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REVISION OF THE FERN GENUS POLYPODIOPTERIS (POLYPODIACEAE)

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SUMMARY

The present revision deals with the systematics of the genus *Polypodiopteris* which is endemic to Borneo and is a precursor for the Flora Malesiana treatment of the family Polypodiaceae which will appear in the near future. It includes the recognition, the description and a full synonymy of three species with pectinate fronds, irregularly anastomosing veins, and lacking any soral paraphyses. Certain characters suggest a relationship with the genus *Selliguea*, but no conclusions can be made before the revision of that genus is finished.

SYSTEMATIC POSITION AND TAXONOMIC HISTORY OF POLYPODIOPTERIS

Copeland (1909) considers this group of species, because of less structural specialisation, as the primitive form of *Goniophlebium*, from which *Schellolepis* (see Rödl-Linder, 1990) is a derived group. He assumed the venation pattern as a generalised one, in-between *Goniophlebium* and *Phymatodes* and cited Maxon who saw these Bornean ferns as "best possible support for his judgement as to the affinity of *Phymatodes* (and *Selliguea*) to *Goniophlebium* ..." Christensen (1934) doubted a close relationship with *Goniophlebium*, due to the irregularity of the venation and saw the group rather close to *Polypodium taeniatum* (*Selliguea*). Referring to the pectinate fronds and the rather simple but irregular venation, Copeland (1947) created the genus *Polypodiopsis* to accommodate the group of three Bornean species instead of including them in *Crypsinus* (*Selliguea*). Due to an earlier application of this name for a genus of the Taxaceae, Reed (1948) altered this generic name into *Polypodiopteris*.

Tryon and Lugardon (1991) assume a close relationship between *Polypodiopteris* and *Selliguea* untenable on the basis of gross differences in the leaves, even though the spores resemble those of *Selliguea*. They suggest a possible relationship with *Pleopeltis* which cannot be confirmed here.

The morphology of the rhizome scales as well as of the spores suggest rather a relationship with the genus *Selliguea*. However, *Polypodiopteris* has a typical venation pattern (Fig. 1a, b) with excurrent veins only and lacks any soral paraphyses, whereas in *Selliguea* recurrent veins and hairy soral paraphyses are common. A revision of *Selliguea* (in preparation, Hovenkamp) will hopefully elucidate further details.

MATERIAL AND PRESENTATION OF DATA

Dried specimens of 33 collection numbers, partly with duplicates, were studied from the following herbaria (abbreviations follow the Index Herbariorum): A, BM, BO, GH, K, L, MICH, NY, P, PNH, UC, US. Selected specimens were also examined from BAS and RO.

The description of the species refers to characters recognised only in dry herbarium material of adult sporophytes. Living material has not been encountered. Information on the habitat has been taken from herbarium labels. Notes are added for special remarks and additional data, when necessary. Details are illustrated in the figures.

POLYPODIOPTERIS

Polypodiopteris C.F. Reed, Amer. Fern J. 38 (1948) 87; Hennipman in Kramer et al., Pteridophytes and Gymnosperms 1 (1990) 228. — *Polypodiopsis* Copel., Gen. Fil. (1947) 210, nom. illeg., non Carrrière, Traité gén. conif. éd. 2 (1867) 710. — Type species: *Polypodiopteris proavita* (Copel.) C.F. Reed (basionym *Polypodium proavitum* Copel.).

Moderate-sized, epiphytic. *Rhizome* long creeping, terete, 2–6 mm in diam., chalky, clothed with scales, phyllopodia more or less prominent, 0.3–2 cm apart; anatomy: ground tissue parenchymatous, number of vascular strands 7–13, related to diameter of rhizome, arranged in a regular circle, dark bundle sheaths absent, black sclerenchyma strands longitudinal, present in specific numbers 30–>100, scattered in the ground tissue. *Rhizome scales* inserted in invaginations, different shades of brown, adpressed or apically spreading, densely set, persistent, peltate or pseudopeltate (note 1), narrowly deltoid, up to 6.5 mm long, apex acute or filiform, auricles round, clathration of cell walls absent (opaque) or in apical part present (semi-clathrate), cells dark yellow, clathrate marginal protrusions absent or present. *Fronds* monomorphic, articulate to rhizome, petiolate, petiolar scales rare, and then basally, stipe grooved, glabrous, in cross section near base 1–3 mm across, index length of stipe/length of blade 0.2–0.8, blade firm herbaceous, index length/width 2.5–6, widest basally or somewhat above base, pectinate, lateral pinnae adnate, in an angle of 60–90° towards the rhachis, 0.3 to three times of own width apart from each other, number relative to length of blade, linear, apically obtuse to acute, margin undulate, crenate or serrate, flat or revolute, lowermost pinnae equally long or (in one

