Stamm 1978).

These species differ from each other mainly in scale size, as well as in length and shape of lobes. Seeds may also differ in shape and size.

Unluckily, all the specimens from Odrowąż were preserved with only the lower surface visible, so that the seeds were not observable. Reymanówna (1992) described and illustrated a specimen of *Swedenborgia* sp. from Odrowąż, and mentioned circular seed scars on the adaxial side of the scale. This specimen was unfortunately not available for the present investigation.

Identification of our material is not easy, because of its state. The morphology of the macrosporophylls from Odrowąż, their size, shape and size of lobes, and proportions between stalk and lobes, correspond best to *S. cryptomerides*. Our specimens also resemble *Swedenborgia* sp. from Iran (Schweitzer and Kirchner 1996). *S. benkertii* could be taken into consideration as well, but it is larger and its lobes are wider (size variability?). Since *Swedenborgia* scales are attributed to *Podozamites*, determination as *S. benkertii* would have been possible if the *Podozamites* leaves described above had belonged to *P. distans*.

Among other known species, *S. minor* is much smaller, *S. major* has elongated, strongly acute lobes.

Cheirolepidiaceae
Hirmeriella Hörhammer 1933
Hirmeriella muensteri (Schenk) Jung 1968
(Pl. 5, Fig. 9)

REMARKS: *Hirmeriella muensteri* occurs in large numbers in Odrowąż: shoots, male and female cones. For details see Barbacka *et al.* 2007.

GENERAL DISCUSSION ON THE FLORA AND ENVIRONMENT

The palaeoenvironment of the Odrowąż succession may be reconstructed on the basis of both macro- and microflora. The palynological study of the sediments containing the macroflora was published separately (Ziaja 2006). Sixty-three taxa of spores and pollen grains were recognised. One taxon of dispersed pollen grains (*Classopollis*) was found *in situ* in the male cone of *Hirmeriella muensteri*. Other taxa were described as dispersed sporomorphs.

Most of the plant groups represented by macroflora have corresponding taxa in the microflora. However, some taxa of the microflora do not have a macroremain counterpart, e.g., Bryophyta, some species of Lycophyta and Coniferophyta. These differences might be caused partly by bad preservation of the macroremains (more probable in the case of the Bryophyta and vegetative organs of Lycophyta), but also by transport of pollen grains by water, wind or animals (Coniferophyta) from outside (upland areas).

In the Early Jurassic, the study area was a part of a vast land area, with numerous freshwater basins; the Odrowąż succession is interpreted as a sequence deposited by a meandering river (Pieńkowski 1998).

Based on the material collected, the richness of the vegetation in the area was quite low. Out of the total number of 491 specimens examined, 15 leaf species and 4 species of reproductive organs were recognized. The quantitative relationship of the leaf species is shown in Text-fig. 2: *Pterophyllum alinae* sp. nov., *Hirmeriella muensteri* and *Neocalamites lehmannianus* dominate the assemblage. Ferns are less common but taxonomically more diverse: *Thaumatopteris brauniana*, *Todites princeps*, *Goepertella microlobus*, *Phlebopteris angustiloba* and *Todites princeps* forma *trilobata.* Rhizomes are common, but their affiliation is uncertain.

The other elements are less common. Seed ferns are represented by a single species, *Pachypteris lanceolata*; bennettites, besides the dominant species *Pterophyllum alinae* sp. nov., by *Otozamites brevifolius*; cycads by *Paracycas minuta* sp. nov.; and conifers, besides *Hirmeriella muensteri*, by rare *Podozamites* cf. *schenkii* and *Podozamites* sp. Text-figs 3 and 4 show the co-occurrence of the main vegetation elements. *H. muensteri* co-occurs with *Pterophyllum alinae* sp. nov. in most cases (59%) or occurs alone (35.8%). It is rarely associated with other elements: with *Neocalamites* 2.4%, with fern rhizomes 1.7 %, and with *Pachypteris lanceolata* 0.8%. It has never been found together with ferns (Text-fig. 3).

P. alinae sp. nov. co-occurs mostly with *Hirmeriella* (43.4%), occurs alone (23%), occurs with other subordinate species (mainly various ferns) (16.1%), with *Neocalamites* (8.8%), and with fern rhizomes (8.7%) (Text-fig. 4).

Podozamites does not occur with ferns, and *Neocalamites* usually occurs alone or accompanied by *Hirmeriella* and/or *Pterophyllum*.

