

A review of the fern genus *Polystichum* (Pteropsida: Dryopteridaceae) in Madagascar and the Mascarene region

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KEY WORDS
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ABSTRACT

The fern genus *Polystichum* Roth (Dryopteridaceae) in Madagascar and the Mascarene region is reviewed. Eight species are recorded, six being endemic to the region. Of these four are endemic to Madagascar. The Madagascar species remain poorly known.

RÉSUMÉ

Révision du genre *Polystichum* (Pteropsida: Dryopteridaceae) de Madagascar et des Mascareignes.

MOTS CLÉS
Polystichum,
Dryopteridaceae,
Madagascar,
Mascareignes.

Révision des fougères de Madagascar et des Mascareignes appartenant au genre *Polystichum* Roth (Dryopteridaceae). Huit espèces sont retenues, dont six endémiques de Madagascar. Les espèces malgaches demeurent peu connues.

INTRODUCTION

A review of the fern genus *Polystichum* in Madagascar and the Mascarene region (the Madagascar and Comore archipelagos) is provided. *Polystichum* is a genus of between 160 (TRYON & TRYON 1982) and 200 species (DAIGOBO 1972), occurring throughout the temperate parts of the world as well as the montane tropics, but is mostly absent from the lowland tropics.

Madagascar has been separated from Africa for at least 100 million years and is well known for its high level of endemism. RAVEN & AXELROD (1974) ascribed the rich Madagascar flora to a now submerged Madagascar plateau that connected it with India and Antarctica, thus allowing for migration between these now distant continents until the late Cretaceous. LEROY (1978), on the other hand, considered the rich Madagascar flora as an autochthonous flora that has differentiated princi-

pally from the original Gondwanan stock and through the immigration of newcomers by long-distance dispersal. LEROY (1978) illustrated the close relationship between the floras of Madagascar and that of eastern and southern Africa.

Mauritius, Rodrigues and La Réunion form the Madagascan archipelago and are found some 800-920 km east of Madagascar. All three islands are of volcanic origin with Mauritius being the oldest, about 7.8 million years (MCDUGALL & CHAMALAUN 1969). La Réunion is estimated to be approximately 3 million years old (BADRE & CADET 1978), whilst Rodrigues, the smallest of the islands is thought to be the summit of a volcano, extinct since the Pliocene-Palaeocene eras (LORENCE 1976). *Polystichum* occurs on Mauritius and La Réunion, but has never been recorded from Rodrigues.

The Comoro archipelago comprises the four volcanic islands of Anjouan, Mayotte, Mohéli and Grande Comore. The archipelago is situated in the middle of the Mozambique Channel, 300 km from the African mainland. Grande Comore is the largest and also the most recent of the islands in the archipelago (WHITE 1983); *Polystichum* has been recorded from this island but not from the

other three. Two primary centres of pteridophyte diversity occur in the region, one in Madagascar and the other in the La Réunion-Mauritius area (RAKOTONDRAINIBE et al. 1996).

CHRISTENSEN (1932) reported four *Polystichum* species for Madagascar, whilst TARDIEU-BLOT (1958) reported five. Of the eight *Polystichum* species recorded for the study area, four are endemic to Madagascar, whilst one species, *P. crinulosum*, is believed to be endemic to Mauritius. *Polystichum ammifolium*, endemic to the region, occurs on Madagascar, Mauritius and La Réunion. The remaining two species, *P. luctuosum* and *P. wilsonii*, are widespread, occurring in Africa, the Indian subcontinent and extending to southeast Asia.

Comparative morphological studies suggest that two of the Madagascan endemics are related to African taxa, however the Madagascan species remain poorly known.

Size range and means (in brackets) are provided for indusia and spores whereas the range and mode (in brackets) are provided for the number of indurated annulus cells per sporangium. The terminology used in describing palea characteristics follow ROUX (2000).

TAXONOMIC TREATMENT

Key to the species

1. Lamina 1-pinnate 2
- 1'. Lamina 2-pinnate to 3-pinnate 3
2. Lamina lanceolate to narrowly oblong, with 12-15-stalked pinna pairs; 1-3 proliferous buds are borne abaxially on the rachis near the frond apex; pinnae oblong-attenuate, lanceolate to trullate, to 66 mm long 5. *P. maevaranense*
- 2'. Lamina ovate-lanceolate, with up to 28-stalked pinna pairs; proliferous buds absent; pinnae linear-attenuate to narrowly oblong-attenuate, to 135 mm long 3. *P. kalambaitrense*
3. Lamina with 1-5-paleated proliferous buds along the rachis near the frond apex 4
- 3'. Lamina never with proliferous buds along the rachis 6
4. Paleae at the stipe base concolorous or bicolorous, chartaceous, often somewhat rugose 5
- 4'. Paleae at the stipe base bicolorous, chartaceous to crustaceous, never rugose 7. *P. tsaratananense*
5. Sporangium stalk glandular; indusium black-centred 2. *P. crinulosum*
- 5'. Sporangium stalk eglandular; indusium stramineous throughout 6. *P. pauciaculeatum*
6. Larger rhizome and stipe base paleae with long twisted uniseriate hairs along the apical margins and on the surface; indusium cupulate when dry 4. *P. luctuosum*
- 6'. Larger rhizome and stipe paleae margins widely to closely fimbriated but never with long twisted uniseriate hairs along the margins or on the surface; indusium flat or folded when dry but never conspicuously cupulate 7
7. Lamina 2-pinnate, narrowly elliptic; paleae on the pinnules filiform or subulate-hastate with few short straight or angular outgrowths proximally 8. *P. wilsonii*
- 7a. Lamina 2- to 3-pinnate, narrowly ovate to ovate-lanceolate; paleae on the pinnules subulate to narrowly triangular, with long, simple, basally directed outgrowths proximally 1. *P. ammifolium*

1. *Polystichum ammifolium* (Poir.) C. Chr.

Cat. Pl. Madag., Pterid.: 31 (1932); Dansk Bot. Ark. 7: 69 (1932). — *Polypodium ammifolium* Poir., in Lam., Encycl. 5: 554 (1804). — *Aspidium ammifolium* (Poir.) Desv., Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. Gesammten Naturk. 5: 321 (1811); Desv., Mém. Soc. Linn. Paris 6: 250 (1827). — Lectotype (here designated): *Commerson s.n.*, Isle-de-France (Mauritius), (P-LA; iso-, BOL, NBG, photo!).

Aspidium stramineum Kaulf., in Spreng., Syst. Veg., ed. 16: 105 (1827). — *Polystichum stramineum* (Kaulf.) C. Presl, Tent. Pterid.: 83 (1836). — Type: *Sine coll. s.n.*, Mauritius [erroneously given as C. B. S. (Caput Bonae Spei)], missing.

Hypopeltis mauritiana Bory, in Bél., Voy. Indes Or.: 67 (1833). — *Polystichum mauritanum* (Bory) Fée, Mém. Foug. 5: 278 (1852). — Type: *Bory de Saint-Vincent s.n.*, les grands bois de l'île Maurice (Mauritius), *n.v.*

Polystichum schizolobium Fée, Mém. Foug. 7: 99 (1857). — Type: *De Montbrison s.n.*, Bourbon (La Réunion), *n.v.*

Polystichum vestitum Sieber, Fl. Mauritiana, ed. 1, suppl. n. 48, nom. nud., non (G. Forst.) Sw. (1801).

Polystichum sieberianum C. Presl, Tent. Pterid.: 83 (1836), nom. nud.

Aspidium aculeatum auct.: Baker, Fl. Mauritius: 492 (1877); Cordem., Fl. Réunion: 71 (1895); non (L.) Roth (1799).

Plants terrestrial or epilithic. Rhizome suberect, short, to 140 mm long, to 15 mm in diameter, beset with roots, crowded, persistent stipe bases, and paleae. Fronds crowded, caespitose, up to 16 per plant, erect to suberect or arching, to 1.4 m long; stipe proximally castaneous or stramineous throughout, adaxially sulcate, to 600 mm long, to 8 mm in diameter, densely paleated, the paleae at the stipe base ferruginous, membranous, sessile or short-stalked, filiform, narrowly linear to narrowly oblong-attenuate, entire or with few widely spaced short marginal outgrowths, the apex terminates in an acicular cell or a small thin-walled cell, to 50 × 2 mm, the paleae higher up appear heteromorphous, the larger paleae concolorous or bicolorous, stramineous or ferruginous, membranous or centrally castaneous, nitid and crustaceous, sessile, ovate-attenuate to narrowly ovate-attenuate, cordate to cordate-imbricate, the margins closely set with short and/or long fimbriae or with short, forked

marginal outgrowths which reduce in size and number towards the apex, the apex entire, terminating in a long or short acicular cell, to 15 × 6 mm, the smaller paleae ferruginous, membranous, sessile or short-stalked, ovate-attenuate to narrowly triangular or subulate, mostly cordate-imbricate, the margins proximally with long twisted, simple or branched outgrowths, the apex entire, terminating in an acicular cell; lamina 2- to 3-pinnate, with up to 32 pairs of stalked pinnae, narrowly ovate to ovate-lanceolate, to 790 mm long, pinnae opposite or alternate, closely spaced, proximally often somewhat more widely spaced, the proximal pinnae slightly reduced; rachis stramineous, adaxially sulcate, densely paleated, the paleae appear heteromorphous, stramineous or ferruginous, membranous to chartaceous, the larger paleae sessile, oblong-attenuate, narrowly ovate-attenuate, narrowly triangular to subulate, the margins closely set with short simple or branched straight or curved marginal outgrowths which reduce in size and number towards the apex, the apex entire, the smaller paleae short-stalked, cordate to cordate-imbricate, the margins usually with a few long simple or branched outgrowths proximally, the apices are always entire, terminating in a long acicular cell or a short subulate cell (rarely also in a short oblong-obtuse thin-walled cell), to 9 × 3 mm; pinnae short-stalked, 1-pinnate to 2-pinnate, with up to 21 pairs of stalked pinnules, oblong-attenuate to narrowly oblong-attenuate, often slightly to strongly auriculate acroscopically, the middle pinnae to 170 mm long, to 62 mm wide; pinna-rachis stramineous, adaxially sulcate, moderately to densely paleated, the paleae ferruginous, membranous, ovate-attenuate to subulate, the larger paleae sessile, the smaller short-stalked, truncate to cordate-imbricate, the margins proximally closely or widely set with short and/or long, simple or forked marginal outgrowths which reduce in size and number towards the apex, the apex entire, terminating in a long acicular cell (rarely also in a short oblong-obtuse thin-walled cell), to 5 × 1 mm; pinnules opposite or alternate, closely spaced, often slightly imbricate, short-stalked proximally, sessile towards the pinna apex, firmly herbaceous, dark green adaxially, slightly paler abaxially, inae-

quilateral, ovate, narrowly ovate, trullate or oblong-attenuate, basiscopically cuneate, acropically cuneate to truncate and auriculate, shallowly lobed or deeply incised to form lanceolate, narrowly elliptic, ovate to obovate lobes, the proximal acroscopic auricle free or nearly free, the margins crenate to doubly serrate, pungent or aristate, the proximal acroscopic pinnule to 35×14 mm, often reaching beyond the pinna-rachis above, adaxially moderately beset with stramineous to ferruginous, membranous, short-stalked, subulate to narrowly triangular paleae, the margin proximally with long, simple, largely basally directed marginal outgrowths, the apex always entire and terminating in a long acicular cell, to 1.8 mm long, abaxially moderately set with stramineous to ferruginous, membranous, short-stalked, subulate to narrowly triangular paleae, proximally with long, simple, largely basally directed marginal outgrowths, the apex always entire, terminating in a short fusiform cell or a long acicular cell (rarely also in a small thin-walled cell), to 2.7 mm long. Venation evident or obscure. Sori circular, to 1.5 mm in diameter, terminal or nearly terminal on abbreviated vein branches, generally uniseriate or sometimes biseri-ate, discrete but confluent at maturity in smaller lobes; sporangium with 12(-13-)21-indurated annulus cells; indusium stramineous to ferruginous, often also dark-centred, persistent, circular, simple or repand, maximum radius 0.36(-0.57-)0.89 mm; spores dark brown, perispore smooth or forming low, reticulate ridges, sparsely echinulate, variously perforated, exospore $22(-45.58-)62 \times 22(-30.82-)40$ μm . Chromosome number unknown. — Figs. 1, 3A-C.

