MARATTIOPSIS VODRAZKAE SP. NOV. (MARATTIACEAE) FROM THE CAMPANIAN OF THE HIDDEN LAKE FORMATION, JAMES ROSS ISLAND, ANTARCTICA.

JIŘÍ KVAČEK
National Museum, Prague, Department of Palaeontology, Václavské nám. 68, 115 79 Praha 1, the Czech Republic; e-mail: jiri.kvacek@nm.cz

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Abstract. A new fossil eusporangiate fern *Marattiopsis vodrazkae* J. Kvaček, sp. nov. has been recovered from the Hidden Lake Formation, the Campanian of James Ross Island, Antarctica. Its fertile and sterile pinnules are described and compared to the other species of the fossil genus *Marattiopsis* Schimper and the living genera *Marattia*, *Ptisana* and *Eupodium* (Marattiaceae). In contrast to the other species of the genus *Marattiopsis, M. vodrazkae* is characterised by stalked synangia, a smaller number of sporangia per synangium, generally small sized pinnules, and the absence of *venuli recurrentes*. It shows a mosaic of characters present in the living Marattiaceae: it shares stalked sporangia with the genus *Eupodium* and some species of *Marattia* and exhibits a suture (an abscission scar at pinnule bases), a character typical for the genus *Ptisana*. Additionally, *M. vodrazkae* provides important palaeoenvironmental signals for climate reconstructions, arguing for warm (paratropical to warm-temperate) and humid climatic conditions on the Antarctic Peninsula and adjacent volcanic islands during the Campanian.

■ Marattiaceae, Campanian, Cretaceous, James Ross Island, Antarctica

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Introduction

Ferns of the family Marattiaceae belong to the most ancient groups of pteridophytes. They represent an early diverging group of eusporangiate ferns (e.g. Smith et al. 2006, Taylor et al. 2009) with several genera having records extending into the mid-Carboniferous (Millay 1990). The most remarkable synapomorphies of the marattioids are large, thick walled sporangia fully or partially fussed into synangia (Murdock 2008).

The extensive fossil record of the Marattiaceae comes particularly from the Permian, Triassic and Jurassic strata of Europe (e.g. Lundblad 1950, Harris 1961, van Konijnenburg van Citter 1975), and Asia (e.g. Kawasaki 1939, Kilpper 1964, Hill et al 1985, Schweitzer et al. 1997, Wang 1999). Their occurrences in the Southern Hemisphere are restricted to Argentina (e.g. Arrondo and Petriella 1980, Escapa et al. 2014), Brazil (Tavares et al. 2014) and Antarctica (Delevoryas et al. 1992). Since the Cretaceous their fossil record is much reduced (e.g. Collinson 2001). Therefore the record described in this paper of the Marattiaceae from the Late Cretaceous of Antarctica is of particular interest.