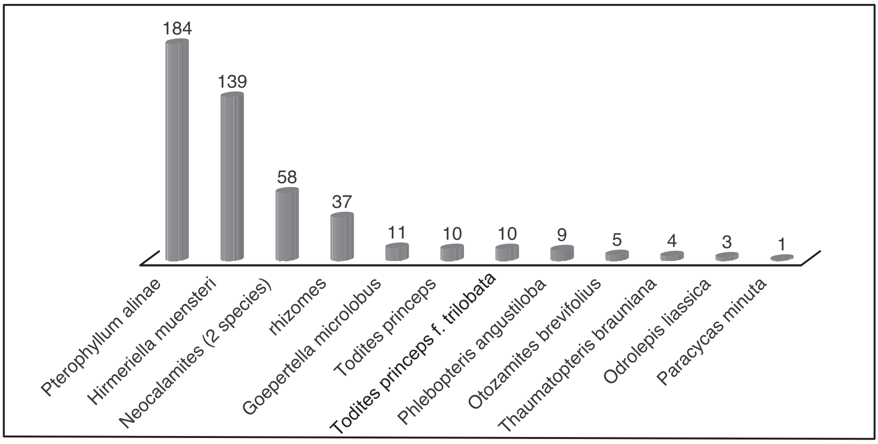
Ferns usually co-occur with *Pterophyllum*. It should be emphasised that some elements are very rare, so their relationships are uncertain. From the above comparison, *Hirmeriella* appears to have been the most specialised element in the community, growing either alone or together with *Pterophyllum*. The latter was associated with more plant taxa, commonly with *Neocalamites* and fern rhizomes, and therefore probably occupied a wider ecological niche. *Hirmeriella* might also have grown at a slightly higher level (more upland) than *Pterophyllum*; its branches etc. are quite strong and have a better preservational potential than the other species.

Fragmentation of the two dominant species is similar, with slight divergence. Fragments of both species were grouped according to their size: small, up to 20 mm long, medium, 20–30 mm, and large, more than 30 mm (Text-fig. 5). In both species, the small fragments predominate; both species show combinations of different size fragments on the same slabs, but in the large category only *Hirmeriella* reached a size above 100 mm (2 pieces).

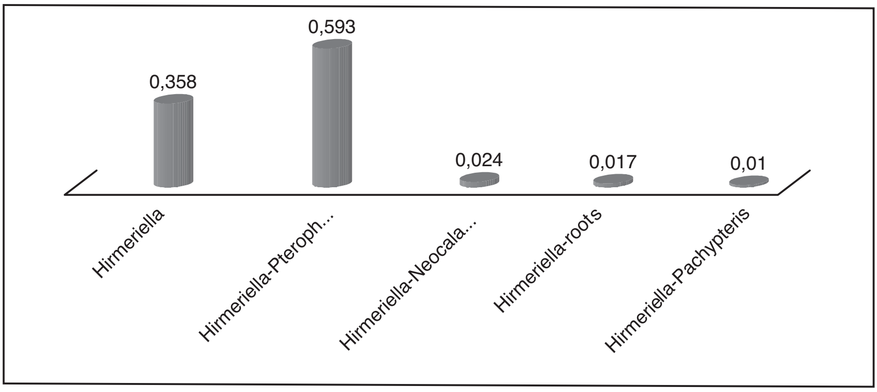
The degree of fragmentation and regular co-occurrence of both species indicate that they were transported from similar, shorter or longer distances; they possibly appeared together over quite a large area. The leaves/shoots, although broken during transport, were not damaged (lack of typical detritus).

The most significant disproportion in size of the remains is shown by the combination of large *Neocalamites* and small *Pterophyllum*, which probably is an effect of the transport of *Pterophyllum* leaves to the basin where *Neocalamites* was living.

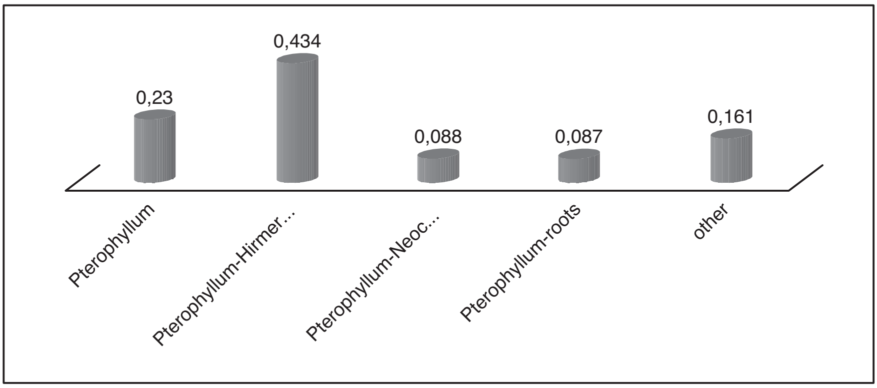
The largest fragments belong to *Neocalamites* (found also with roots preserved *in situ*) and fern rhizomes (more than 150 mm long) as well as two rare