MATERIAL EXAMINED. — MADAGASCAR: *Rakolomalala s.n.*, région de Sambirano (P). — MAURITIUS: *Ayres s.n.*, without precise locality (L); *Bewsher s.n.*, without precise locality (B, SAM); *Boivin s.n.*, without precise locality (P); *Bory de Saint-Vincent s.n.*, without precise locality (L); *Bouton s.n.*, without precise locality (B); *Commerson s.n.*, without precise locality (L, P); *Düring 1825*, without precise locality (B); *Düring s.n.*, without precise locality (B 96919); *D'Urville 152*, without precise locality (B); *Guého 11453*, Mt. Corps de Garde, (P); *Lorence 346*, Le Pouce Mt., E windward flank, 650 m (MO); *Lorence 390*, Mt. Lagrave, S flank, c. 650 m (MO); *Sieber s.n.*, Fl. Maur. n. 48 (B); *Sieber s.n.*, Syn. fil. n. 34, without precise locality

(B, K, L, MO, P, S); *Sieber s.n.*, without precise locality (L); *Vesco s.n.*, without precise locality (P); *sine coll.*, without precise locality (B 96913); *sine coll.*, without precise locality (B 96928); *sine coll. s.n.*, without precise locality (S); *sine coll.*, without precise locality (B 96914); *sine coll.*, without precise locality (B 97038); *sine coll. s.n.*, without precise locality (BR). — LA RÉUNION: *Badré 854*, Îlet à Guillaume (P); *Badré 978*, route de la montagne St. Denis, à La Possession (P); *Badré 1053bis*, Cirque de Salazie, sentier vers La Nouvelle, 1300-1400 m (P); *Badré 1118*, Pas de Bellecombe (P); *Bathe s.n.*, without precise locality (P); *Bernier 1*, Cilaos (P); *Bernier 93*, without precise locality (P); *Bernier s.n.*, without precise locality (P); *Berter s.n.*, without precise locality (B); *Billiet & Jadin 422*, route vers le Piton Maïdo, 1600 m (BR); *Billiet & Jadin 511*, environs du gîte de la Caverne Dufour, entre Cilaos et Piton des Neiges, 2400 m (BR); *Billiet & Jadin 581*, plaine d'Affouches, 1200 m (BR); *Billiet & Jadin 618*, forêt de Bébour, 1400 m (BR); *Billiet & Jadin 807*, Dos d'Âne, rempart de la rivière Sainte-Suzanne, 1200 m (BR); *Billiet & Jadin 820*, plaine des Chicots, environs du gîte de la Roche Écrite, 1800 m (BR); *Billiet & Jadin 887*, Bébour, rivière des Marsouins (BR); *Billiet & Jadin 895*, Piton Maïdo, 2200 m (BR); *Boivin 891*, without precise locality (B, P); *Boivin 892*, without precise locality (B, L); *Bosser 11453*, sentier du volcan, c. 2000 m (P); *Bosser 11474*, sentier du Bras Cabot, plaine des Palmistes, 1400-1500 m (P); *Bosser 11710*, La Roche Écrite, 2200-2300 m (P); *Bosser 20437*, montée de la plaine des Affouches, 1000-1100 m (P); *Bosser 21205*, haut de Brass-Panon, 600 m (P); *Cadet 43*, Grande Montée, 1500 m (P); *Cadet 1553*, massif de la Fournaise, 2200 m (P); *Cadet 1664*, Grand Coin, Dos d'Âne, 800 m (P); *Cadet 1942*, pentes du Cirque de Cilaos (P); *Decken s.n.*, prope Caverne de Musard (B); *Delavary s.n.*, plaine du Piton des Neiges (P); *De l'Isle 371*, ravine du Bras Piton, plaine des Palmistes (K); *De Lessert s.n.*, without precise locality (B); *De Sloover P2*, au pied du Piton de la Grande Montée, 1600 m (BR); *De Sloover P38*, Piton de Maïdo, 2150 m (BR); *Gaudichaud s.n.*, without precise locality (P); *Gimalac 70R*, sentier du Piton des Neiges, 3000 m (BR); *Hombroton s.n.*, without precise locality (P); *Houdllet s.n.*, without precise locality (B); *Keller s.n.*, Brûlé de St. Denis (B); *Kersten 100*, without precise locality (B); *Kersten 101*, zweihohen Cap Augéas à Caverne de Musard (B); *Kersten 102*, Hellbourg (B); *Olivier s.n.*, without precise locality (BR); *Onraedt 155*, Réserve Forestière de Bébour, \pm 1600 m (MO); *Onraedt 69R36*, plaine des Cafres, au Piton des Forges (BR); *Onraedt 69R80*, plaine des Cafres, aux sources Reilhac, 1550 m (BR); *Onraedt 69R82*, plaine des Palmistes, au Piton Desforges, 1550 m (BR); *Onraedt 69R107*, route forestière de Tévelare, 1300 m (BR); *Onraedt 69R122*, plaine des Cafres, au Piton Desforges, 1550 m (BR); *Onraedt 69R155*, Réserve Forestière de Bébour, 1600 m (BR); *Onraedt 70R*, plaine des

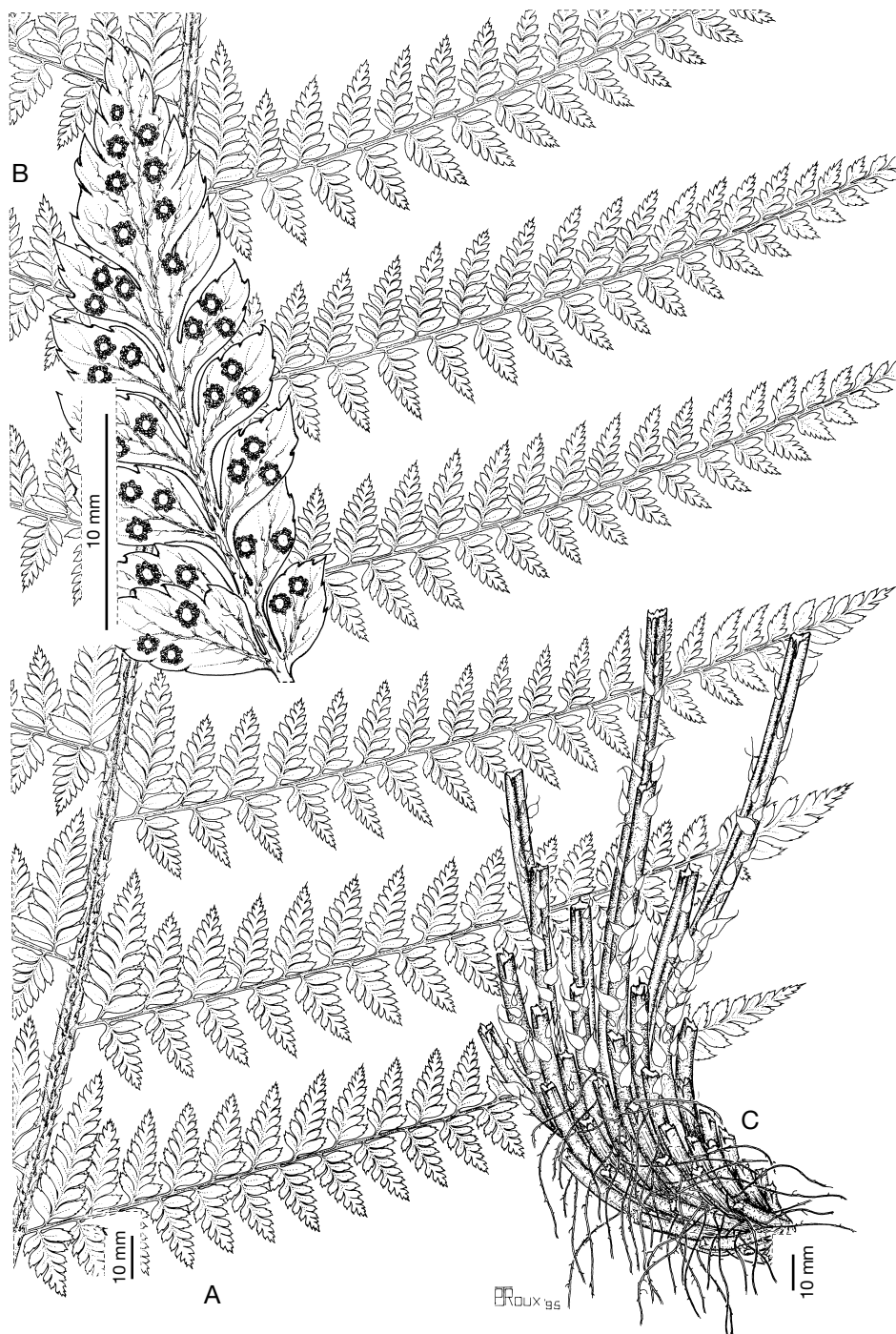


Fig. 1. — *Polystichum ammifolium*: **A**, middle pinnae of lamina; **B**, abaxial surface of a basal acroscopic pinnule; **C**, rhizome. A-B, Cadet 1164 (P); C, Guého 11453 (P).

Osmondes, au Trou Caron, c. 1000 m (BR); *Lépervanche-Mézière s.n.*, without precise locality (P); *Lotzy T11*, Salazie, 1000 m (M); *Raub 10235*, Petite plaine (BM); *Richard 94*, without precise locality (B); *Richard 321*, without precise locality (P); *Williams 3449*, walk down to cascade de Bras Rouge, Cilaos (NBG); *Vieillard s.n.*, without precise locality (B 97037); *Vieillard & Deplanche s.n.*, without precise locality (L, P); *sine coll. 43*, without precise locality (BR); *sine coll. 321*, without precise locality (B); *sine coll. 361*, without precise locality (P); *sine coll. sn.*, without precise locality (B); *sine coll. s.n.*, without precise locality (BR); *sine coll. s.n.*, without precise locality (L).

WITHOUT INDICATION OF ISLAND. — *Sine coll.*, s.loc. (B 96927); *sine coll.*, s.loc. (P [A only]); *sine coll.*, s.loc. (B 96929 [A only]); *sine coll. 692*, s.loc. (B); *sine coll. 82*, s.loc. (P); *Bory de Saint-Vincent s.n.*, s.loc. (P [3 sheets]); *sine coll. s.n.*, s.loc. (P); *Splitgerber s.n.*, Pr. b. sp. (L); Sieber flora mixta n. 286, s.loc. (L).

POIRET (1804) first described the species as *Polypodium ammifolium*, based on a COMMERSON collection made during his stay on Mauritius during the 1770's. Two sheets of this plant are currently housed in the Lamarck Herbarium in Paris. The sheet numbered 626, named "*polyp. ammifolium*", is here selected as the lectotype. Later authors evidently overlooked this name resulting in the species being described or listed under different names by KAULFUSS (1827), BORY DE SAINT-VINCENT (1833), SIEBER (exsicc.) and FÉE (1857). CHRISTENSEN (1905) initially considered the species to be a form of *P. aculeatum* (L.) Roth, but in 1932 recognized it as a distinct species.

