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MATONIACEAE

(Masahiro Kato, Tokyo, Japan)

Matoniaceae C. Presl, Gefässb. Stipes Farrn (1847) 32; Copel., Gen. Fil. (1947) 173; Holttum, Revis. Fl. Malaya 2 (1955) 58; K.U. Kramer in Kubitzki (ed.), Fam. & Gen. Vasc. Pl. 1 (1990) 183.

Rhizomes creeping, dorsiventral, polycyclic-solenostelic, densely covered by light-brown or brown hairs. *Leaves* alternate on the dorsal side of rhizome; stipes polished, glabrous; lamina either pedate with pectinate pinnae, or alternately pinnate with pinnae consisting of resting buds or bud-derived leaflets and linear, simple or forked pinnules; veins free or anastomosing in soriferous parts. *Sori* round or elliptic, in one row on either side of costule or midrib; indusia thick-stalked, peltate, thick in central portion and membranous and inrolled in marginal portion; sporangia in one or a few layers around receptacle, consisting of short, thick stalk and capsule with incomplete oblique annuli. *Spores* tetrahedral, trilete. Gametic chromosome number n = 25 or 26.

DISTRIBUTION

The family *Matoniaceae* is restricted to Malesia.

HABITAT AND ECOLOGY

The family has two markedly different ecological preferences: *Matonia* grows in more or less open places in often mossy mountain ridges or summits, and *Phanerosorus* on vertical walls of limestone rocks or caves.

TAXONOMY AND AFFINITY

The family shows a unique combination of vegetative and reproductive characters, and affinities to other families are remote and uncertain. Molecular data suggest that *Matoniaceae*, like other primitive families, diverged near the base of a phylogenetic tree of leptosporangiate ferns [Hasebe et al., Proc. Acad. Nat. Sc. USA 91 (1994) 5930–5934]. The family consists of two genera, *Matonia* and *Phanerosorus* which are distinct in leaf organization and also differ in sori, sporangia, spores, and gametophytes. The leaves of *Phanerosorus* resemble those of young plants of *Matonia* [Tansley & Lulham, Ann. Bot. 19 (1905) 475–519].

FOSSILS

Fossils of 11 or more genera are known from the Upper Triassic and Upper Cretaceous. In contrast to the present narrow range, they were widely distributed throughout the world: Eurasia, Australia including Tasmania, Africa and Madagascar, North and South Americas, and Greenland. Fossil leaves resemble those of extant *Matonia*.

KEY TO THE GENERA

1a. Leaves pedate; pinnae pectinate ..... **Matonia** *(p. 290)*
b. Leaves pinnately compound; pinnae bearing resting buds or bud-derived leaflets; pinnules linear, simple or forked ..... **Phanerosorus** *(p. 292)*

MATONIA

Matonia R. Br. in Wall., Pl. Asiat. Rar. (1829) 16, t. 16; Copel., Gen. Fil. (1947) 172; Holttum, Revis. Fl. Malaya 2 (1955) 59, f. 13; K.U. Kramer in Kubitzki (ed.), Fam. & Gen. Vasc. Pl. 1 (1990) 183, f. 95, 96; M. Kato, Blumea 38 (1993) 167–172. — Type species: *Matonia pectinata* R. Br.

Rhizomes creeping, branched, tricyclic-solenostelic, densely hairy, hairs brown, multicellular, uniseriate, up to 5 mm long. *Leaves* borne alternately in two rows on the dorsal side of rhizome; stipe brown to chestnut-brown, hairy at base, glabrous above, much longer than lamina; lamina umbrella-like and perpendicular to stipe, pedate with a central pinna, coriaceous; pinnae 10–30, pectinate, deeply lobed, linear, marginal pinnae shorter; costae glabrous or hairy underneath; pinna-segments linear-oblong, entire, polished on the adaxial surface, often glaucous, papillate on the abaxial surface; veins forming costal areoles, forked, usually free or sometimes weakly anastomosing in sterile portions of segments, regularly anastomosing in soriferous portions (sori supplied by 5–7 veinlets branched from circular veins). *Sori* round, in one row along each side of costa or midrib; indusia 1–1.1 mm in diam., peltate, hemispherical, thick in central portion and membranous and inrolled in marginal portion, margin 0.4 mm broad; sporangia 5–10 in one layer; capsules globose-polygonal; annuli meandering. *Spores* tetrahedral, trilete, pale. — **Fig. 1a–c.**

Distribution — *Malesia.*

Taxonomy — Two species. In Blumea 38 (1993) 167–172 a statistical analysis is given the outcome of which justifies their separation.