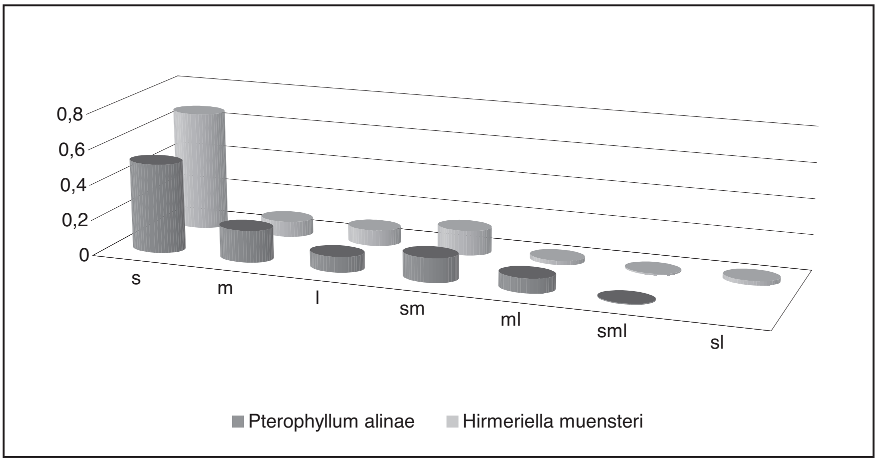
Text-fig. 2. The elements of flora from Odrowąż in quantitative values



Text-fig. 3. Co-occurrence of *Hirmeriella muensteri* (Schenk) Jung 1968, with other remains



Text-fig. 4. Co-occurrence of *Pterophyllum alinae* sp. nov. with other remains



Text-fig. 5. Percentage of different length categories in *Hirmeriella muensteri* (Schenk) Jung 1968 and *Pterophyllum alinae* sp. nov. Size categories: s-small, up to 20 mm; m-medium, between 20 and 30 mm; l-large, more than 30; and their combinations on the same slabs records: *Otozamites brevifolius* and *Pachypteris lanceolata* (110 and 85 mm long, respectively). Relatively well preserved are the conifer *Podozamites* cf. *schenkii* (about 50 mm), and the ferns *Todites princeps* (about 30 mm) and *T. princeps* forma *trilobata* (about 60 mm) even though these three forms were delicate. The other ferns occur only as small pieces of pinnae. The presence of single large fragments of leaves might indicate that they occupied the neighbourhood of the depositional basin or marshy territory near the river, where they could fossilize. The presence of secreting trichomes (of hydatode type) in both *Otozamites* and *Pachypteris* leaves and the fine structure of *Podozamites* support this hypothesis, since the structure of the trichomes converges with those of recent angiosperms living in a humid environment.

Hirmeriella and *Pterophyllum* might have formed a humid dense forest along the river bank over a large area, where *P. alinae* sp. nov.*,* due to its delicate cuticle with large stomata, might have been the understorey.

With the exceptions of *Thaumatopteris*, with usually large leaves (the pinnules of *Thaumatopteris* are narrow), the majority of species found in Odrowąż have small or narrow leaves/pinnules. The small and narrow pinnules might suggest dry conditions if they had not been so delicate. Most of the leaves, especially the ferns, *Paracycas minuta* sp. nov. and *Pterophyllum alinae* sp. nov. have thin, fine leaves with delicate cuticle. Species like *Otozamites brevifolius* and *Pachypteris lanceolata* that had a relatively thick cuticle, possessed hydatode-like structures.

Hirmeriella muensteri has long been regarded as having xeromorphic features such as the thick cuticle, protective rim around the sunken guard cells and the structure of the female cone (Reymanówna 1991a, b, 1992; Ziaja and Wcisło-Luraniec 1999; Thévenard *et al*. 2004). An alternative opinion suggests its growth in a wet environment. Alvin (1982) pointed to the wide adaptation of the Cheirolepidiaceae, from dry uplands to maritime environments, but also to growing along rivers or freshwater lakes. Clement-Westerhof and van Konijnenburg-van Cittert (1991) also agreed with the opinion that at least *H. muensteri* preferred non-arid environments. The specimens from Odrowąż have well-developed papillae at the leaf margins, especially large near the leaf apex and directed towards the top. Papillae directed to the apex also cover the surface of cones scales, particularly the male ones. According to Wilkinson (1979b), such type of papillae may have played a role in removing water from the surface of leaf/scale, which suggests an environment with a high air humidity.

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PLATES 1–5

PLATE 1

1 – *Neocalamites lehmannianus* (Goeppert) Weber, 1968; KRAM-P PM 68/1251.
2 – Diaphragm belonging probably to *Neocalamites lehmannianus* (Goeppert) Weber, 1968; KRAM-P PM 68/1101.
3 – *Odrolepis liassica* gen. et sp. nov., holotype, KRAM-P PM 68/119/I.
4-6 – *Odrolepis liassica* gen. et sp. nov., details of particular sporophylls: 4 – base, 5 – apex of sporophyll, 6 – complete sporophyll, KRAM-P PM 68/119/I.
7-8 – *Todites princeps* (Presl) Gothan, 1914; KRAM-P PM 68/1089.
9-10 – *Todites princeps* (Presl) Gothan 1914, forma *trilobata*, forma nov., KRAM-P PM 68/1097 and KRAM-P PM 68/1075 respectively.
10 – *Goepertella microloba* (Shenk) Oishi and Yamasita, 1936; KRAM-P PM 68/1008.