KAULFUSS (1827) described *Aspidium stramineum*, giving the origin as C.B.S. (Caput Bonae Spei). The collector of the material was not indicated, but currently it is accepted that the material upon which KAULFUSS based the species originated from Mauritius (BOJER 1837; HOOKER 1862; KUHN 1868). The current location of KAULFUSS's pteridophyte collection, that was acquired by RÖMER (STAFLEU & COWAN 1979) is not known and therefore the collector of the material cannot be determined. Two sheets inscribed by W.J. HOOKER as "*Aspid. stramineum* Kaulf. n. sp." are currently housed in the Kew Herbarium. These specimens originated from Mauritius and are duplicates of SIEBER's *Synopsis filicum exsiccatae* (number 34). Although

HOOKER (1862) stated that SIEBER *Synopsis filicum* number 34 is *Aspidium stramineum* Kaulf. there is no proof that KAULFUSS based the species on a SIEBER collection and thus authentic material of *Aspidium stramineum* remains unlocated.

BORY DE SAINT-VINCENT also obtained material from Mauritius and in 1833 described the plant as *Hypopeltis mauritiana*. Neither the type, nor any other material that can be considered original, of this species has yet been located. There is no doubt, however, that the plants are of the same species because BORY DE SAINT-VINCENT described the stipe and rachis as "*squamoso-tomentosis*" and the pinnules as "*argutè crenatis, supernè mucronatis*". The only other *Polystichum* species occurring on Mauritius, *P. crinulosum*, does not conform to this description.

FRANS W. SIEBER spent eleven weeks on Mauritius during late 1822 and early 1823 (GUNN & CODD 1981). In the exsiccatae of his Flora Mauritiana he listed the plant as *Aspidium vestitum*. Since the epithet had already been used by SWARTZ (1801), PRESL renamed the plant *P. sieberianum* citing SIEBER's Flora Mauritiana, ed. 1, suppl. n. 48 exsiccata. SIEBER, however, did not provide diagnoses for his plants but merely lists them in his exsiccatae. Since PRESL did not provide a diagnosis either, both names are invalid under Art. 32.1 (GREUTER et al. 2000).

FÉE (1857) based his description of *P. schizobium* on a collection made by DE MONTBRISON on La Réunion. The type of this collection appears to be missing as a search in BASSA, BORD, FI, L, NTM, P, PC and STR proved fruitless.

DIAGNOSTIC FEATURES AND RELATIONSHIPS. — *Polystichum ammifolium* is characterized by the closely and minutely fimbriated margins of the larger stipe and rachis paleae. Perhaps more diagnostic, however, are the paleae that occur adaxially and abaxially on the lamina which bear long, mainly basally directed, marginal outgrowths. Similarly structured paleae have been observed in *P. vestitum* (G. Forst.) C. Presl from New Zealand and may suggest an affinity. *Polystichum ammifolium* belongs to section *Lasiopolystichum* Daigobo.

VARIATION. — Two forms can be distinguished within *Polystichum ammifolium*. The Mauritian form is characterized by shorter and broader fronds and is generally less dissected than the La Réunion form. The pinnules of the Mauritian form are generally ovate to broadly ovate in outline and shallowly and obtusely lobed. The most diagnostic feature of this form is the stipe which is densely covered by large chartaceous and stramineous, ovate to broadly ovate paleae. The La Réunion form has much longer and narrower and generally more deeply dissected pinnules of which the margins are sharply dentate to aristate. The paleae on the stipe are conspicuously dimorphic with the larger paleae more widely spaced, membranous and stramineous or centrally dark brown, nitid and crustaceous. In spite of these variations the paleae do not differ micromorphologically. Also, the paleae occurring on the lamina surfaces do not differ. It is therefore suggested that the forms be retained as a single species. CORDEMOY (1895) recognised two morphological forms on La Réunion, but conferred no formal taxonomic status to them.

DISTRIBUTION AND ECOLOGY. — *Polystichum ammifolium* is confined to Madagascar, Mauritius and La Réunion. On Mauritius the species occurs at elevations between 500-650 m in dry evergreen thickets and in lower montane wet forests (LORENCE 1978). Dry evergreen thickets that are now confined to the western mountain slopes and flanks fall within the rain shadow area and receive an annual precipitation of 1000-1600 mm. The lower montane wet forests are largely confined to the central plateau of the island and are characterized by a much richer flora. Annual precipitation in these forests range between 1800 and 4200 mm.

On La Réunion the species occurs at elevations ranging from 600-2200 m and grows in a number of plant communities. The principal zones, as defined by BADRÉ & CADET (1978), in which the species occurs are megathermic dry sector vegetation, lowland forests, high altitude hygrophyllic formations and high altitude ericoid vegetation. Although the species largely occurs on moist forest floors it is also found in rock crevices, especially of lava fields at higher elevations.

In Madagascar the distribution of the species appear to be restricted, having been recorded only from the northern Sambirano region.

2. *Polystichum crinulosum* (Desv.) J.P. Roux

Novon 6: 202 (1996). — *Aspidium crinulosum* Desv., Mém. Soc. Linn. Paris 6: 249 (1827). — Lectotype (designated by ROUX 1996): *Sine coll. s.n.*, habitat in insula Mauriti (Mauritius), (P!; iso-, B 96929!); only known material.

Plants terrestrial. Rhizome unknown but probably short and erect to suberect. Stipe castaneous, adaxially sulcate, to 3 mm in diameter at the lamina base, densely paleated, the paleae appear heteromorphous, the larger paleae bicolorous, centrally ebeneous, nitid and crustaceous with a narrow ferruginous to stramineous, membranous margin, sessile, ovate to narrowly ovate, cordate, the margins moderately beset with short, straight, simple or branched, emarginate or forked outgrowths which reduce in size and number towards the apex, the apex terminates in a short acicular cell or a small elliptic thin-walled cell, to 8 × 4 mm, the smaller paleae ferruginous to stramineous, chartaceous, sessile, narrowly ovate to narrowly triangular-hastate, cordate, the margin proximally with a few short, straight, simple or curved, emarginate or forked outgrowths which reduce in size and number towards the apex, the apex terminates in a short acicular cell or a small thin-walled cell; lamina 2-pinnate, with up to 24 pairs of stalked pinnae, narrowly ovate, to 440 mm long, the pinnae opposite to alternate, closely spaced, proximally somewhat more widely spaced, the proximal pinnae reduced; rachis with proliferous buds near the apex, castaneous to stramineous, adaxially sulcate, densely paleated, the paleae ferruginous to castaneous, chartaceous, or proximally often centrally ebeneous, nitid, crustaceous, with a narrow ferruginous, membranous margin, sessile, narrowly ovate to subulate-hastate, cordate to cordate-imbriate, the margins proximally moderately beset with short straight or curved, often emarginate marginal outgrowths which reduce in size and number towards the apex, the apex is

often multiseriate and eglandular or it terminates in a short acicular cell, or a small thin-walled cell, to 3.5×1 mm; pinnae 1-pinnate, with up to 16 pairs of stalked pinnules, oblong-attenuate, slightly auriculate acroscopically, the middle pinnae to 125 mm long, to 25 mm wide; pinna-rachis stramineous, adaxially sulcate, densely paleated, the paleae ferruginous, chartaceous, sessile, narrowly ovate to subulate-hastate, cordate, the margins proximally with short straight or curved, simple or branched outgrowths which rapidly reduce in size and number towards the apex, the apex terminates in a short acicular cell or a small thin-walled cell, to 3×0.8 mm; pinnules opposite to alternate, closely spaced but not overlapping, short-stalked proximally, sessile towards the apex, firmly herbaceous, dark green adaxially, slightly paler abaxially, inaequilateral, ovate to rhombic, basiscopically cuneate, acroscopically cuneate to truncate and auriculate, shallowly obtusely lobed to serrate, the proximal acroscopic pinnules deeply incised acroscopically to form a nearly free broadly obovate lobe, to 14×7 mm, adaxially glabrous, evidently glabrous abaxially. Venation obscure adaxially, evident abaxially. Sori circular, to 1.5 mm in diameter, medial or supramedial on modified vein branches, essentially uniseriate, discrete at maturity; sporangium with 12(-14-)16-indurated annulus cells, stalk glandular; indusium stramineous, black centred, persistent, circular, shallowly repand, maximum radius 0.87(-0.97-)1.07 mm. Spores dark brown, perispore folded to form a close reticulum of inflated and compressed ridges, the ridges echinulate, the ridges and areas between perforated, the exospore $30(-35.32-)42 \times 24(-27.8-)34$ μm . Chromosome number unknown. — Figs. 2, 3D-G.

DESVAUX described the species in 1827, giving the locality as “Habitat in montosis. C. Bonae spei” (Caput Bonae Spei). The sheet selected as lectotype of the species (ROUX 1996), however, gives the locality as “Habitat in insula Mauritiï”. The latter locality is taken as correct as the species does not conform to any of the known African taxa.

KUHN (1868) considered the name to be synonymous with *Polystichum ammifolium* (Poir.)

C. Chr., whilst CHRISTENSEN (1905) believed it to be a form of *P. aculeatum* (L.) Roth. It is, however, distinct from any of the known taxa from the region.

DIAGNOSTIC FEATURES AND RELATIONSHIPS. — *Polystichum crinulosum* is characterized by the presence of proliferous buds on the rachis near the frond apex, the presence of glandular cells along the sporangium stalk and the palea morphology. The paleae apices are generally short and blunt and often multiseriate and eglandular, terminating in a short acicular cell or a small thin-walled cell. The palea morphology suggests that it should be included in section *Metapolystichum* Tagawa.

DISTRIBUTION AND ECOLOGY. — *Polystichum crinulosum* is known only from Mauritius, and nothing is known about its ecology. DESVAUX merely states “Habitat in montosis”. The species is known only from the type collection. Because of the large-scale destruction of the natural vegetation of the island, the species may well now be extinct.

3. *Polystichum kalambatitrense* Tardieu

Notul. Syst. (Paris) 15: 165 (1956); Tardieu, in Humbert, Fl. Madag., fam. 5: 320 (1958). — Type: *Humbert 11914*, Madagascar, massif du Kalambatitra, Mt. Analasitendrika, 1650-1800 m (holo-, P!).