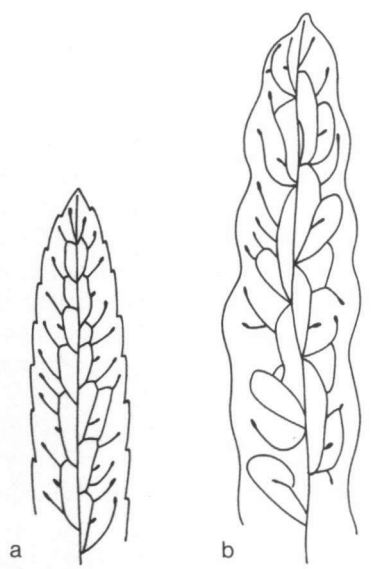

Fig. 1. Venation patterns. – a. *Polypodiopteris colorata* (Copel.) C.F. Reed (*Mogea 3897*). – b. *P. proavita* (Copel.) C.F. Reed (*Brooks*, ii-1908). Both × 2.

species) reduced, apical segments continuously reduced in length, terminal segment adnate, conform. *Laminar indument:* glandular hairs rarely present, 2 cells long. *Stomata* (co-)polocytic. *Venation* (Fig. 1a, b): badly visible (note 2), 1 (or 2) series of areolae at each side of costa, irregularly shaped, included free veins rarely present, then minute with an hydathode at its end; marginal free veins simple, excurrent with terminal hydathodes. *Sori* exindusiate, uniserial at each side of costa, situated slightly closer to costa than to margin, usually on the connecting veins flanking the costa, rarely terminal on short, excurrent veins, superficial or slightly sunken, on hydathodes, round, c. 2 mm in diam. (note 3); receptacular paraphyses absent; sporangial capsule index length/width 1–1.2, annulus vertical, indurated cells 10 or 11, cells in total 18–20. *Spores* (Fig.2a–c) bilateral, oblong (polar view), plano-convex (lateral view), brown, exospore thin, surface smooth, perispore thick, c. 0.9 µm in diam., surface shallowly ornamented (pusticulate), usually building echinae (note 4), blunt or swollen, globules few or many.

Distribution – Various mountain ranges all over Borneo: from Central Kalimantan through Sarawak to Mt Kinabalu, Sabah,.

Habitat & Ecology – Primary and secondary forests; montane; on steep slopes; epiphytic; altitude 600–2500 m.

Notes – 1. It has not been observed before that the rhizome scales of *P. colorata* and *P. proavita* are pseudopeltate and peltate on one rhizome.

2. The venation is visible in *Mogea 3897* (L) and *Iwatsuki et al. B-2503* (L), two specimens which have presumably been treated with alcohol before drying. In some of the mounted fronds the usually firm herbaceous texture is in these cases transparent.

3. The only specimen with measurable sori is *Clemens 32467* (GH). The size is assumed to be about the same in all three species of the genus.

4. In the case of *P. proavita*, echinae have not been observed. However, there is a chance that all the spores studied are in a slightly premature stage and echinae are built later. Some spores of *P. brachypoda* and *P. colorata* have only a few echinae which are easily overlooked. Others, however, have many echinae which can be up to c. 7 µm long (Fig. 2a, b).