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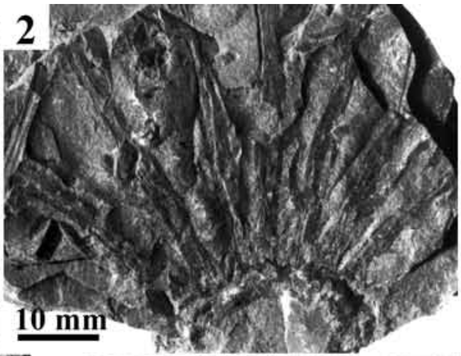
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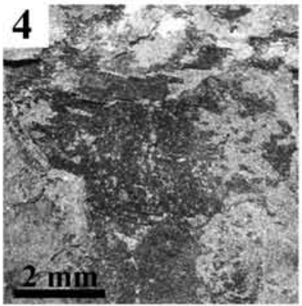
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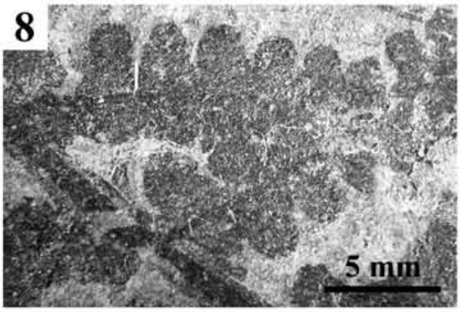
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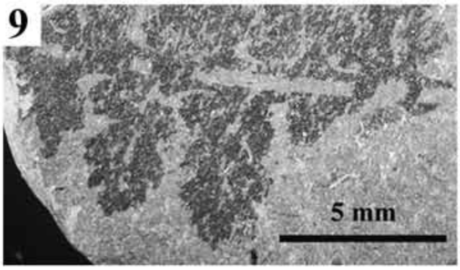
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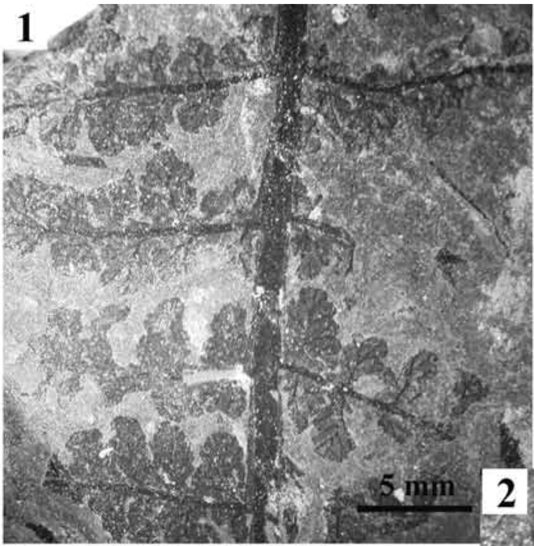
PLATE 2

1 – *Todites princeps* (Presl) Gothan 1914, forma *trilobata*, forma nov., KRAM-P PM 68/1133.
2 – *Todites princeps* (Presl) Gothan 1914, forma *trilobata*, forma nov., details of venation, KRAM-P PM 68/1133.
3 – *Phlebopteris angustiloba* (Presl) Hirmer and Hörhammer 1936; KRAM-P PM 68/155.
4 – *Goepertella microloba* (Shenk) Oishi and Yamasita, 1936; KRAM-P PM 68/1047.
5 – *Goepertella microloba* (Shenk) Oishi and Yamasita, 1936; KRAM-P PM 68/1050, fragment of pinnula, SEM picture.
6 – *Thaumatopteris brauniana* Popp 1863; KRAM-P PM 68/140 , in the corner detail of venation.
7 – Rhizome, KRAM-P PM 68/1143.
8 – *Pachypteris lanceolata* Brongniart 1828; KRAM-P PM 68/1082.
9 – *Pachypteris lanceolata* Brongniart 1828; KRAM-P PM 68/2.
10 – *Pachypteris lanceolata* Brongniart 1828; the specimen from fig. 8, upper cuticle.
11 – The same specimen as fig. 8, detail of stoma.