Plants terrestrial. Rhizome decumbent, to 10 mm in diameter, beset with roots, closely spaced persistent stipe bases and paleae, the paleae ferruginous, membranous to chartaceous, broadly attached, lanceolate to narrowly ovate, cordate, the margins closely beset with short straight or curved outgrowths, the apex terminates in a long flagelliform cell, to 10×4 mm. Fronds crowded, 4 or 5 per plant, suberect to arching, to 1.11 m long; stipe proximally castaneous, stramineous higher up, adaxially sulcate, to 455 mm long, to 5 mm in diameter, moderately beset with conspicuously larger and smaller paleae, the larger paleae ferruginous, membranous, broadly attached, ovate to broadly ovate, cordate to cordate-imbricate, the margins closely

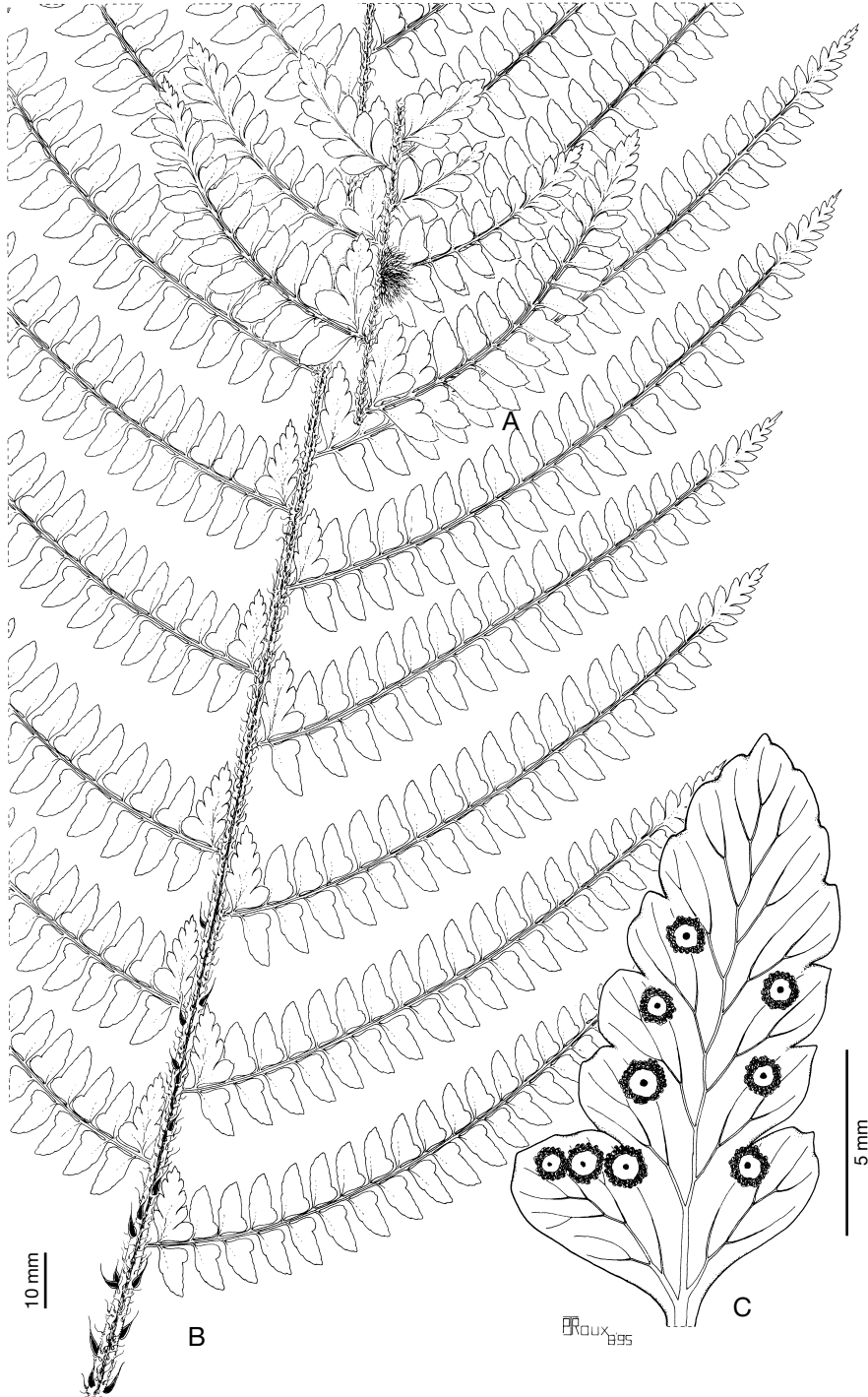


Fig. 2. — *Polystichum crinulosum*: A, distal pinnae showing proliferous buds; B, basal part of lamina; C, abaxial surface of a fertile pinnule. All drawn from s.coll. s.n. (P).

beset with small curved outgrowths, the apex terminates in a long flagelliform cell, to 17×8 mm, the smaller paleae ferruginous to castaneous, membranous, sessile or short-stalked, narrowly lanceolate to narrowly ovate, cordate-imbricate, the margins proximally closely beset with long, simple or branched, flagelliform outgrowths, distally the outgrowths become more widely spaced and rigid, pointing basally or apically, the apex terminates in a long acicular or flagelliform cell, or a small thin-walled cell, to 6.8×0.9 mm; lamina 1-pinnate, with up to 28 pairs of stalked pinnae, herbaceous to coriaceous, ovate-lanceolate, to 650×230 mm; rachis stramineous, adaxially sulcate, moderately to densely paleated, the paleae ferruginous to castaneous, membranous, broadly attached or short-stalked, lanceolate to narrowly triangular, cordate or cordate-imbricate, the margins proximally closely beset with long, simple or branched flagelliform outgrowths, distally the outgrowths are shorter, more widely spaced and curved or straight, the apex terminates in a long flagelliform cell, to 8×2 mm; pinnae opposite to alternate, proximally widely spaced, more closely spaced distally but never overlapping, linear-attenuate to narrowly oblong-attenuate, proximally short-stalked, broadly attached towards the lamina apex, inaequilaterally truncate, with or without an acroscopic auricle, the auricle obtuse, often incised near to the costa, then broadly elliptic, the margins proximally subentire, serrate to serrate-dentate distally, or obtusely lobed, the lobes serrate-dentate, dull green adaxially, slightly paler abaxially, to 135 mm long, to 18 mm wide, adaxially sparsely beset with taeniform paleae along the costa, to 8.5 mm long; abaxially sparsely paleated largely along the costa, the paleae ferruginous to stramineous, membranous, short-stalked, narrowly triangular; narrowly trullate or narrowly triangular-hastate, cordate, proximally with a few short, rigid outgrowths or with a few long flagelliform outgrowths, to 5.5 mm long; costa flexuose distally, sulcate adaxially, pronounced abaxially. Venation free, evident abaxially and adaxially. Sori circular, to 2 mm in diameter, terminal or near-terminal on abbreviated vein branches, near the costa on smaller pinnae; sporangium with 11(-13)-13-indurated annulus cells; indu-

sium ferruginous to castaneous, persistent, repand or unequally lobed, maximum radius $0.36(-0.43)-0.58$ mm; spores brown, the perispore forms a close reticulum of inflated ridges, the ridges crested, the ridges and areas between echinulate, minutely perforated. Chromosome number unknown. — Figs. 3H, I, 4.

MATERIAL EXAMINED. — MADAGASCAR: *Humbert 11914*, massif du Kalambatitra, Mt. Analasitendrika, 1650-1800 m (P), type; *Humbert 12158*, massif de l'Ivakoany, 1250-1550 m (BR, P).

DIAGNOSTIC FEATURES AND RELATIONSHIPS. — TARDIEU-BLOT (1956a) suggested that *Polystichum kalambatitrense* was closely related to *P. falcinellum* (Sw.) C. Presl from Madeira and *P. macleae* (Baker) Diels from South Africa. Although *P. falcinellum* is a species with 1-pinnate fronds, there appears to be no affinity between these taxa as it differs markedly from *P. kalambatitrense* in indusium and paleae morphology. *Polystichum kalambatitrense* appears to be related to *P. macleae* because of the similarity in the size and morphology of the indusia and paleae. Unlike *P. macleae*, where some proximal marginal outgrowths of the paleae terminate in a small thin-walled cell, the marginal outgrowths in *P. kalambatitrense* terminate either in an acicular cell or a long flagelliform cell. In *P. kalambatitrense* the stipe paleae rarely terminate in a thin-walled cell whereas in *P. macleae* they regularly do so. The epidermal cell length and the guard cell length are larger for *P. kalambatitrense* ($50(-56.8)-70$ μm) than for *P. macleae* ($32(-46.03)-60$ μm).

VARIATION. — *Polystichum kalambatitrense* shows some variation in pinna morphology. In some plants the acroscopic auricle on the proximal pinnae is incised near the costa whereas in others the pinnae are barely acroscopically developed. The pinna margins also vary from entire to proximally slightly repand to serrate, or obtusely lobed with the margins of the distal lobes serrate-dentate.

DISTRIBUTION AND ECOLOGY. — *Polystichum kalambatitrense* is endemic to Madagascar and

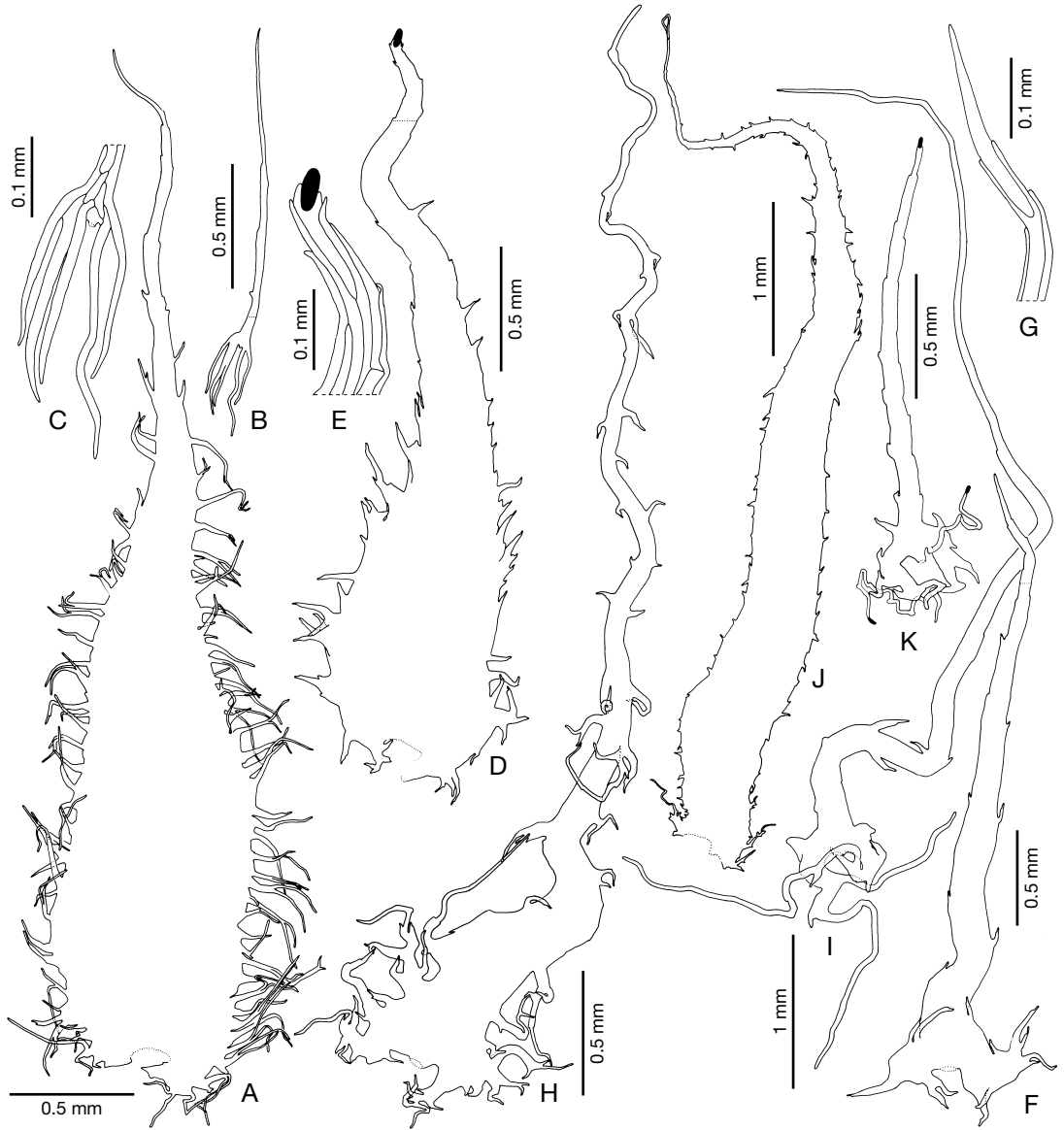


Fig. 3. — Stipe and lamina paleae in *Polystichum* species. — *Polystichum ammifolium*: A, stipe palea, *Boivin* 822 (B); B, lamina palea (adaxial surface), *Rakolomalala* s.n. (P); C, basal part of B showing the cellular structure. — *Polystichum crinulosum*: D, stipe palea, *s.coll.* s.n. (P); E, apex of D showing the cellular structure; F, rachis palea, *s.coll.* s.n. (P); G, apex of F showing the cellular structure. — *Polystichum kalambatitense*: H, stipe palea, *Humbert* 12158 (P); I, lamina palea (abaxial surface), *Humbert* 11914 (P). — *Polystichum luctuosum*: J, stipe palea, *Roux* 2268 (NBG); K, lamina palea (abaxial surface), *McDonell* 34 (BM).

appears to be restricted to the southern part of the central mountain range. The species is confined to forests along the Kalambatitra mountain range, where on Mount Analatsitendrika it grows

at elevations between 1650 and 1800 m. To the south, on the l'Ivakoany mountain range, the species grow at elevations between 1250 and 1550 m.