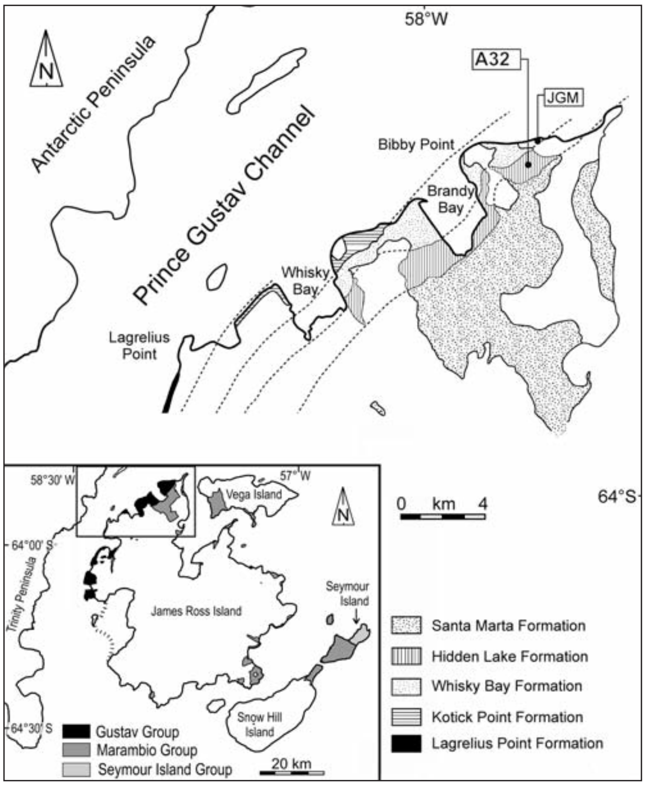
Material and methods

The studied material is derived from the Late Cretaceous locality on James Ross Island (Kvaček and Sakala 2012, Sakala and Vodrážka 2014). The material comes from the Hidden Lake Formation of the Gustav Group in the Larsen Basin, sometimes termed the James Ross Basin (Elliot 1988). The basin was formed as a back-arc basin during Late Mesozoic - Early Cenozoic (e.g., Hathway 2000). Sediments of the Hidden Lake Formation occur in the north-western part of James Ross Island (Text-fig. 1). The formation represents the lowermost unit of the Gustav Group (Whitham et al., 2006). It consists of a 400 m thick layer of coarse-grained volcanoclastic conglomerates, sandstones, siltstones and mudstones (Whitham et al. 2006). The sand-dominated sediments are interpreted as deposits of a shallow marine deltaic environment within a fan delta shelf setting (Elliot 1988, Pirrie 1991). Palaeontological and Sr-isotope data suggest a Coniacian age for the formation (e.g. McArthur et al. 2000, Riding and Crame 2002, Crame et al. 2006).

The flora of the Hidden Lake Formation is dominated by angiosperms (Hayes et al. 2005, Cantrill and Pool 2012, Sakala and Vodrážka 2014). However, pteridophytes are also well represented (Kvaček and Sakala 2012). A preliminary description of the Hidden Lake Formation flora is in preparation by the present author (Kvaček and Vodrážka in prep.).

This study is based on the collections gathered during austral summer seasons between December 2008 – March 2009 by the present author and between January – March 2010 by Radek Vodrážka (CGS), whilst at the Czech Antarctic Johann Gregor Mendel Research Station (63° 48' 5.6" S, 57° 53' 5.6" W) situated on the northern coast of James Ross Island. The material is housed in the Czech Geological Survey (CGS) and the Instituto Antártico Argentino (IAA) in Buenos Aires.

The studied specimens were photographed using a Canon EOS 6D camera with a Canon 100 macro lens and Olympus



Text–fig. 1. Geographical and geological situation in the James Ross Island region. The locality No. 32 and the position of the Johann Gregor Mendel Czech Antarctic Station (JGM) are indicated. Modified from Sakala and Vodrážka (2014).

SZX 12 stereomicroscope equipped with an Olympus DP 72 camera. Details of fossil and recent synangia and spores were documented using a Hitachi S 3700-N SEM in low vacuum mode.

Systematic palaeobotany

Family **Marattiaceae** KAULF.

Genus: ***Marattiopsis*** **SCHIMPER 1869**

Type: *Marattiopsis crenulata* LUNDBLAD 1950, typ. cons. prop. (Bomfleur et al. 2013).

D i s c u s s i o n . Earlier records of Triassic and Jurassic members of the Marattiaceae were described under the name *Marattiopsis* SCHIMPER or the recent genus *Marattia* SW. s.l. However, the latter genus in its earlier sense has been identified as polyphyletic (Murdock 2008) and therefore subdivided into three genera *Marattia* SW *s. s.*, *Ptisana* MURDOCK and *Eupodium* (J. SM.) HOOKER. Due to this fact Bomfleur et al. (2013) reintroduced the genus *Marattiopsis* SCHIMPER for the fossil material which could not be assigned unequivocally to either *Marattia*, *Ptisana* or *Eupodium*.

Marattiopsis vodrazkae J. Kvaček, sp. nov.

Pl. 1, figs 1–10, Pl. 2, figs 1, 2

H o l o t y p e: CGS No. AN 491 (pl. 1, figs 1–3) designated here.