1



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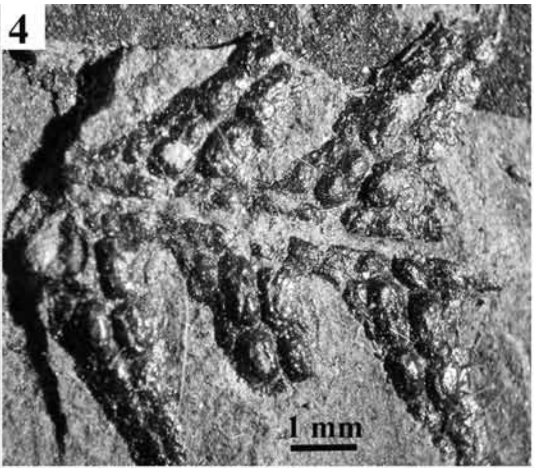

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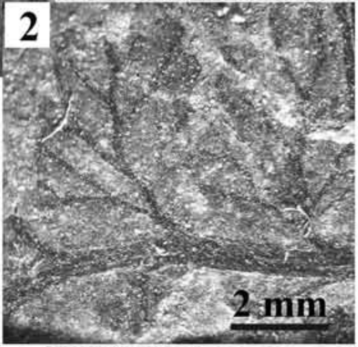

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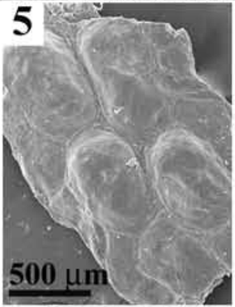

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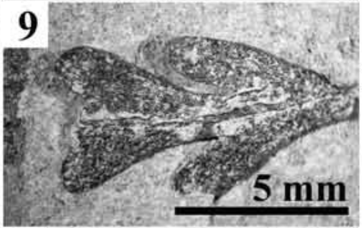

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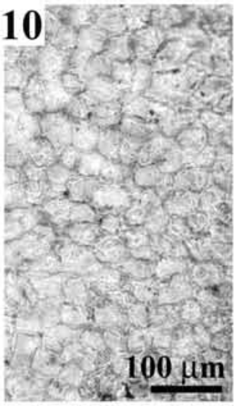

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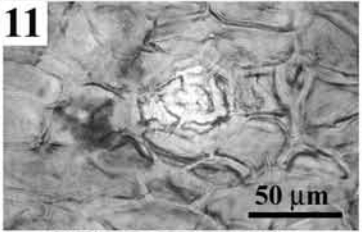

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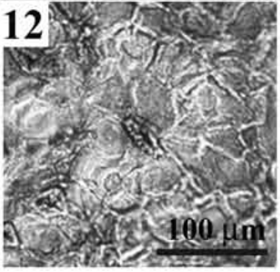

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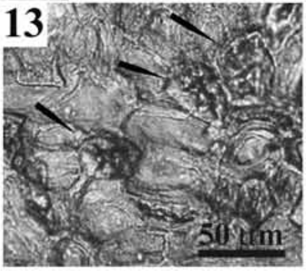
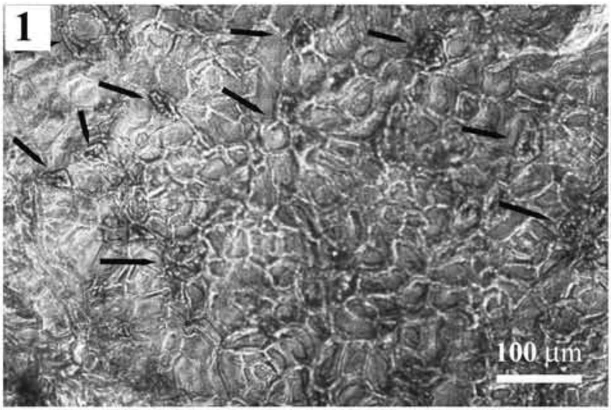