Habitat & Ecology — In open places often in clearings, and in and at edge of mossy forest on mountain ridges or summits; from lowland to mountain.

Chromosome number — According to Manton in Holttum, Ferns of Malaya (1955), n = 26.

Gametophytes — The gametophytes grown in culture are massive, with a thick central cushion and much folded, glabrous wings on both sides of it. Antheridia and archegonia are massive, composed of many cells, and of a primitive type. See Stokey & Atkinson, Phytomorphology 2 (1952) 138–150.

KEY TO THE SPECIES

1a. Number of pinnae 19 or more, rarely fewer in extremely small leaves; pinna-segments usually strongly oblique and falcate; costae glabrous beneath at maturity .. .. **1. M. pectinata**
b. Number of pinnae 15 or less, rarely up to 17; pinna-segments subpatent or oblique, straight or only moderately falcate; costae usually hairy beneath .... **2. M. foxworthyi**

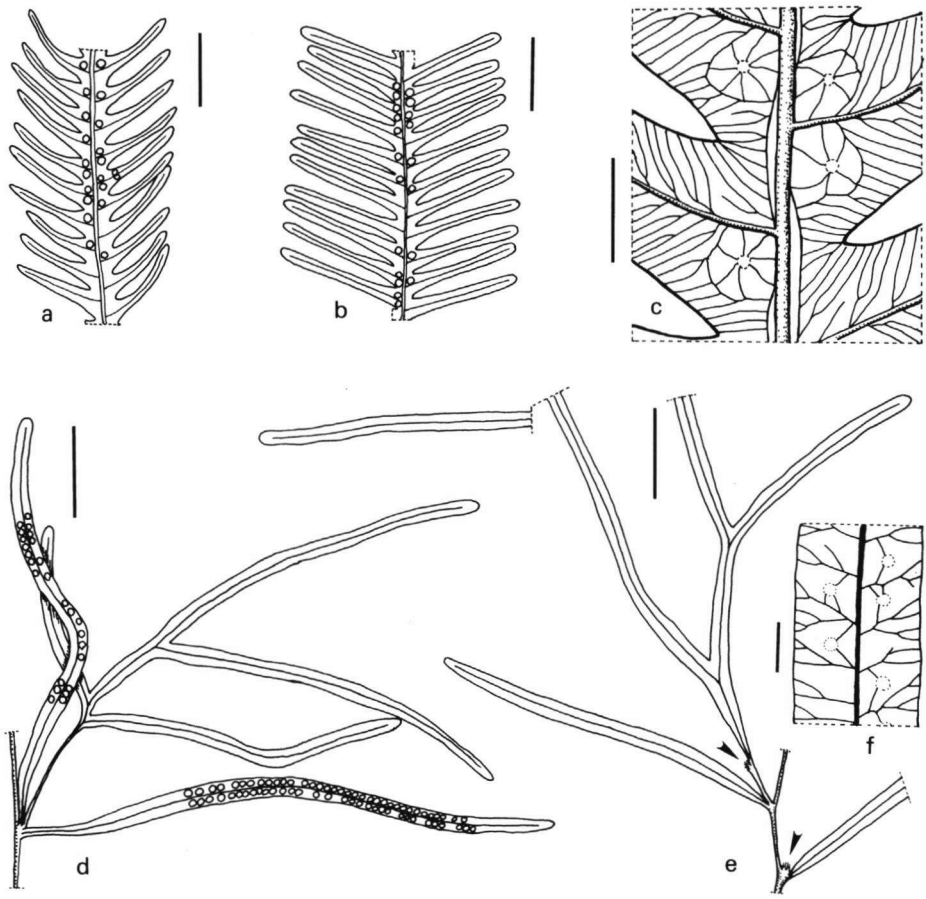

Fig. 1. *Matonia pectinata* R. Br. a. Part of pinna; c. part of pinna showing venation. — *M. foxworthyi* Copel. b. Part of pinna. — *Phanerosorus sarmentosus* (Baker) Copel. d. Pinna consisting of a pair of lateral primary pinnules and a forked secondary one. — *P. major* Diels. e. Two pinnae; the upper pinna consists of a basiscopic primary pinnule and a bud-bearing secondary one, the lower one consists of a basiscopic pinnule and a bud; f. part of fertile pinnule showing venation. — Scale bars = 2 cm for a, b, d, e; 2 mm for c, f.