4. *Polystichum luctuosum* (Kunze) T. Moore

Index Fil.: 95 (1858); Christensen, Dansk Bot. Ark. 7: 68 (1932); Tardieu, Fl. Madag., fam. 5: 320 (1958); Roux, Bull. Nat. Hist. Mus. Lond. (Bot.) 30: 37 (2000). — *Aspidium luctuosum* Kunze, Linnaea 10: 548 (1836). — *Polystichum lobatum* var. *luctuosum* (Kunze) Christ, Ber. Schweiz. Bot. Ges. 3: 34 (1893). — Types: *Ecklon s.n.*, in monte Katriviersberg in sylvis, (syn-, LZ, delet.); *Ecklon s.n.*, ad fontes fl. Katrivier prope Philipstown, in sylvis montium, (syn-, LZ, delet.).

Aspidium tsus-simense Hook., Sp. Fil. 4: 16 (1862). — *Polystichum tsus-simense* (Hook.) J. Sm., Hist. Fil.: 219 (1875). — Type: *Wilford s.n.*, Island of Tsus Sima, in the Straits of Korea (holo-, K [2 sheets]; NBG!-photo).

Plants terrestrial, epilithic, or rarely as low-level epiphytes. Rhizome short, erect to suberect, to 10 mm in diameter, densely beset with roots, persistent stipe bases, and paleae, the paleae castaneous, chartaceous, the larger paleae broadly attached, ovate, narrowly ovate, or lanceolate, cordate, with long twisted uniseriate, gland-tipped hairs on the apical margin and surface, the apex flagelliform, terminating in an oblong thin-walled cell, to 10.5 × 3.3 mm, the smaller short-stalked, narrowly triangular to subulate, cordate, the margins proximally with numerous long and twisted uniseriate hairs, distally with widely spaced apically and basally directed marginal outgrowths that become smaller apically, the apex flagelliform, terminating in a small thin-walled cell. Fronds crowded, caespitose, 7-16 per plant, suberect to arching, to 0.93 m long; stipe proximally castaneous, stramineous distally, adaxially sulcate, to 450 mm long, to 5 mm in diameter, densely paleated, the proximal paleae castaneous, chartaceous to crustaceous, broadly attached, ovate, cordate, the margins proximally entire or with a few short and/or long uniseriate hairs, distally with numerous multicellular hairs as for the rhizome paleae, the distal paleae short-stalked, narrowly oblong, narrowly triangular or subulate, cordate to hastate, the margins bearing a few long and/or short multicellular hairs proximally, distally with widely and irregularly spaced outgrowths reduced in size and number towards apex, the apex flagelliform, terminating in a small thin-walled cell, to 15 × 1.5 mm; lamina 2-pinnate to 2-pinnate-pinnatifid, with up to 25-stalked

pinna pairs, to 480 mm long, firmly herbaceous to coriaceous, olive-green adaxially, paler abaxially, narrowly ovate to ovate, the proximal pinnae slightly reduced, often somewhat deflexed; rachis stramineous, adaxially sulcate, densely paleated, the paleae dark brown to black, glossy, chartaceous to crustaceous, short-stalked, narrowly triangular to subulate, cordate to hastate, the auricles usually bearing long and twisted multicellular and uniseriate hairs some of which terminate in a thin-walled cell, the margins either distally with short, widely and irregularly spaced outgrowths that reduce in size and number towards the apex, or more or less entire in smaller paleae, to 7 mm long; pinnae short-stalked, 1-pinnate to 1-pinnate-pinnatifid, with up to 12-stalked pinnule pairs, narrowly lanceolate, proximally widely spaced, distally often somewhat overlapping, to 173 mm long; pinna-rachis stramineous, adaxially sulcate, densely beset with paleae similar to, but less complex than those on the rachis; pinnules widely spaced to overlapping, the proximal acroscopic pinnule the largest, often significantly longer than the next, to 40 mm long, to 12 mm wide, inaequilateral, narrowly trullate to rhomboid, basiscopically cuneate, acroscopically truncate and auricled, often somewhat falcate, lobate-serrate, aristate, the proximal pinnules short-stalked, often acroscopically incised to or nearly to the costa, the costa adaxially sulcate, glabrous, abaxially sparsely beset with castaneous, chartaceous, narrowly triangular-hastate to subulate-hastate paleae, cordate to cordate-imbricate, proximally with long and/or short filiform outgrowths that often terminate in a thin-walled cell, the apex always terminating in a small thin-walled cell, to 0.3 mm long. Venation obscure. Sori circular, c. 1.2 mm in diameter; terminal or near-terminal on abbreviated vein branches, essentially uniseriate; sporangium stalk eglandular, capsule with 10(-13)-19-indurated annulus cells; indusium peltate, circular, entire, repand or crenulate, persistent, brown, pale brown and often dark-centred before drying, cupulate when dry, maximum radius 0.5(-0.73)-0.95 mm. Spores 32 per sporangium, brown, the perispore unevenly folded to form narrow and broad reticulate ridges, the ridges and areas between ridges echinulate, spicu-

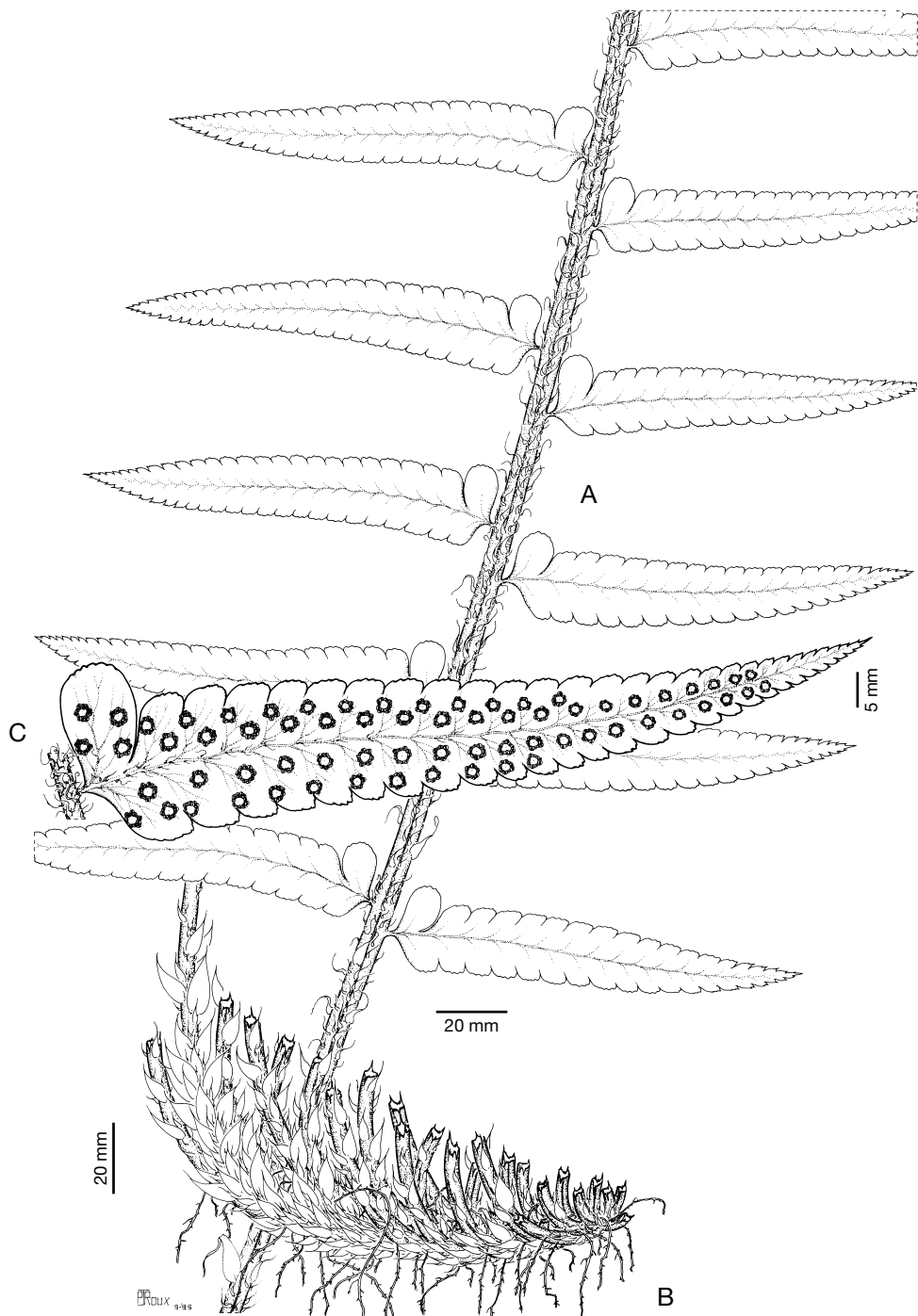


Fig. 4. — *Polystichum kalambatitrense*: A, basal part of the lamina; B, rhizome; C, abaxial surface of a fertile pinna. Humbert 11914 (P).

late or verruculate, exospore 30(-38.84-)50 × 22(-28.2-)36 µm. Chromosome number 2n = 123, apogamous. — Figs. 3J,K.

MATERIAL EXAMINED. — MADAGASCAR: *Humbert & Swingle 4798*, environs d'Ambositra, Mt. Vatomavy (BM, P); *Perrier de la Bâthie 13656*, massif de l'Andringitra, 1200 m (P); *Herb. Jard. Bot. Tananarive 3229*, Merina (P); *H.P.B. s.n.*, Manongarivo, 1200 m (P). — LA RÉUNION: *Cadet 4129*, Thermes de Cilaós, 1200 m (P).

DIAGNOSTIC FEATURES AND RELATIONSHIPS. — Diagnostic of *Polystichum luctuosum* is the olive-green colour of the adaxial surface of the lamina and the darker veins seen in live plants. It is also separated from other taxa in the region by the usually very dark and narrow paleae occurring along the stipe and rachis. The larger rhizome and stipe base paleae bear long filiform outgrowths along the margin and paleae surface. Indusia are large, persistent, and entire, and take on a cupulate form when mature. *Polystichum luctuosum* is furthermore a triploid apomict with 32 spores per sporangium and has a somatic chromosome number of 2n = 123. *Polystichum luctuosum* belongs to section *Xiphopolystichum* Daigobo.

VARIATION. — *Polystichum luctuosum* shows little variation in stipe, lamina and basal pinna length within the study area. A comparison of these parts with Asian material shows that African (including Madagascar) plants are slightly larger than plants from Asia (ROUX 1998).

DISTRIBUTION AND ECOLOGY. — The species occurs on La Réunion and the central parts of Madagascar at elevations to 1200 m. *Polystichum luctuosum* also occurs on the Indian subcontinent, extending to Pakistan, China, Vietnam, South Korea and Japan (Honsyu, Sikoku and Kyusyu). In South Africa, *Polystichum luctuosum* occurs from the Eastern Cape, through KwaZulu-Natal to the north-eastern parts of the Free State, Mpumalanga and the Northern Province. It also extends to the lower western parts of Lesotho and the higher lying part of Swaziland with isolated populations occurring along the eastern escarpment in Zimbabwe.

Polystichum luctuosum mostly occurs epilithically along streams, but often also as a low-level epiphyte in moist forests. Plants often also grow on rocks away from water and in fairly dry conditions.