KEY TO THE SPECIES

1a. Rhizome scales shortly toothed, light red-brown, gradually narrowed from a sometimes broader base, only near the top becoming filiform or apex acute. Lamina at most 36 cm long, margin of pinnae revolute. Sclerenchyma strands of rhizomw 80–>100 ..... **1. P. brachypoda**

b. Rhizome scales toothed or ciliate, darker brown to nearly black, above the broad base suddenly narrowed and filiform for the upper half. Lamina up to 30 cm or up to 60 cm long, margin of pinnae flat or revolute 2

2a. Pinnae at a distance of 0.5–1.5 of their width, margin flat, lamina up to 30 cm long, sclerenchyma strands in rhizome 30–40 ..... **2. P. colorata**

b. Pinnae at a distance of 1–3 times their width, margin revolute, lamina up to 60 cm long, sclerenchyma strands > 90 ..... **3 P. proavita**

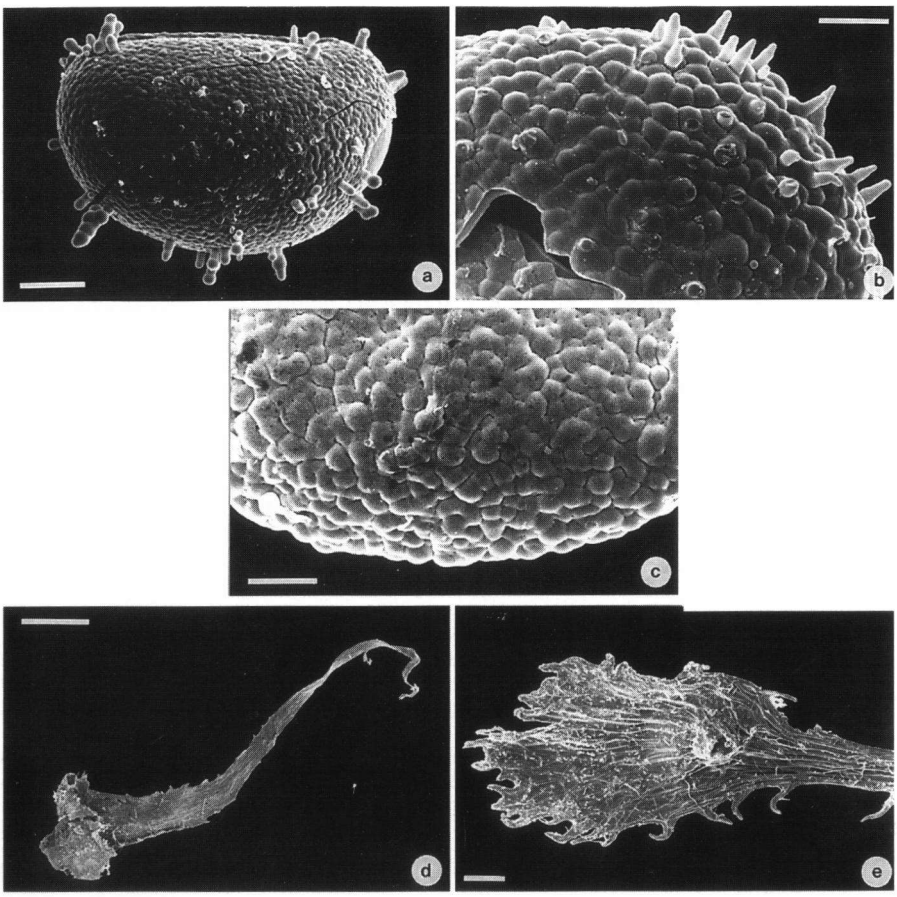

Fig. 2a–c. Spores (SEM). – a. *Polypodiopteris brachypoda* (Copel.) C.F. Reed (*de Vogel 8670*), lateral view, perispore thick, partly cracked, surface pusticulate, with blunt, sometimes swollen echinae. – b. *P. colorata* (Copel.) C.F. Reed (*Clemens 30747*), detail, perispore thick, broken, surface pusticulate, building blunt, partly swollen echinae. – c. *P. proavita* (Copel.) C.F. Reed (*Brooks*, ii-1908), detail, perispore surface pusticulate, echinae absent. — Fig. 2d & e. Rhizome scales (SEM). – d. *P. brachypoda* (Copel.) C.F. Reed (*Clemens 32467*), entire scale: opaque, continuously narrowing towards apex, base bent, marginal protrusions not clathrate. – e. *P. proavita* (Copel.) C.F. Reed (*Clemens 22381*), basal part of scale: semi-clathrate, contracted above base, base flat, marginal protrusions clathrate. — Scale bars: a = 10 μm; b & c = 5 μm; d = 500 μm; e = 100 μm.