1. Matonia pectinata R. Br.

Matonia pectinata R. Br. in Wall., Pl. Asiat. Rar. 1 (1829) 16, t. 16; Bedd., Ferns Brit. India 2 (1866) 186, pl. 186; Handb. Ferns Brit. India (1883) 19, f. 8; Copel., Sarawak Mus. J. 2 (1917) 388; Holttum, Revis. Fl. Mal., ed. 2, 2 (1968) 59, f. 13; Parris et al., Pl. Mt Kinabalu 1 (1992) 93, p.p., excl. specim. ex Kinabalu; M. Kato, Blumea 38 (1993) 172. — Type: *Farquhar s.n.* (K or CAL), Peninsular Malaysia, Malacca, Mt Ophir (at present Johor, G. Ledang), anno 1815.

Rhizome (excluding hairs) up to 8.5 mm (mean 6.4 mm) thick. *Leaves:* stipes brown or chestnut-brown, glabrous, up to 115(–180) cm (mean 82 cm). Lamina up to 50(–75) by 55(–80) cm (mean 35 by 42 cm), pedate; pinnae up to 30 (mean 22), deeply pectinate; central pinnae up to 50(–75) by 3.5(–5.5) cm (mean 35 by 2.7 cm); costae gla-

brous on the abaxial side but rarely hairy in young leaves; segments usually strongly oblique and falcate, linear-oblong, up to 6.2(–7.3) mm (mean 5.4 mm) broad at base. Annulus cells of *sporangia* 17–24 (mean 19.3). *Spores* 48–68 mm in diameter (mean 53 mm); surface granulate. — **Fig. 1a, c.**

Distribution — *W Malesia:* Peninsular Malaysia, Sumatra, Lingga Archipelago, Riau Archipelago. See note.

Habitat — In exposed area or in scrub on mountain ridges or on summits; altitude (90–)750–2000 m.

Note — One specimen (*Lobb 481*, BM) was assumedly collected in Java, but most certainly this is a wrong location. The report from New Guinea [Tan & Tolentino, Philipp. J. Sc. 116 (1987) 435–443] is perhaps due to misidentification.

2. Matonia foxworthyi Copel.

Matonia foxworthyi Copel., Philipp. J. Sc., Bot. 3 (1908) 343, pl. 2; Sarawak Mus. J. 2 (1917) 388; Alderw, Philipp. J. Sc., Bot. 11 (1916) 114; C. Chr. & Holttum, Gard. Bull. Str. Settlem. 7 (1934) 223; K. Iwats. & M. Kato, Acta Phytotax. Geobot. 35 (1984) 61; Tan & Tolentino, Philipp. J. Sc. 116 (1987) 536, pl. 2; M. Kato, Blumea 38 (1993) 171. — Type: *Foxworthy 372* (holotype destroyed, MICH iso), Borneo, Sarawak, Mt Po.

Rhizome (excluding hairs) up to 7 mm thick (mean 5.8 mm). *Leaves:* stipes brown or chestnut-brown, glabrous, up to 150 cm long (mean 85 cm). Lamina up to 45(–55) by 50(–60) cm (mean 35 by 41 cm), pedate; pinnae up to 15(–17) (mean 13), pectinate; central pinnae up to 45(–55) by 5(–6) cm (mean 36 by 3.9 cm); costae hairy beneath with brown or chestnut-brown crisped hairs, glabrous in very old leaves; pinna-segments linear-oblong, up to 6.2(–7.8) mm (mean 5.3 mm) broad at the base, subpatent or oblique, straight or only moderately falcate. Annulus cells of *sporangia* 14–25 (mean 18.7). *Spores* 50–70 mm in diameter (mean 61 mm); surface granulate. — **Fig. 1b.**

Distribution — *Malesia:* Borneo (Sarawak, Sabah, Kalimantan), Philippines (Mindoro, Sibuyan), Moluccas (Ambon), New Guinea (Irian Jaya).