5. *Polystichum maevaranense* Tardieu

Notul. Syst. (Paris) 15: 166 (1956); in Humbert, Fl. Madag., fam. 5: 319 (1958). — Type: *Humbert & Capuron 25019*, Madagascar, Centre-Nord: montagnes au nord de Mangindrano (haute Maevarano) jusqu'au sommet d'Ambohimirahavavy (partage des eaux Mahavavy-Androranga), 1900 m (holo-, P!; iso-, L!); only known material.

Plants terrestrial. Rhizome short, erect to suberect, to 6 mm in diameter, beset with closely spaced persistent stipe bases, roots, and paleae, the paleae densely impregnated, ebeneous to black, crustaceous with a narrow ferruginous membranous margin, nitid, broadly attached, linear-lanceolate, the margins with widely spaced short outgrowths, the apex terminating in an acicular cell, to 7 × 1.2 mm. Fronds caespitose, to 6 per plant, suberect to arching, to 610 mm long; stipe proximally castaneous, brown higher up, adaxially sulcate, to 310 mm long, to 3 mm in diameter, proximally densely paleated, the paleae similar to those on the rhizome, to 15 × 2 mm, distally moderately paleated, the paleae dark brown, short-stalked, narrowly triangular, cordate to cordate-imbricate, the margin proximally with simple or branched, straight or curved outgrowths, the apex entire, terminating in an acicular cell; lamina 1-pinnate, lanceolate to narrowly oblong, with 12-15 pinna pairs, the proximal pinnae not reduced, the proximal pinna pair deflexed, to 250 mm long; rachis brown, sulcate adaxially, densely paleated, the paleae castaneous to ferruginous, short-stalked, narrowly linear-attenuate, narrowly triangular, or subulate, cordate to cordate-imbricate, often hastate, the margin proximally beset with simple or branched, straight or curved outgrowths, the apex entire, subulate, terminating in an acicular cell, to 8 mm long, proliferous near the apex, with 1-3-paleated buds per frond borne abaxially in the axils of the distal pinnae, the paleae ferrugi-

neous, broadly attached, lanceolate to narrowly ovate, cordate, the margins with short marginal outgrowths, the apex terminates in an acicular cell, to 3×0.7 mm; pinnae glossy green adaxially, pale green abaxially, approximate to alternate, proximally widely spaced, distally more closely spaced but not overlapping, proximally short-stalked, distally sessile, firmly herbaceous to coriaceous, to 66 mm long, to 18 mm wide, proximally oblong-attenuate, distally lanceolate to trullate, strongly inaequilateral, auriculate acroscopically, the auricle on the proximal pinnae incised near to the costa, broadly elliptic, the pinnae obliquely lobate, serrate, pungent, adaxially glabrous or with a few subulate paleae along the sulcated costa, abaxially moderately beset with stiff ferruginous, short-stalked, subulate to narrowly triangular paleae, with a few simple or branched outgrowths at the base, the apex terminates in an acicular cell, to 2 mm long. Venation obscure. Sori essentially uniseriate, often pluriseriate proximally, medial to inframedial, circular, to 1.5 mm in diameter; sporangium with 10(-13)-14-indurated annulus cells; indusium stramineous, persistent, minutely repand, maximum radius 0.58(-0.6)-0.65 mm; spores brown, perispore smooth to glebose, variously perforated, echinulate, exospore 30(-33.68)-40 \times 22(-14.96)-28 μ m. Chromosome number unknown. — Fig. 6A-C.

DIAGNOSTIC FEATURES AND RELATIONSHIPS. — *Polystichum maevaranense* is characterized by a thin suberect rhizome, rhizome and stipe paleae that are crustaceous, dark brown to black and glossy, the long stipe and the narrowly lanceolate pinna outline. The proliferous buds are borne along the rachis in the distal part of the frond. Also, the palea morphology distinguishes it from any other taxon in the region.

Polystichum maevaranense is poorly known and the material at hand is insufficient for it to be confidently placed in any section hitherto described.

DISTRIBUTION AND ECOLOGY. — A little-known species endemic to Madagascar, where it is reported to grow at an elevation of 1900 m in wet forests on gneiss laterites in the northern part of the island.

6. *Polystichum pauciaculeatum* Bonap.

Notes Prérid. 7: 206 (1918). — Type: *d'Alleizette 30*, Madagascar, Mandraka (holo-, P!).

Polystichum coursii Tardieu, Mém. Inst. Sci. Madagascar, sér. B, Biol. Vég. 7: 42 (1956); Tardieu, in Humbert, Fl. Madag., fam. 5: 324 (1958). — Type: *Cours 4225*, Madagascar, Bemainty à Androndramanitra (holo-, P!).

Plants terrestrial. Rhizome short, erect to suberect, to 15 mm in diameter, beset with roots, closely spaced persistent stipe bases, and paleae, the paleae ferruginous to castaneous, chartaceous. Fronds caespitose, to 9 per plant, suberect to arching, to 1.19 m long; stipe proximally castaneous, distally stramineous, adaxially sulcate, to 615 mm long, to 5 mm in diameter, sparsely to densely paleated, the paleae at the stipe base ferruginous, chartaceous, broadly attached, narrowly linear, often somewhat rugose, cordate, the margins with short, widely spaced outgrowths (rarely also with unicellular glandular cells), the apex terminates in an acicular cell or small thin-walled cell, to 40×3 mm, the paleae higher up the stipe appear heteromorphous, ferruginous to castaneous, chartaceous, the larger paleae broadly attached, ovate to lanceolate, cordate to cordate-imbricate, the margins proximally fimbriate, entire towards the apex, the fimbriae short or long, straight or curved, and simple or branched, the apices usually forked, the paleae apices often flagelliform, terminating in a small thin-walled cell or an acicular cell, to 25×6 mm, the smaller paleae short-stalked, hastate, cordate to cordate-imbricate, with numerous long marginal outgrowths proximally, the apex entire, subulate, always terminating in an acicular cell; lamina 2-pinnate to 3-pinnate, with up to 28 pairs of stalked pinnae, narrowly ovate to narrowly elliptic, to 685 mm long, bearing 1-5 ferruginously paleated proliferous buds along the rachis near the apex, the pinnae opposite to alternate, closely to widely spaced, proximal pinnae slightly to strongly reduced, often somewhat deflexed; rachis stramineous, adaxially sulcate, often somewhat flexuose towards the apex, sparsely to densely paleated, the paleae ferruginous, chartaceous, short-stalked, lanceolate to subulate, cordate to cordate-imbricate, the margins proximally fimbri-

ate, entire towards the apex in larger paleae, the fimbriae restricted to the proximal part in smaller paleae, the fimbriae short or long, straight or curved and simple or branched, the apices often forked, the apex usually entire, flagelliform or acicular, often terminating in a small thin-walled cell, to 8×2 mm; pinnae 1-pinnate to 2-pinnate, with up to 18 pairs of stalked pinnules, oblong-attenuate, proximally often slightly auriculate acroscopically, to 180×33 mm; pinna-rachis stramineous, adaxially sulcate, sparsely to densely paleated, the paleae ferruginous, chartaceous, narrowly ovate to subulate, short-stalked, cordate to cordate-imbricate, the margins fimbriate, the fimbriae similar to those of the paleae on the stipe and rachis, the apex entire, flagelliform or acicular, usually terminating in an acicular cell (rarely terminating in a small thin-walled cell), to 4.5×1 mm; pinnules opposite to alternate, closely to widely spaced, proximally short-stalked, sessile towards the apex, firmly herbaceous, dark green adaxially, slightly paler abaxially, inaequilateral, broadly ovate to rhombic, basiscopically cuneate, acroscopically truncate and auriculate, the larger pinnules commonly deeply incised at the base and thus forming a nearly free auricle, the margins serrate, aristate, to 27 mm long, adaxially sparsely beset with twisted stramineous paleae chiefly along the costa, subulate or proximally with one or more short or long marginal outgrowths, the apical cell is always acicular, to 4 mm long, abaxially moderately paleated, the paleae stramineous, membranous, short-stalked, subulate to narrowly triangular, proximally with a few short or long, simple or branched marginal outgrowths, the apex always terminates in an acicular cell, to 2.2 mm long. Venation evident or obscure. Sori circular, to 1.5 mm in diameter, terminal or near-terminal, essentially uniseriate, discrete to slightly confluent at maturity; sporangium with 11(-13)-30-indurated annulus cells; indusium stramineous, persistent, circular to amorphous, usually simple but often with a small or large wing, repand to erose, maximum radius $0.43(-0.64)-0.9$ mm; spores castaneous, the perispore folded to form inflated tubercules and ridges, echinulate to verruculate, closely perforated, exospore $30(-37.89)-48 \times 20(-27.06)-44$ μm . Chromosome number unknown. — Figs. 5, 6D-F.

MATERIAL EXAMINED. — MADAGASCAR: *Baron 2161*, without precise locality (P); *Benoist 986*, Ankaratra, Manjakatempo (P); *Bosser 10985*, Ankaratra (Manjakatempo), 2000 m (P); *Capuron 4*, Angavokely (P); *Cours 4225*, Bemaity à Androndramanitra, 800-850 m (P); *d'Alleizette 30, 84*, Mandraka (P); *Decary 13363*, Manjakatempo (P); *Decary 17542*, forêts au sud d'Ambositra (P); *Hildebrandt 3766*, Ost-Imerina: Andrangaloaka (B [4 sheets], K, P); *Hodgkin & Stanfield s.n.*, Central Plateau, (K [3 sheets]); *Humbert 3243*, Pic d'Ivohibe (Bara), 1500-2000 m (P); *Humbert 3730*, massif de l'Andringitra (Iratsy): vallées de la Riambava et de l'Antsiforta et montagnes environnantes, 2000 m (P); *Humbert 6096*, massif de l'Andohahelo: vallée de Ranohela, 1200-1800 m (P); *Humbert 11121*, Tampokesta au N d'Ankazobe: forêt d'Ambohitantely, 1600 m (P); *Humbert & Capuron 28402*, environs d'Ambatofinandrahana (Betsileo) au km 300 de la route Tananarive-Fianarantsoa, 1550-1600 m (BOL, BR, L, P [2 sheets]); *Humbert & Capuron 30273*, massif de l'Ankaratra, forêt de Manjakatempo, 1700-2200 m (P); *Leandri et al. 3396*, massif de l'Andringitra: forêts de Imaiso, 1500-2000 m (P); *Onraedt 10M87*, Ambatofitorahana, 35 km au sud d'Ambositra, 1600 m (BR); *Perrier de la Bâthie 7928*, massif de l'Andringitra, 2000-2400 m (P); *Perrier de la Bâthie 13362*, Mt. Tsiafajavona (Ankaratra), 2000-2400 m (P); *Pool s.n.*, Antananarivo (K); *Rabarijaona s.n.*, recueillies dans la forêt d'Ankeramadinika (district de Manjakandriana, 1300 m (P); *Ramuaria 1871*, forest near Ankerameduika (K); *Rauh 7669*, wald 30 km südlich Ambositra (M); *Viguiet & Humbert 1699*, province du Vakinankaratra, district d'Ambatolampy, Est d'Ankaratra, du Tsiafajavona, 1800-1900 m (P); *Waterlot 834*, Angavo, Tananarive (P); *Herb. Jard. Bot. Tananarive 4761*, Forêts du Tritondroina, 1800 m (P); *sine coll. s.n.*, Mandraka (Herb. PIC.SERM. 15765).

Polystichum pauciaculeatum was first collected by D'ALLEIZETTE in December 1905, but was not formally described until 1918 by BONAPARTE who suggested that it belonged to the *P. aculeatum* group. TARDIEU-BLOT (1956a, 1956b), in her treatment of the Madagascan *Polystichum* species, and later also in the flora of Madagascar and the Comores (1958), makes no reference of this species. *Polystichum coursii*, here considered synonymous with *P. pauciaculeatum*, was suggested to belong to the *P. setiferum* group of species (TARDIEU 1956b). Several collections belonging to this species were cited as belonging to *P. pungens* (Kaulf.) C. Presl by CHRISTENSEN (1932). *Polystichum pungens* is, however, confined to South Africa (ROUX 2000).