PLATE 3

1 – *Pachypteris lanceolata* Brongniart 1828; KRAM-P PM 68/1082, lower cuticle, general view, distribution of trichome basis (arrows).
2 – *Otozamites brevifolius* Braun in Muenster 1843; KRAM-P PM 68/1094.
3 – *Otozamites brevifolius* Braun in Muenster 1843; KRAM-P PM 68/284.
4 – *Otozamites brevifolius* Braun in Muenster 1843; KRAM-P PM 68/1.
5 – *Otozamites brevifolius* Braun in Muenster 1843; KRAM-P PM 68/284, lower cuticle from the pinnula margin.
6 – *Otozamites brevifolius* Braun in Muenster 1843; the same specimen as fig. 2, lower cuticle.
7 – *Otozamites brevifolius* Braun in Muenster 1843; the specimen from fig. 3, pinnula margin with secretory cells (arrows), fluorescent microscope picture.
8 – *Otozamites brevifolius* Braun in Muenster 1843; KRAM-P PM 68/284, cuticle fragment, with spherical trichome (white arrow) and stoma surrounded by papillae (black arrow), SEM picture.
9 – *Otozamites brevifolius* Braun in Muenster 1843; KRAM-P PM 68/284, detail of trichome from fig. 8, SEM picture.
10 – *Pterophyllum alinae* sp. nov., holotype, KRAM-P PM 68/1088.
11-12 – *Pterophyllum alinae* sp. nov., holotype, pinnae in natural size.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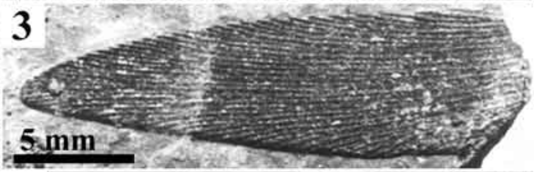
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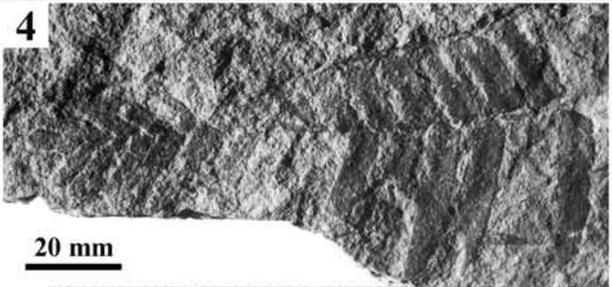
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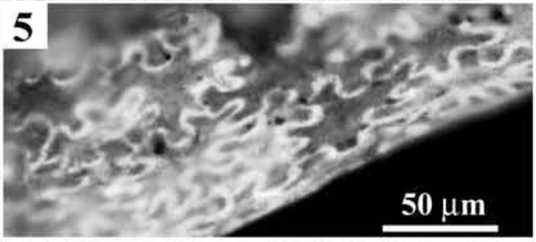
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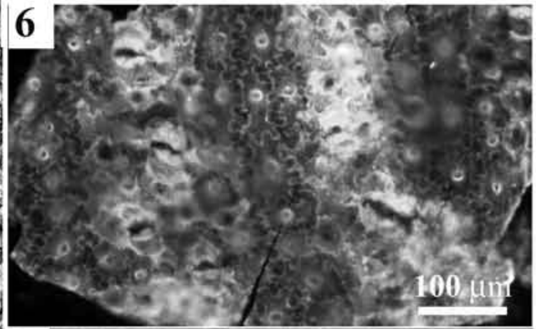
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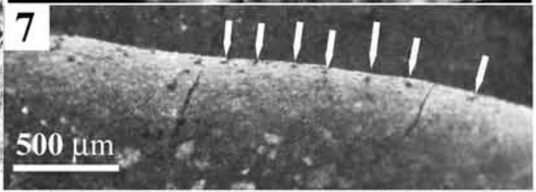
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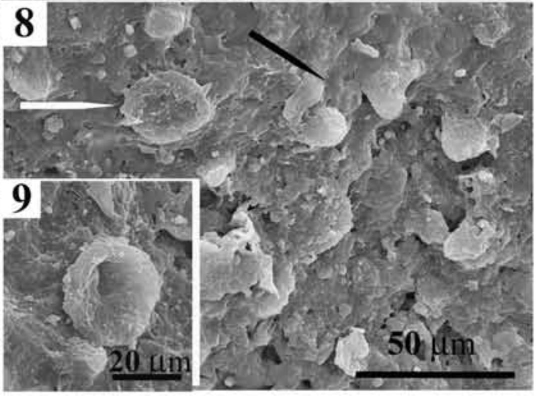
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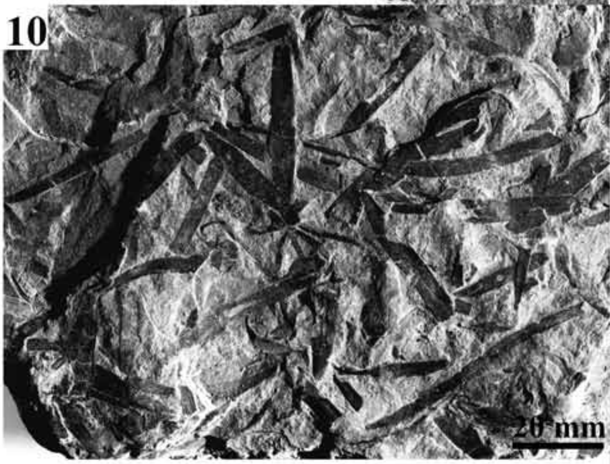
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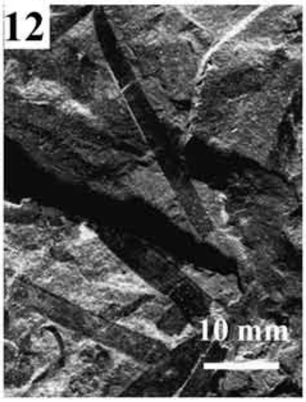
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PLATE 4

1 – *Pterophyllum alinae* sp. nov., holotype, KRAM-P PM 68/1088, lower cuticle with stomata.