P a r a t y p e: CGS No. AN 493 (pl. 1, fig. 7) designated here.

T y p e l o c a l i t y: A32-2; James Ross Island, Antarctica.

T y p e h o r i z o n: Coniacian, Late Cretaceous, Hidden Lake Formation.

E t y m o l o g y: After my colleague Radek Vodrážka who intensively collected fossils on James Ross Island in the period 2009-2011.

O t h e r m a t e r i a l: James Ross Island, Antarctica locality A32-2: AN 492, AN 495, AN 506ab (CGS); IAA 005-008, IAA 022; locality A32-1: IAA 083; locality A32-3: IAA 043.

D i a g n o s i s. Isolated pinnules oblong to oblong-lanceolate, tapering gradually towards the apex; base with basiscopic auricle and short petiolule; apex acute, pinnule margins varying from undulate, denticulate to dentate, venation simply pinnate, eucamptodromous consisting of one vein order. Lateral veins commonly forking immediately at, or near, the midrib, leaving the midrib at an acute angle. Synangia shortly stalked consisting of two deeply divided valves. Each valve consisting of 5–6 sporangia. Spores *in situ* monolete, granular to delicately rugate.

D e s c r i p t i o n . The holotype (Pl. 1, fig. 1) is an exceptionally well preserved specimen showing two synangia born on a pinnule fragment (40 x 50 mm). One synangium is broken longitudinally, another one perpendicularly (Pl.1, fig. 1). The synangia are arranged in the central part of the pinnule lamina (Pl. 1, fig. 2). The longitudinally broken synangium (Pl. 1, fig. 3) shows an elliptic valve with six sporangia. The valve is 1.6 mm long and 1 mm high. Each sporangium is elongate ovoid, 1 mm long and 0.2–0.5 mm in diameter. The synangium length occupies about 20–35% of the pinnule width (Pl.1, fig. 1). In the transversal section the synangium is deeply divided into two valves, bilaterally symmetrical and spindle-shaped. The valves are erect, ovate, pointed in apical parts. Both valves are born on a short common stalk 0.2 mm in length (Pl. 1, fig. 1). The sporangium walls consist of elongate cells (Pl. 2, fig. 1). Spores *in situ* 25–32 μm in diameter are probably not mature. They are tightly pressed together and arranged in diades (Pl. 2, fig. 2). They are monolete, ellipsoid in equatorial outline showing a granular, rugate exospore (Pl. 2, fig. 2).

The lamina fragment of the holotype shows the same venation pattern and dentate margin as other isolated pinnules. Sterile material is typified by the paratype (Pl. 1, fig. 7) showing an oblong-lanceolate sterile pinnule nearly 20 mm in length with a vein density of 14 veins per cm. Its base is asymmetrical with a relatively well pronounced basiscopic auricle. Venation of each pinnule is pinnate, the robust main midrib reaching the pinnule apex. Robust lateral veins in basal and medial parts of the pinnule fork immediately at, or near, the midrib. Each lateral vein terminates in a tooth. Paired veins unite two adjacent teeth into pairs which form a characteristic double dentate pattern (see Pl. 1, fig. 7).

Other material comprises a number of isolated pinnules. The fertile pinnules (IAA 006, 007) usually do not have preserved synangia (Pl. 1, fig. 10). However, their scars or impressions show an arrangement of six to ten synangia in

Table 1. Comparison of species diagnostic characters of the genus *Marattiopsis*.