1. **Polypodiopteris brachypoda** (Copel.) C.F. Reed

Polypodiopteris brachypoda (Copel.) C.F. Reed, Amer. Fern J. 38 (1948) 87. — *Polypodiopsis brachypoda* (Copel.) Copel., Gen. Fil. (1947) 210. —.*Polypodium 'brachypodium'* Copel., Philipp. J. Sci., C 12 (1917) 62; C. Chr. & Holttum, Gard. Bull. Sing. 7 (1934) 305; Dansk Bot. Ark. 9, 3 (1937) 40. — Type: *Topping 1823*, Borneo, Mt Kinabalu, Gurulau Spur, 21-xi-1915 (PNH †, lecto MICH; iso GH, MICH).

Epiphytic. *Rhizome* 2.5–4 mm in diam., phyllopodia 0.5–2 cm apart, sclerenchyma strands 80–>100. *Rhizome scales* (Fig. 1d) reddish brown, opaque, peltate, continuously narrowing towards apex, apex acute, spreading, base ± round, bent, index 5.2–8.3, 5–6.5 by 0.7–1 mm, margin shortly dentate. *Fronds:* blade index length/width 3.1–6, maximum length 36 cm, lateral pinnae regular in length, margin crenate to serrate, revolute, distance between each other 0.3–1.5 times the width, lower pinnae equally long as medial ones, index length of stipe/length of blade 0.2–0.7. *Venation:* areolae uniserial, irregularly shaped, included free veins absent. *Sori* superficial. *Spores* (Fig. 2a): length 75–87 µm, perispore pusticulate, echinae present, blunt and/or swollen, globules few or many.

Distribution – Sabah: Crocker Range from the SW up to Mt Kinabalu.

Habitat & Ecology – Primary forest (oak-laurel, *Leptospermum–Dacrydium*), disturbed forest with secondary growth (Magnoliaceae), 8–30 m high, terrain sloping to steep, soil whitened sandstone and shale or thick humus layer; altitude 1350–2500 m.

Notes – 1. Fifteen specimens (plus duplicates) seen.

2. Remarkable is the rather soft appearance of the rhizome scales.

2. **Polypodiopteris colorata** (Copel.) C.F. Reed

Polypodiopteris colorata (Copel.) C.F. Reed, Amer. Fern J. 38 (1948) 87. — *Polypodiopsis colorata* (Copel.) Copel., Gen. Fil. (1947) 210. — *Polypodium coloratum* Copel., Philipp. J. Sci., Bot. 3 (1909) 347; C. Chr., Dansk Bot. Ark. 9, 3 (1937) 39, **q.n.s.** — Type: *Hewitt 35*, Borneo, Sarawak, Mt Po., vii-1906 (MICH).

Epiphytic. *Rhizome* 2–4 mm in diam., phyllopodia 0.5–2 cm apart, sclerenchyma strands 30–40. *Rhizome scales* reddish brown, semi-clathrate, pseudopeltate and/or peltate, contracted above base, apex filiform, spreading, base ± round or overlapping, flat, index 4.2–6.7, 3.5–6.1 by 0.7–0.9 mm, margin toothed or ciliate. *Fronds:* blade index length/width 2.5–3.3, maximum length 30 cm, lateral pinnae regular in length, margin crenate to serrate, flat, distance between each other 0.5– 1.5 times the width, lower pinnae equally long as medial, index length of stipe/length of blade 0.4–0.8. *Venation* (Fig. 1a): areolae uniserial, irregu-larly shaped, included free veins absent. *Sori* slightly sunken. *Spores* (Fig. 2b): length 65–70 µm, perispore colliculate, echinae present, blunt and/or swollen, globules few.