Habitat — In more or less open places often in clearings, and in and at edge of mossy forest on mountain ridges or summits; altitude (420–)750–2100 m.

Notes — 1. New Guinean specimens [*van Royen & Sleumer 7204* (L), *Kanehira & Hatusima 14039* (BO)] have small leaves with 11 pinnae and hairy costae.

2. One specimen (*Anonymous collector*, BM) was collected from Mt Ophir, Peninsular Malaysia, where many specimens of *M. pectinata* have been collected; detailed field observation and new collection is needed.

PHANEROSORUS

Phanerosorus Copel., Philipp. J. Sc., Bot. 3 (1908) 344, pl. 3; Gen. Fil. (1947) 172; K.U. Kramer in Kubitzki (ed.), Fam. & Gen. Vasc. Pl. 1 (1990) 183, f. 95. — Type species: *Phanerosorus sarmentosus* (Baker) Copel.

Rhizomes creeping, branched, dicyclic-solenostelic, densely hairy; hairs light-brown, multicellular, uniseriate, up to 4 mm long. *Leaves* pendulous, pinnately compound,

pinnately lobed at apex; stipes straw-coloured, glabrous throughout, round on the abaxial side and somewhat flattened on the adaxial side; rachis, like stipe, stramineous and glabrous, narrowly winged on both lateral-adaxial sides as the uppermost part of the stipe; pinnae alternate, mostly consisting of two opposite primary pinnules and densely hairy buds sunken in a crater between them, or consisting of basiscopic primary pinnules and buds, or sometimes of secondary pinnules (devoid of primary pinnules) and buds near the base of pinnule or bud-derived leaflet, upper pinnae simpler than the middle; buds borne singly at the apex of pinna or up to nine additional buds borne near the base of leaflet stipes, dormant or developed into leaflets which are variable from small, single or forked secondary pinnules to large leaf-like leaflets; primary pinnules (the edge of which is decurrent to the rachis-wing) and secondary pinnules (whose edge is not continuous with the rachis-wing) near the base of leaflets simple to twice forked; pinnule-segments linear, up to 5 mm broad when fertile, up to 6(–7) mm broad when sterile, subcoriaceous or coriaceous, entire or subundulate at edge, polished on the adaxial surface, often glaucous and papillate on the abaxial surface; veins in sterile pinnule-segments free, once or twice forked, in fertile ones 2–4 times forked, soriferous veins usually anastomosing, veins in sterile portions free. *Sori* round or elliptic and hemispherical, in one median or inframedian row on each side of midrib, supplied by 1–3 veinlets; indusia peltate, thick in central portion and membranous and inrolled in marginal portion; sporangia about 20 in two or rarely three, more or less regular layers, consisting of a short, thick stalk and an elliptic-globose capsule with incomplete oblique annulus. Spores tetrahedral, trilete, pale. — **Fig. 1d–f.**

Distribution — Two species, both in *Malesia.*

Habitat & Ecology — Calcicolous and hanging from steep limestone cliffs or rocks, often at caves; locally abundant.

Morphology — The leaf morphology of *Phanerosorus* is similar to that of the small leaf of young *Matonia* plants [Tansley & Lulham, Ann. Bot. 19 (1905) 475–519], in particular in that the pinna-segments of young *Matonia* plants are unequally forked, as are the pinnules of *Phanerosorus*. The remarkable difference in leaf morphology of the genera is suggested to be due to heterochrony (paedomorphosis).

There are two kinds of leaf buds. One is a terminal bud at the apex of a pinna, and the other is an adventitious bud near the base of bud-derived secondary pinnules or leaflets. Leaf buds may develop into leaflets ranging from simple pinnules to large leaf-like leaflets; thus the leaves can grow indeterminately.

Chromosome number — According to Walker & Jermy, n = 25 [Fern Gaz. 12 (1982) 209–213].