taxon	Diagnostic characters						
	pinnule base	pinnule margin	no. of veins per cm	*venuli recurrentes*	synangium length/ pinnule width	no. of sporangia pairs per synangium	reference
M. aganzhenensis (Yang et al) Escapa, Bomfleur, Cuneo, Scasso	rounded	entire	10–16	absent	12.5	20	Yang et al. 2008
M. anglica Thomas	contracted and rounded	entire	10–12	not known	33	30	van Konijnenburg-van Cittert 1975
M. angustifolia Prynada	unknown	entire-undulate	13	present	25	unknown	Prynada 1938
M. asiatica Kawasaki	rounded	entire-undulate	13–16	present	17	10–40	Kawasaki 1939
M. barnardii (Schweitzer, van Konijnenburg – van Cittert, van der Burgh) Escapa, Bomfleur, Cuneo, Scasso	cordate, slightly auriculate	undulate-serrate	8–14	absent	20–30	8–16	Schweitzer et al. 1997
M. crenulata Lundblad	unknown	crenulate-undulate	9	present	5–6	10	Lundblad 1950
M. curvinervis (Lorch) Escapa, Bomfleur, Cuneo, Scasso	unknown	unknown	26–34	present	20–33	unknown	Lorch 1967
M. hoerensis Schimper (Schimper) Schimper	asymetrically auriculate	entire-dentate	8–14	present	20	unknown	Schimper 1869
M. intermedia (Münster) Weber	unknown	unknown	12–16	unknown	unknown	unknown	Weber 1968
M. muensteri (Göppert) Schimper	rounded	entire	10	present	10–20	uknown	Schimper 1869
M. patagonica Escapa, Bomfleur, Cuneo, Scasso	asymetrically auriculate	undulate-serrulate	8–16	present	12–20	8–20	Escapa et al. 2014
M. vodrazkae sp. nov.	asymetrically auriculate	serrate, undulate	10–14	absent	20–35	5–6	Kvaček herein

three to five pairs per pinnule. They were born on lateral veins nearby the midrib (Pl. 1, fig. 10). With respect to the sterile pinnules, a completely preserved pinnule is invaluable , with a low vein density (10 veins per cm), a denticulate - undulate margin, asymmetrical auriculate base and acute apex (Pl. 1, fig. 8). Further material (Pl. 1, fig. 4) displays pinnule fragments (18 x 8 mm) showing a nearly symmetrical, slightly cordate base with a delicate fragment of petiolule and fragmentarily preserved apex. Marginal teeth are blunt, inconspicuous forming an undulate margin. The specimen AN 506a (Pl. 1, fig. 5) shows an undulate-denticulate margin and asymmetrically auriculate base with a well pronounced short petiolule. The specimen AN 495 shows an apical fragment of a pinnule with bifurcating terminal part of the midrib (Pl. 1, fig. 6). The specimen IAA 008 shows a well preserved asymmetrical auricule with a suprabasal vein bent backwards (Pl. 1, fig. 9).

D i s c u s s i o n. *Marattiopsis vodrazkae* is known only from the Hidden Lake Formation on James Ross Island. It is unusual within the genus in having remarkably smaller pinnules than the rest of the *Marattiopsis* species. However, its typical type of sporangia forming synangia and the characteristic occurrence of only isolated pinnules with basiscopic auricles argue for inclusion of this material into the genus *Marattiopsis*.

The type species *Marattiopsis crenulata* LUNDBLAD from the Triassic of Sweden (Lundblad 1950) proposed by Bomfleur et al (2013) differs from the present material in having marginally arranged synangia and remarkably larger sized pinnules. It also differs in lacking short stalked synangia.