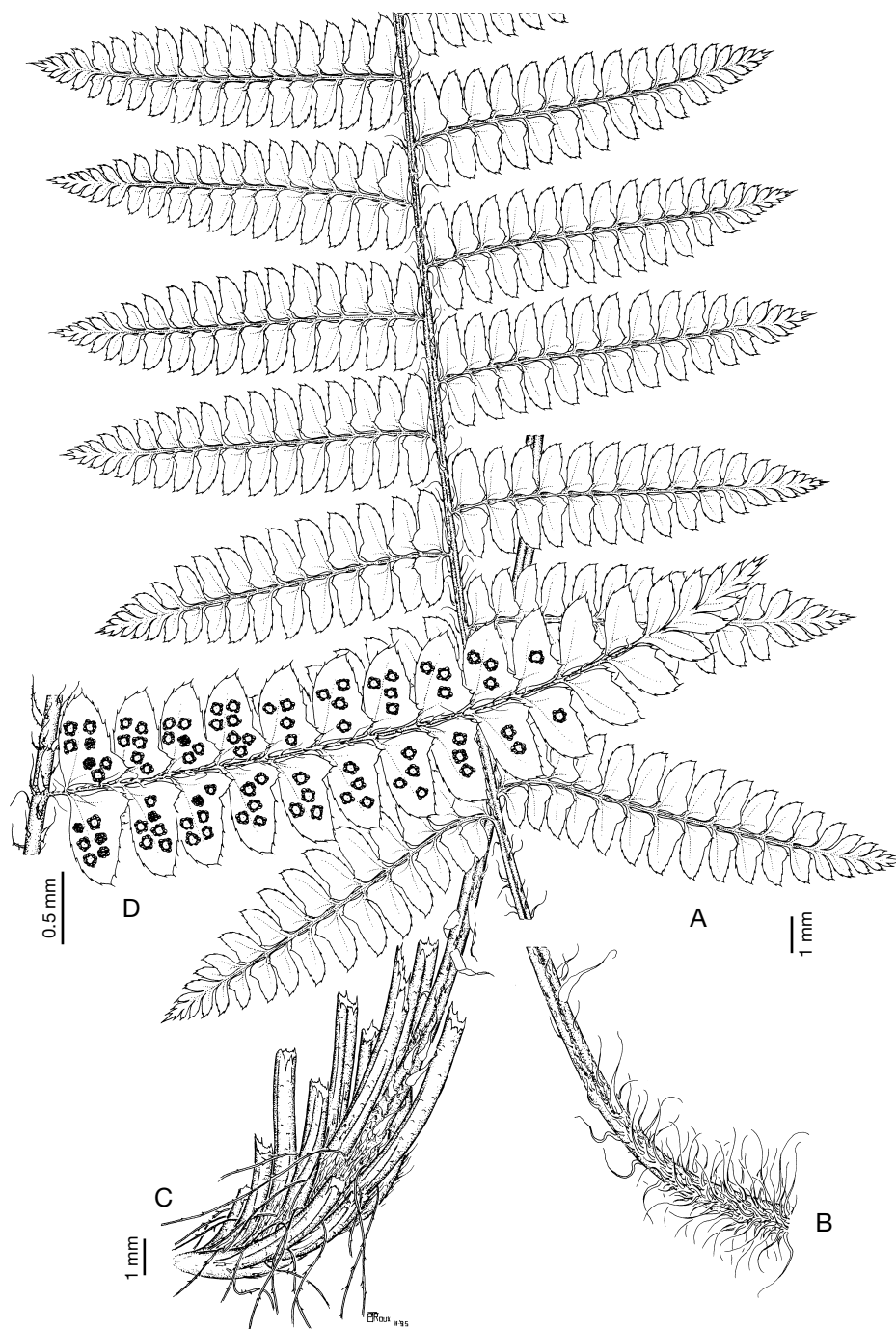


Fig. — 5. *Polystichum pauciaculeatum*: **A**, basal part of the lamina; **B**, stipe base; **C**, rhizome; **D**, abaxial surface of a fertile pinna. A-B, Cours 4225 (P); C-D, Capuron 4 (P).

BONAPARTE (1918), in describing *P. pauciaculeatum*, does not mention that the species is proliferous. The type specimen does, however, possess poorly developed buds that are easily overlooked. Similarly, the type of *P. coursii* also has poorly developed proliferous buds.

DIAGNOSTIC FEATURES AND RELATIONSHIPS. — Considering palea morphology, *Polystichum pauciaculeatum* is related to *P. kilimanjaricum* and *P. tsaratananense*. It can, however, be separated from these species by the usually ferruginous, somewhat rugose, very long and narrow stipe base paleae and the firmly textured, often castaneous, ovate to lanceolate paleae with closely but shortly fimbriated margins that extend to the rachis. *Polystichum pauciaculeatum* belongs to section *Metapolystichum* Tagawa.

VARIATION. — *Polystichum pauciaculeatum* shows extreme variation in a large number of features. Perhaps the most apparent is the frond architecture and palea density. Stipe length ranges from 90 to 612 mm, whereas the lamina length varies between 370 and 685 mm. The proximal pinnae in some plants are widely spaced and hardly reduced whereas in others they are strongly reduced, resulting in a narrowly elliptic lamina outline. Pinnules also vary significantly in size and division. In some plants the proximal acroscopic pinnules are divided near the base to form an almost free auricle, but in others both the acroscopic and basispic pinnules are divided to the base forming free, broadly ovate to rhombic segments.

Variation in palea density is especially striking. Some plants are sparsely paleated whereas others are densely beset with stramineous to ferruginous paleae along the stipe, rachis and pinna-rachises. The morphology of the paleae, however, shows little variation. The larger paleae along the rachis are generally stramineous to ferruginous, but in some plants they are centrally castaneous.

The number of proliferous buds along the rachis also varies significantly. Although only one or two buds per frond are generally well developed (rarely up to five), there are many more, but these are usually undeveloped and easily overlooked.

DISTRIBUTION AND ECOLOGY — *Polystichum pauciaculeatum* is endemic to Madagascar and confined to the central highlands. The species is adapted to a wide range of habitats and occurs at elevations ranging from 800 to 2400 m. It is largely a forest species occurring in lowland rain forests, moist montane forests and montane bushland and thickets. On Mount Ankaratra it grows in volcanic-derived soils whereas to the south, on Mt. Andringitra, it grows in soils of granitic origin.

7. *Polystichum tsaratananense* Tardieu

Mém. Inst. Sci. Madagascar, sér. B, Biol. Vég. 7: 44 (1956); in Humbert, Fl. Madag., fam. 5: 322 (1958). — Type: *Humbert 18144*, Madagascar, massif du Tsaratanana, montagnes entre le haut Sambirano et le haut Maivarano (entre Mangindrano et Ampanompia), 1400-1800 m. Forêt ombrophile sur latérite de gneiss (holo-, P!).

Plants terrestrial. Rhizome short, erect to suberect, to 10 mm in diameter, densely beset with roots, closely spaced persistent stipe bases, and paleae, the paleae ferruginous, dark brown or ebeneous with narrow pale brown margins, nitid, chartaceous to crustaceous, broadly attached, narrowly linear-attenuate to narrowly lanceolate, cordate, the margins beset with widely spaced, short, apically or basally directed outgrowths, the apex terminates in a long acicular cell, to 20×0.3 mm. Fronds caespitose, suberect to arching, to 1.1 m long; stipe proximally castaneous, stramineous higher up, sulcate adaxially, to 370 mm long, to 6 mm in diameter, densely beset with paleae appearing heteromorphic, the larger paleae ferruginous and chartaceous throughout or crustaceous, nitid, and black to dark brown with a narrow pale brown margin, broadly attached, cordate, the margins closely beset with short simple or branched, straight or curved outgrowths, the apex terminates in an acicular cell, to 25×4 mm, the smaller paleae ferruginous to stramineous, chartaceous, sessile or short-stalked, ovate to narrowly triangular, cordate to cordate-imbricate, the margins closely beset with simple or branched, short or long, straight or curved out-

growths that become more widely spaced distally, the apex terminates in an acicular cell or rarely in a small oblong thin-walled cell; lamina 2-pinnate to 3-pinnate, with up to 27 pairs of stalked pinnae, ovate-lanceolate, often with a paleated proliferous bud abaxially in a distal pinna axil, to 800 mm long, the proximal pair not or slightly reduced, somewhat deflexed; rachis stramineous, sulcate adaxially, densely paleated, the paleae ferruginous to stramineous, chartaceous, short-stalked, narrowly ovate, ovate-lanceolate, oblong-attenuate or subulate, cordate to cordate-imbricate, the margins closely beset with short or long, simple or branched, straight or curved outgrowths, entire towards the apex in smaller paleae, terminating in an acicular cell, to 10×2 mm; pinnae 1-pinnate, with up to 13 pairs of stalked pinnules, broadly to narrowly oblong-attenuate, opposite to alternate, short-stalked, widely spaced or slightly imbricate, firmly herbaceous, to 190×50 mm, the proximal acroscopic pinnule usually longer than the next; pinna-rachis stramineous, sulcate adaxially, closely paleated, the paleae ferruginous to stramineous, chartaceous, short-stalked, narrowly lanceolate, narrowly oblong or subulate, cordate to cordate-imbricate, proximally closely beset with long and short, simple or branched, usually twisted outgrowths, entire towards the apex, the apex terminates in an acicular cell, to 6×1 mm, rarely also bearing paleated proliferous buds near the pinna apex; pinnules opposite to alternate, proximally short-stalked, sessile distally, imbricate or not, inaequilateral, ovate, obliquely rhomboid or falcate, basiscopically narrowly cuneate, acroscopically cuneate to truncate and auriculate, the larger pinnules lobate-serrate, the smaller pinnules serrate to doubly serrate, aristate, to 35 mm long, adaxially sparsely beset with simple filiform paleae terminating in an acicular cell, to 2.8 mm long, abaxially sparsely set with stramineous, short-stalked, filiform to subulate paleae with a few straight and simple or branched marginal outgrowths, the apex terminates in an acicular cell, to 2.5 mm long. Sori circular, to 1.5 mm in diameter; sporangium with 12(-14-)16-indurated annulus cells; indusium stramineous, subentire, maximum radius 0.34(-0.42-)

0.53 mm; spores unknown. Chromosome number unknown. — Fig. 6G-J.

MATERIAL EXAMINED. — MADAGASCAR: *Humbert 18144*, montagnes entre le haut Sambirano et le haut Mairarano, 1400-1800 m (P); *Humbert 18475*, massif du Tsaratanana, plateau supérieur et hauts sommets de l'Amboabory à l'Antsianongatalata, 2000-2700 m (P); *Humbert 18266*, massif du Tsaratanana et haute vallée du Sambirano, ± 2000 m (P [2 sheets]); *Perrier de la Bâthie 7642*, massif de Manangarivo, 1200 m (P [2 sheets]); *Humbert & Capuron 25035*, montagnes au nord de Mangindrano (haute Maevarano), jusqu'au sommet d'Ambohimirahavavy, 1900 m (L, P [3 sheets]); *Rauh s.n.*, Mandraka-Schlucht (M).

DIAGNOSTIC FEATURES AND RELATIONSHIPS. — *Polystichum tsaratananense* is characterized by the narrow, crustaceous, dark brown to black stipe paleae. Although the stipe paleae in some plants are ferruginous to stramineous, at least some paleae at the stipe base are usually densely impregnated. The short, curved, marginal outgrowths of the paleae and the small, subentire to repand indusia are also diagnostic.