2 – *Pterophyllum alinae* sp. nov., holotype, lower cuticle with unusually irregular cells.

3 – *Pterophyllum alinae* sp. nov., holotype, upper cuticle.

4 – *Pterophyllum alinae* sp. nov., stoma, detail from fig. 1.

5 – *Paracycas minuta* sp. nov., holotype, KRAM-P PM 68/293, in the corner natural size.

6 – *Paracycas minuta* sp. nov., holotype, upper cuticle, KRAM-P PM 68/293.

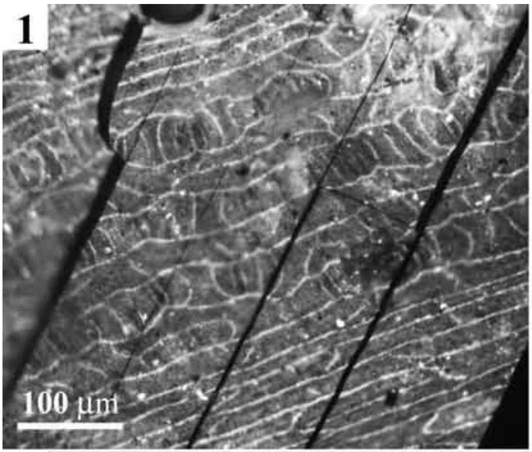
7 – *Paracycas minuta* sp. nov., stoma with papillae on the lower cuticle, holotype, KRAM-P PM 68/293.

8-9 – *Piroconites kuespertii* Gothan 1914; KRAM-P PM 68/233.

10 – *Piroconites kuespertii* Gothan 1914; fluorescent microscope picture of the section of compressed synangia, light stripes are cuticle layers, KRAM-P PM 68/233.

11 – *Piroconites kuespertii* Gothan 1914; the thin cuticle from the surface of synangium, fluorescent microscope picture.

1



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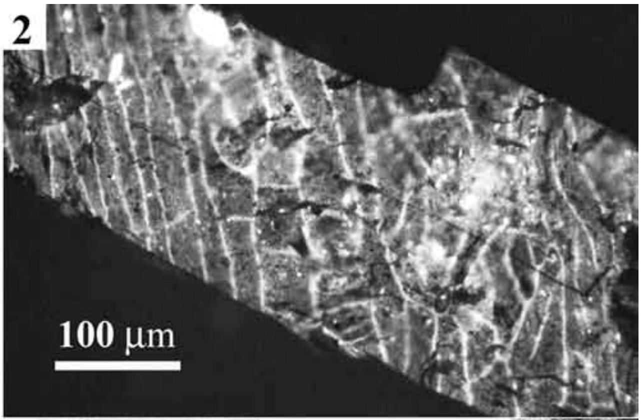

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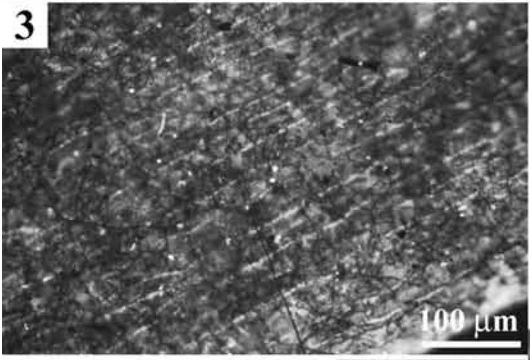

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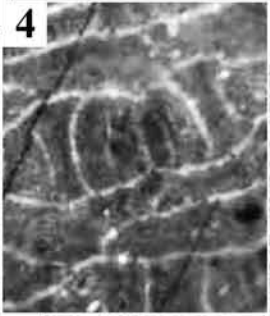

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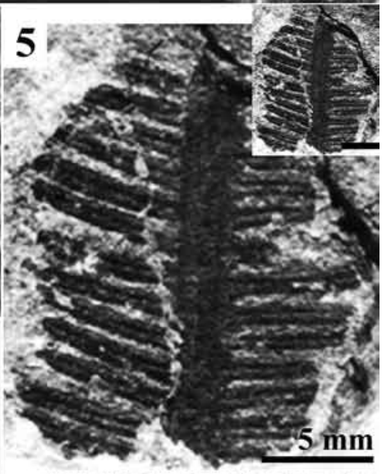

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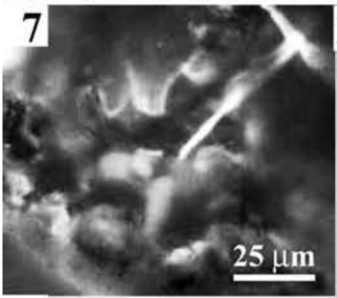

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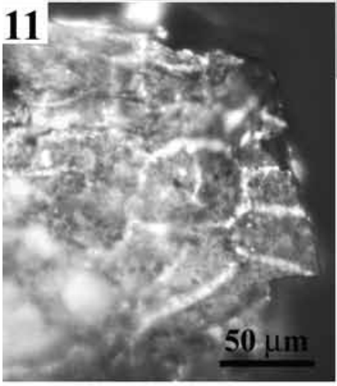