Yang (et al 2008) and Esacpa (et al 2014) suggested a list of diagnostic characters which can help us compare *M. vodrazkae* sp. nov. with the other species of the genus. The characters are in particular the type of pinnule margin, vein density, presence or absence of *venuli recurrentes*, number of septa per sporangium and ratio of synagium length to pinnule width (Tab. 1). *M. vodrazkae* differs from all of the listed species in several important characters. It has short stalked synangia, 5–6 septa pairs per synangium and remarkably small pinnules. As it is clear from Table 1 *M. vodrazkae* differs from *Marattiopsis aganzhenensis* (YANG, WANG, PFEFFERKORN) ESCAPA, BOMFLEUR, CUNEO, SCASSO. from the Early Jurassic of China (Yang et al. 2008) and *M. anglica* THOMAS from the Jurassic of Great Britain (van Konijnenburg van Cittert 1975) in absence of entire margined pinnules, round, symmetrical base and lower number of sporangia per valve. *M. vodrazkae* differs from *M. angustifolia* PRYNADA from the Jurassic of Russia (Prynada 1938) and *M. asiatica* KAWASAKI from the Triassic of Korea, Japan, Vietnam and China (Kawasaki 1939, Wang 1999), from *M. curvinervis* (LORCH) ESCAPA, BOMFLEUR, CUNEO, SCASSO from the Jurassic of Israel (Lorch 1967), from *M. hoerensis* (SCHIMPER) SCHIMPER from the Triassic of Sweden (Schimper 1869), from *M. muensteri* (GÖPPERT) SCHIMPER from the Rhaeto-Liassic of Germany, from *M. intermedia* (MÜNSTER) WEBER from the Rhaeto-Liassic of Bayreuth (Weber 1968) and from *M. patagonica* ESCAPA, BOMFLEUR, CUNEO, SCASSO from the Early Jurassic of Argentina (Escapa et al. 2014) in the absence of *venuli recurrentes* and lower number of sporangia per valve. *M. vodrazkae* differs from *M. barnardii* (SCHWEITZER, VAN KONIJNENBURG – VAN CITTERT, VAN DER BURGH) ESCAPA, BOMFLEUR, CUNEO, SCASSO from the Rhaeto-Liassic of Iran (Schweitzer et al. 1997) in having a lower number of sporangia per valve, more asymmetrical bases and smaller size of pinnules. Those species of

Marattiopsis based on sterile foliage only are not compared with *M. vodrazkae* due to lack of the important synangia characters .

Comparison with extant material

Within extant taxa, *M. vodrazkae* shares characters with all three species assigned previously to *Marattia* s. l. – *Eupodium*, *Ptisana* and *Marattia* s.s. It shares stalked synangia with the genus *Eupodium*. However, *M. vodrazkae* is most similar to the latter genera *Ptisana* and *Marattia* s.s. The presence of a mosaic of characters present in both the above genera does not allow its attribution to either *Ptisana* or *Marattia*. Within the genus *Marattia* s.s. the species *Marattia douglasii* (Pl. 2, figs 3, 4, 8) shows very similar pinnules with the same pattern of marginal teeth (notably the tendency to form double teeth), but its sporangia are compact and show only shallow dissection. On the other hand, some species of *Marattia* s.s. e.g. *M. cicutifolia* have short stalked synangia as does *M. vodrazkae* (Murdock 2008). *M. vodrazkae* seems to be most similar to some species of the genus *Ptisana* in having a very similar type of synangia. Also the presence of sutures (abscission scars) at the pinnule bases, characteristic of all species of *Ptisana,* argues for a closer relationship. The latter character is an interpretation of the fact that the pinnules of *Marattiopsis* always occur as fragmented isolated pinnules (Escapa et al. 2014). *Ptisana sylvatica* (Pl. 2, figs 5–7) shows deeply dissected synangia possessing the same shape and size as *Marattiopsis vodrazkae* (compare Pl. 2, fig. 1 and fig. 5). However, pinnules of *P. sylvatica* have a serrulate margin and simple veins, characters which are not present in *M. vodrazkae*. This mosaic of characters of both *Marattia* s.s and *Ptisana* present in *M. vodrazkae* resulted in a decision to assign the material to the rather broadly understood genus *Marattiopsis.*

Palaeoclimatic and palaeoecological remarks

M. vodrazkae might be a quite useful climate indicator for the Hidden Lake Formation. It can be used as an important taxon for the NLR method and provides parallel proxy data in addition to CLAMP analysis published by Hayes et al. (2005). From their data, mean annual temperature (MAT) for the Hidden Lake Formation is 13–21°C (mean 17°C) and annual precipitation 594–2142 mm.

Recent members of the family Marattiaceae are typical elements of tropical rain forests (Murdock 2008). However, some species also occur in paratropical, very rarely maritime warm temperate climates (Christenhusz 2007, fig. 2). Tropical to paratropical climates are generally reconstructed also for fossil species of the Marattiaceae (Escapa et al. 2014).