Gametophytes — The gametophytes are long-lived and may occur abundantly together with the sporophytes of various ages on limestone rock surface. See Yoroi & Kato, Amer. J. Bot. 74 (1987) 354–359. Young gametophytes are slender, ribbon-like and one cell thick throughout, and old ones have cushions along the elongate thallus. They are usually monoecious and protandrous. Both young and old gametophytes reproduce vegetatively by proliferation of marginal cells of the thallus.

KEY TO THE SPECIES

1a. Pinna usually consisting of two opposite primary pinnules and a bud or bud-derived leaflet between them ..... **1. P. sarmentosus**

b. Pinna consisting of a bud or bud-derived leaflet and one basiscopic primary pinnule or only of a bud or leaflet (primary pinnules lacking) ..... **2. P. major**

1. Phanerosorus sarmentosus (Baker) Copel.

Phanerosorus sarmentosus (Baker) Copel., Philipp. J. Sc., Bot. 3 (1908) 344, pl. 3; Sarawak Mus. J. 2 (1917) 388. — *Matonia sarmentosa* Baker, J. Linn. Soc. Bot. 24 (1887) 256. — Type: *Hose 216* (K), Borneo, Sarawak.

Rhizomes creeping, branched, up to 3 mm thick, densely covered with light-brown hairs. *Leaves* to 80(–130) cm long including the up to 20 cm long stipe, 25 cm broad; pinnae alternate, up to 22 on either side of rachis, up to 6(–9) cm apart, most pinnae consisting of two opposite primary pinnules and a bud or bud-derived leaflet between them, lower pinnae deciduous; buds one or two per pinna, rarely more; pinnules simple or once or twice forked, up to 20 cm long; pinnule-segments linear, entire or undulate at edge, fertile segments up to 5 mm broad, sterile ones up to 6(–7) mm broad; veins free but anastomosing in soriferous area, 2 or 3 times forked. *Sori* in one row on either side of midrib, supplied by one (veins free) or two or rarely three veinlets; indusial scars slightly raised; indusia brown, round or elliptic, up to 1.6 mm long, 1.4 mm broad, 1.1 mm tall. *Spores* 50–63 mm in diam.; surface granulate-verrucose. — **Fig. 1d.**

Distribution — *Malesia:* Borneo (Sarawak).

Habitat — Epipetric on and hanging from steep limestone cliff or on rock surface; 50–800 m altitude.

2. Phanerosorus major Diels

Phanerosorus major Diels, Notizbl. Bot. Gard. Mus. Berlin-Dahlem 11 (1932) 311; M. Kato, Acta Phytotax. Geobot. 40 (1989) 82. — Type: *Stein 212* (B; GH fragment), New Guinea, Waigeo Isl.

Rhizomes up to 2.5 mm thick, branched, densely covered by light-brown multicellular hairs. *Leaves* clustered or remote, up to 65 by 30 cm including the up to 15 cm long stipe, pinnate; pinnae alternate, up to 7 or 8 on either side of rachis, up to 3 cm apart, each consisting of either basiscopic primary pinnule and a bud or bud-derived leaflet at the base, or only bud or leaflet (primary pinnules lacking), a few lowest ones usually deciduous; pinnules simple to once or twice forked, stalked or sessile, up to 15 cm long (those of young plants longer); pinnule-segments linear, entire or subundulate at edge, coriaceous, fertile segments 3–5 mm broad, sterile segments up to 6(–7) mm broad; buds 1–10 (one primary and the others adventitious) per pinna; veins free, once or twice forked, or anastomosing in soriferous portions. *Sori* in one row along either side of midrib, supplied by 2 or 3 veinlets; scars of indusial stalks prominently raised; indusia brown or dark brown, peltate, thick, round or elliptic, up to 1.9 by 1.4 mm, up to 1.8 mm tall. *Spores* 55–63 mm in diam.; surface granulate. — **Fig. 1e, f.**

Distribution — *Malesia:* Moluccas (Seram), Waigeo, Misool, Aru, NW New Guinea.

Habitat — Epipetric on and hanging from steep limestone cliff or rock surface; from sea level up to 600 m altitude.