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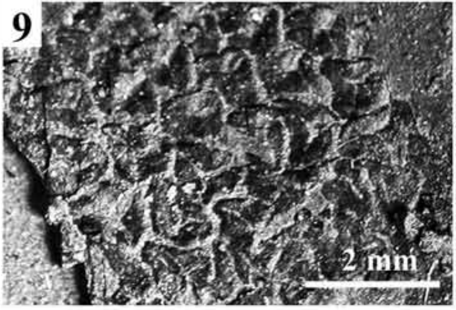

PLATE 5

1, 4 – *Schmeissneria microstachys* (Presl) Kirchner and van Konijnenburg-van Cittert 1994; KRAM-P PM 68/1126; 4 – detail of base.
2 – *Podozamites* cf. s*chenkii* Heer 1876; KRAM-P PM 68/141.
3 – *Podozamites* sp., KRAM-P PM 68/109.
5 – Upper cuticle, fluorescent microscope picture, specimen from fig. 1.
6 – Lower cuticle, fluorescent microscope picture, specimen from fig. 1.
7 – *Swedenborgia cryptomerides* Nathorst 1876; KRAM-P PM 68/276/I.
8 – *Swedenborgia cryptomerides* Nathorst 1876; KRAM-P PM 68/274/I.
9 – *Hirmeriella muensteri* (Schenk) Jung 1968; 68/3036.


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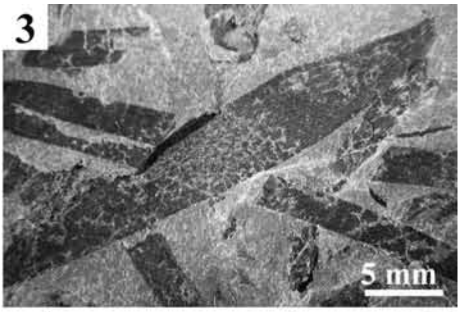
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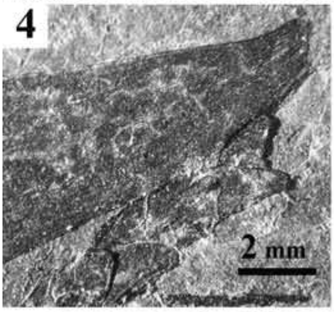
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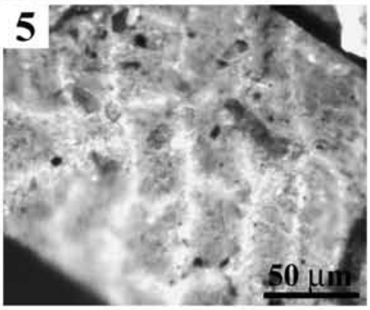
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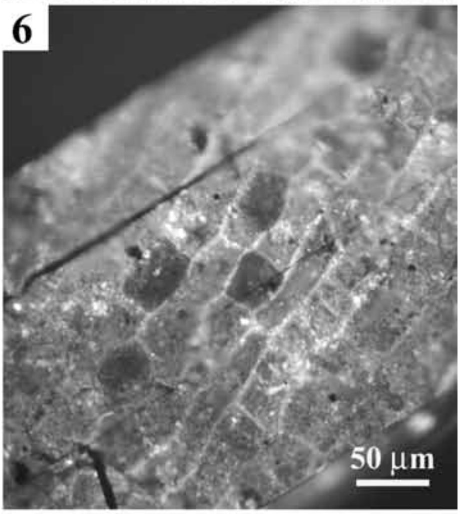
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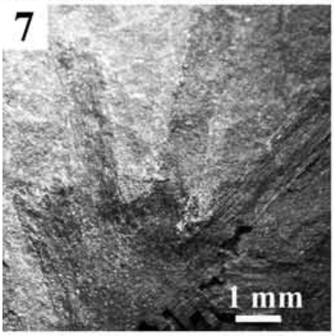
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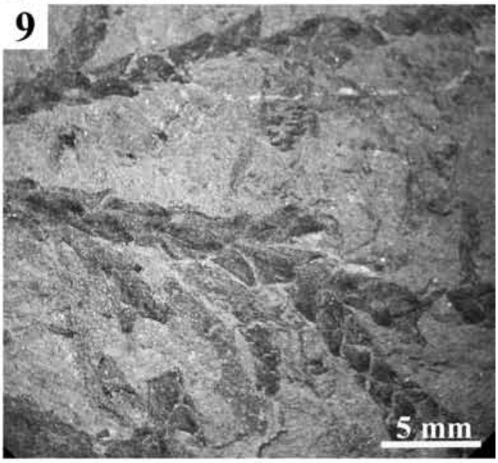
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