As an example of the extremely cool climate tolerated by the Marattiaceae is the maritime warm temperate climate of New Zealand (MAT to 10–16°C, NIWA 2014). The northern island of New Zealand hosts the marattioid fern *Ptisana salicina*. This is the only species of the family present in New Zealand. In a preliminary reconstruction, one might assume that this example could be the closest possibility for reconstruction of climate conditions of the Hidden Lake Formation. This assumption is in concert with conclusions of Hayes et al. (2005) who interpreted the climate of the Hidden Lake Formation as warm temperate (MAT 17°C). Also their rather controversial estimates of high precipitation (annual precipitation of up to 2142 mm, Hayes et al. 2005) appear to be more realistic in the light of typical environments for marattioid ferns.

The palaeoecology of the Hidden Lake Formation flora is not yet fully understood. From preliminary studies summarised in Cantrill and Pool (2012) and reports by Kvaček and Sakala (2012), Kvaček and Vodrážka (in prep.) the vegetation can be reconstructed as warm temperate to paratropical forest rich in fern and bryophyte understory. The above mentioned palaeoclimatic proxy data (Hayes et al. 2005), presence of numerous bryophytes and ferns, including Marattiaceae, strongly argue for rain forest either warm temperate, or paratropical growing on the Antarctic Peninsula during the Campanian.

Conclusions

A new species, *Marattiopsis vodrazkae* J. Kvaček sp. nov., is erected to accommodate isolated fertile and sterile pinnules of marattioid fern material from the Campanian Hidden Lake Formation. It is recognised in having dentate-undulate pinnules with simple pinnate venation and deeply dissected short stalked synangia consisting of 5–6 pairs of sporangia. The present paper reports on the only known megafossil of the Cretaceous *Marattiopsis* in Antarctica. Most other species of *Marattiopsis* differ from the studied material in having sessile synangia or of unknown position, higher number of sporangia per synangium and much larger and elongate pinnules. In general morphology of the pinnules and the number of sporangia per synangium *Marattiopsis vodrazkae* remains close to the species of the recent genera *Ptisana* and *Marattia* s.s. and may represent a stem group of those marattioid ferns.

The occurrence of *M. vodrazkae* has quite important climatic and ecological significance. It confirms predicted estimates for the climate of the Hidden Lake Formation by earlier authors (Hayes et al. 2005) and suggests warm temperate to paratropical rain forest as a possible type of reconstructed vegetation for this part of Antarctica.

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Explanations of the plates

PLATE 1

Marattiopsis vodrazkae J. Kvaček, sp. nov., James Ross Island, Hidden Lake Formation

1. Holotype showing transversely broken synangium born on a dentate leaf, AN 491, scale bar 1 mm.
2. Holotype fragment of dentate leaf bearing synangia, AN 491, scale bar 3 mm.
3. Longitudinally broken synangium, holotype, AN 491, scale bar 1 mm.
4. Pinnule with cordate base and undulate margin, IAA 005, scale bar 5 mm.
5. Small complete pinnule with undulate margin, AN 511b, scale bar 3 mm.
6. Apical part of pinnule, AN 495, scale bar 3 mm.
7. Paratype, pinnule with double dentate margin, AN 493, scale bar 4 mm.
8. Complete pinnule with serrate margin and simple venation, IAA 022, scale bar 5 mm.
9. Pinnule with serrate margin, IAA 008, scale bar 4 mm.
10. Pinnule with undulate margin and remains of partly detached synangia, IAA 007, scale bar 4 mm.

PLATE 2

Marattiopsis vodrazkae J. Kvaček, sp. nov., James Ross Island, Hidden Lake Formation

1. Detail of synangium, holotype, AN 491, scale bar 250 μm.
2. Spores (arrowed), holotype, AN 491, scale bar 50 μm.

Marattia douglasii (C. Presl) Baker, Hawai (Rosenstock 91, coll. NMP)

3. Synangium, scale bar 50 μm.
4. Monolete spores, scale bar 20 μm.
5. Pinnule showing double dentate margin, scale bar 5 mm.