Distribution – Throughout Borneo: mountain ranges from Central Kalimantan through Sarawak to Mt Kinabalu, Sabah.

Habitat & Ecology – Primary, upper montane forest, steep slope to small river, on mossy stem of fallen tree; altitude 1000–1450 m..

Notes – 1. Seven specimens (plus duplicates) seen.

2. Petioles dirty greenish, sporangia light brown (*Mogea 3897*).

3. **Polypodiopteris proavita** (Copel.) C.F. Reed

Polypodiopteris proavita (Copel.) C.F. Reed, Amer. Fern J. 38 (1948) 87. — *Polypodiopsis proavita* (Copel.) Copel., Gen. Fil. (1947) 210. — *Polypodium proavitum* Copel., Philipp. J. Sci., Bot. 3 (Jan. 1909) 347; C. Chr., Dansk Bot. Ark. 9, 3 (1937) 40. — *Polypodium colora-*

tum auct. non Copel.: C. Chr., Dansk Bot. Ark. 9, 3 (1937) 40. — *Polypodium papillosum* auct. non Blume: Ces., Atti Accad. Sc. Fis. (1876) 25. — Type: *Brooks & Hewitt s.n.*, Borneo, Sarawak, Bongo Mt (MICH).

Polypodium cesatianum Baker [J. Bot. (Hooker) 8 (1879) 42, nom. nud.] ex Alderw., Malayan Ferns (Oct. 1909) 603; Copel., Philipp. J. Sci., C 12 (1917) 62; H. Christ, Ann. Jard. Bot. Buitenzorg 2, 5 (1925) 120; C. Chr., Dansk Bot. Ark. 9, 3 (1937) 40. — Type: *Hallier 3312* (BO).

Epiphytic. *Rhizome* 2.6–6 mm in diam., phyllopodia 0.3–1.2 cm apart, sclerenchyma strands > 90. *Rhizome scales* dark brown to black, semi-clathrate, pseudopeltate and/or peltate, continuously narrowing towards the apex or slightly contracted above base, apex filiform, mostly appressed, rarely spreading, shape of base ± round or overlapping, flat, index 4.6–5.5, 2.9–5.7 by 0.6–1.1 mm, margin toothed or ciliate. *Fronds:* blade index length/width 3.1–4.6, maximum length 60 cm, lateral pinnae irregular in length, margin undulate to serrate, revolute, distance between each other 1–3 times the width, lower pinnae reduced, index length of stipe/length of blade 0.3–0.5. *Venation* (Fig. 1b): areolae usually uniserial (partly biserial), irregularly shaped, included free veins sometimes present, then minute with an hydathode at its end. *Sori* superficial. *Spores* (Fig. 2c): length 66–75 µm, perispore pusticulate, echinae absent, globules few to many.

Distribution – Mountain ranges from Kalimantan to Sarawak.

Habitat & Ecology – Evergreen forest, on trunk of tall tree; altitude 600 m.

Notes – 1. Eleven specimens (plus duplicates) seen.

2. Remarkable are the dark rhizome scales, the reduced lower pinnae and the somewhat irregular length of the pinnae throughout the blade.

3. Originally Copeland described only a form with long fronds. There are, however, a number of specimens with short fronds and, therefore, with a quite different appearance. They have generally been wrongly identified, e.g. *Parris 6493, 6564, Curtis s.n. comm. Veitch 9/81* (K), *Brooks s.n.*, iv-1909 (BM), *Beccari s.n.*, 1866 (RO).

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IDENTIFICATION LIST

Collections are referred to the number given to the species in this treatment.

Beaman 10524: 1 — Beccari 189: 3 — Bell 2019: 2.
Clemens 20444: 2; 22381: 3; 28544: 1; 30747: 2; 32467, 33692: 1.
Hewitt 35: 2.
Iwatsuki et al. B2503: 3.
Kidman Cox 2537: 1.
Mogea 3897: 2 — Molesworth Allen 3142: 3.
Parris 6493, 6564: 3; 8474, 9128, 10811, 11281: 1.
Topping, LeRoy 1620, 1823: 1.
de Vogel 8595, 8670: 1.