Ptisana sylvatica (Blume) Murdock, Cameroun, (Kurz 338, coll. NMP)

6. Synangium, scale bar 50 μm.
7. Pinnule showing serrulate margin, scale bar 5 mm.
8. Monolete spores, scale bar 20 μm.

PLATE 1

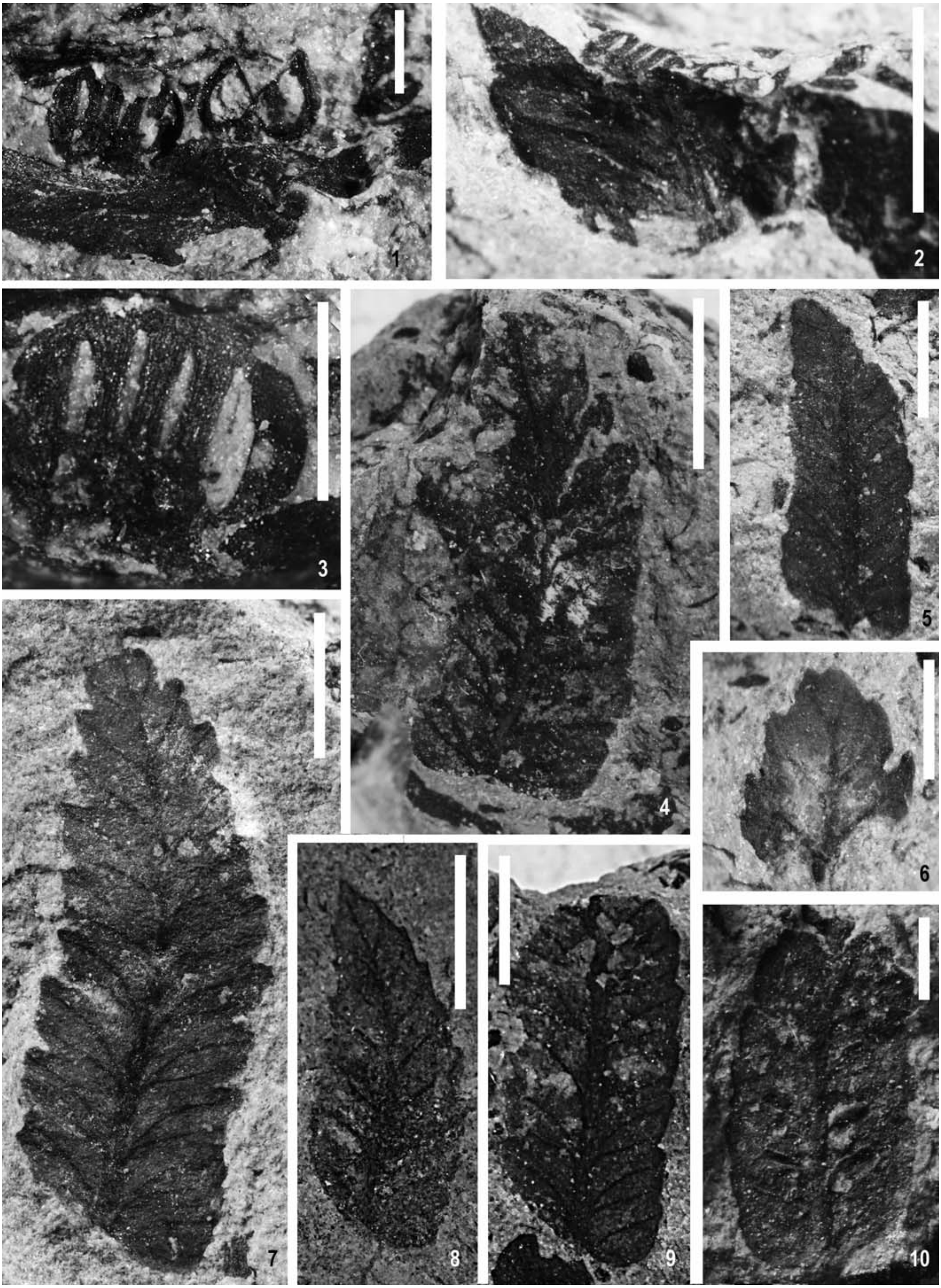

PLATE 2