Based on palea morphology, *P. tsaratananense* appears to have a closer affinity with *P. kilimanjaricum* Pic. Serm. from Africa than with any of the Mascarenes species. Both taxa are characterized by the presence of proliferous buds near the frond apex. In *P. tsaratananense* the rhizome and stipe paleae are generally densely impregnated but are narrower and much longer than in *P. kilimanjaricum*. The paleae in both species terminate mostly in an acicular cell; in *P. tsaratananense* the outgrowths are short and curved whereas in *P. kilimanjaricum* they are long, slender and relatively straight. The indusia of *P. tsaratananense* are also smaller (0.34(-0.42-)0.53) than those of *P. kilimanjaricum* (0.73(-0.87-)1.02). *Polystichum tsaratananense* belongs to section *Lasiopolystichum* Daigobo.

VARIATION. — The degree to which the paleae of the stipe are impregnated shows the highest degree of variation. In some plants only a few paleae at the stipe base are impregnated whereas in others impregnated paleae may extend to the lamina base. Tripinnate fronds in this essentially 2-pinnate species are known but not very common.

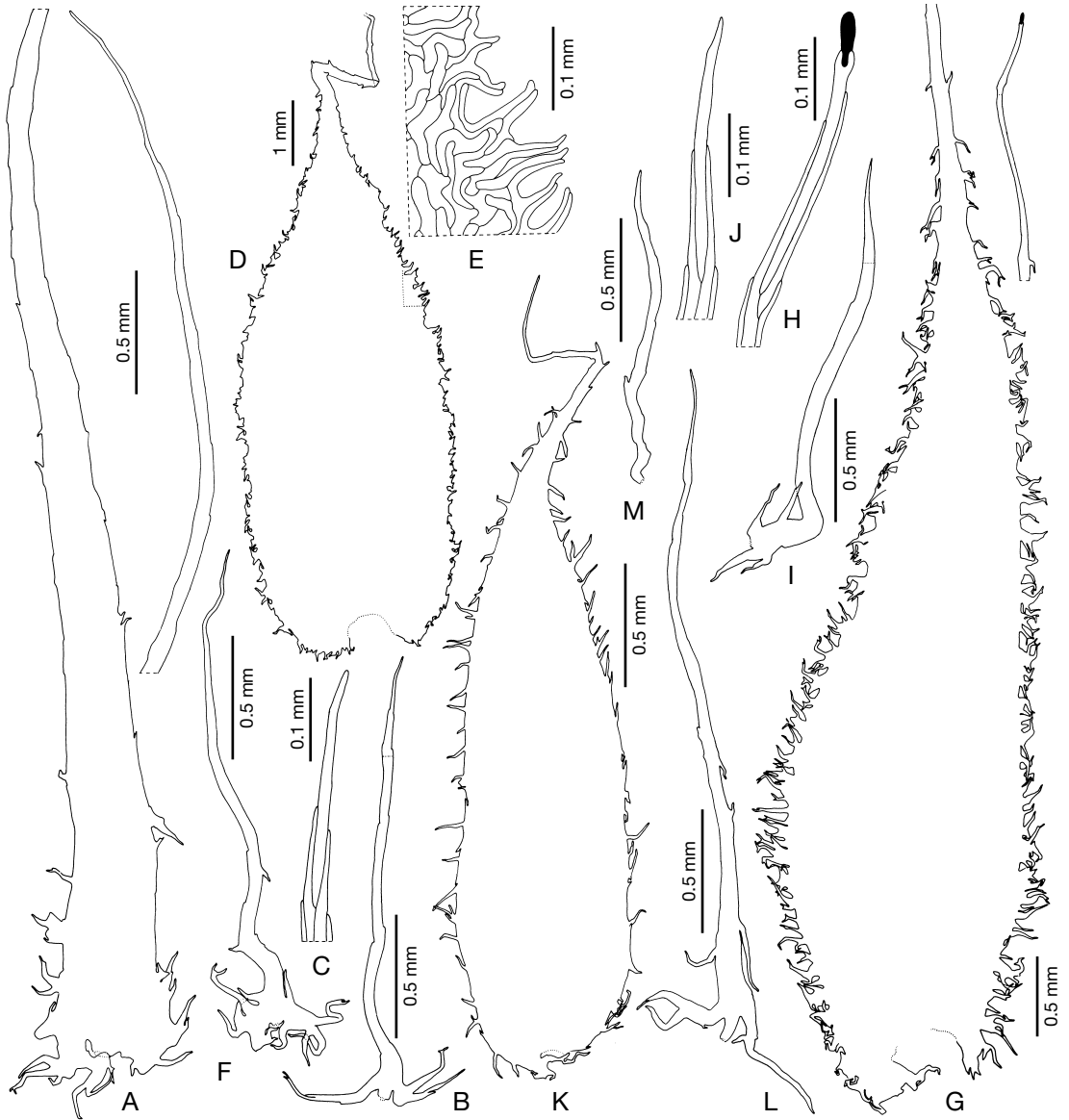


Fig. 6. — Stipe and lamina paleae in *Polystichum* species. — *Polystichum maevaranense*: A, rachis palea; B, proliferous bud palea; C, apex of B showing the cellular structure. Humbert 15019 (P). — *Polystichum pauciaculeatum*: D, stipe palea. Leandri et al. s.n. (P); E, margin of D showing the cellular structure; F, lamina palea, abaxial surface. Humbert 11121 (P). — *Polystichum tsaratananense*: G, stipe palea; H, apex of G showing the cellular structure. Humbert & Capuron 25035 (P); I, lamina palea (abaxial surface); J, apex of I showing the cellular structure. Humbert 18144 (P). — *Polystichum wilsonii*: K, stipe palea; L-M, lamina palea, abaxial surface. K-L, Alluaud 241 (P); M, Esterhuysen 26699 (BOL).

DISTRIBUTION AND ECOLOGY. — *Polystichum tsaratananense* is endemic to Madagascar, where it is confined to the northern part of the central highlands. It is a forest species and essentially con-

fined to elevations between 1200 and 2700 m. At lower elevations the species occurs on gneiss or siliceous soils but on Mount Tsaratanana above 2000 m the soils are basalt-derived.

8. *Polystichum wilsonii* Christ

Bot. Gaz. 51: 353 (1911); Roux, Bull. Nat. Hist. Mus. Lond. (Bot.) 30: 53 (2000). — Type: *Wilson 2614*, China, Szechuan Province, Mupin, woodlands, 4000-6000 ft. (holo-, BM!).

Polystichum lobatum var. *ruwenzoriense* Pirota in di Savoia, Il Ruwensori I: 478 (1909). — *Polystichum fuscopaleaceum* var. *ruwenzoriense* (Pirota) Pic. Serm., Webbia 32: 90 (1977). — Type: *Roccati & Cavalli-Molinelli s.n.*, Ruwensori: Nella foresta scendendo da Kichuchu a Nakitava, (holo-, TO).

Polystichum aculeatum var. *mildbraedii* Brause, Bot. Jahrb. Syst. 53: 379 (1915). — Type: *Mildbraed 7180*, Fernando Poo (Bioko), Nordseite des Pics Sta. Isabel oberhalb Basilé, Grasflur-Region des Gipfels mit viel *Ericinella*, zwischen Gras, c. 2700 m ü. M. (holo-, B!).

Polystichum aculeatum var. *rubescens* Bonap., Notes Ptérid. 14: 214 (1923). — Type: *Alluaud 48*, Tanzania, Kilimanjaro. Zone supér. des forêts, 2760 m (holo-, P!).

Polystichum aculeatum var. *stenophyllum* Bonap., Notes Ptérid. 14: 215 (1923). — Type: *Alluaud 241*, Kenya, Mt. Kenya, versant ouest, forêt inférieure, 2400 m (holo-, P!).

Polystichum fuscopaleaceum Alston, Bol. Soc. Brot., sér. 2, 30: 22 (1956). — *Polystichum setiferum* var. *fuscopaleaceum* (Alston) Schelpe, Bol. Soc. Brot., sér. 2, 41: 216 (1967). — Type: *Keay FHI 28602*, Cameroon, Victoria District, Cameroon Mountain, SW of hut 2, in gully woodland, 9100 ft. (holo-, BM!).

Polystichum alticola Schelpe & N.C. Anthony, Contr. Bolus Herb. 10: 144 (1982). — Type: *E. Esterhuysen 26699*, South Africa, Ladismith, Swartberg, Toverkop, 2160 m (holo-, BOL!; iso-, NBG!, PRE!).

Plants terrestrial or epilithic. Rhizome short, erect to suberect, to 130 mm long, to 10 mm in diameter, rarely branched, beset with roots, crowded, persistent stipe bases and paleae, the paleae castaneous, chartaceous, broadly attached, narrowly linear, the margins with small, widely spaced cellular outgrowths, the apex mostly terminating in an acicular cell, rarely terminating in a small thin-walled cell, to 12 × 1 mm. Fronds caespitose, 8-12 per plant, suberect to arching, to 1.05 m long; stipe proximally castaneous, stramineous higher up, adaxially sulcate, to 450 mm long, to 5 mm in diameter, sparsely to densely paleated, the larger paleae concolorous or bicolorous, chartaceous to crustaceous, broadly attached, often slightly bullate, spreading, extending to the

rachis, broadly ovate-acuminate to ovate-acuminate, cordate to cordate-imbricate, the margins widely to closely fimbriate, the fimbriae generally straight, the apex entire, terminating in an acicular cell, to 23 × 9 mm, the smaller paleae apically or basally directed, stramineous, chartaceous, short-stalked, narrowly triangular to subulate, often somewhat auricled, the margins proximally with long straight, angular or curved outgrowths, distally with few widely spaced, short or long marginal outgrowths, the apex entire, terminating in an acicular cell, to 13 × 7 mm; lamina 2-pinnate, with up to 29-stalked pinna pairs, herbaceous to firmly herbaceous, pale to dark green adaxially, paler abaxially, narrowly elliptic, to 625 mm long, the proximal pinnae reduced, deflexed; rachis stramineous, adaxially sulcate, densely beset with paleae similar to, but smaller than those on the stipe, the paleae restricted to the abaxial surface, to 9 × 3 mm; pinnae 1-pinnate, with up to 12-stalked pinnule pairs, opposite to alternate, proximally widely spaced, distally closely spaced and somewhat overlapping, folded ventrally along the rachis (conduplicate) narrowly triangular to oblong-attenuate, the proximal pinnae to 88 mm long, to 20 mm wide; pinna-rachis stramineous, adaxially sulcate, densely paleated, the paleae short-stalked, narrowly ovate to narrowly triangular, the margins proximally with long straight or angular outgrowths, apically with few widely spaced short or long outgrowths, the apex entire, terminating in an acicular cell; pinnules asymmetric, acroscopically auriculate, narrowly trullate to trullate, to 12 mm long, serrate, long-aristate, adaxially with straight or slightly twisted filiform paleae, simple or proximally with short straight or curved marginal outgrowths, the apex terminating in an acicular cell, abaxially with straight or proximally somewhat twisted, subulate-hastate paleae, the margins with short straight or angular outgrowths at the base, the apex entire, terminating in an acicular cell. Venation evident. Sori circular, c. 1 mm in diameter, terminal or near terminal on abbreviated vein branches; sporangium stalk eglandular, with 11(-15-)24-indurated annulus cells; indusium stramineous, peltate, circular or reniform, repand to erose, often with small central processes, persistent, maximum radius 0.51(-0.75-)1.09 mm.

Spores 64 per sporangium, brown, the perispore smooth or tuberculate, spiculate, closely perforated, exospore $32(-41.74)-52 \times 24(-30.16)-40 \mu\text{m}$. Chromosome number $2n = 164$. — Fig. 6K-M.

MATERIAL EXAMINED. — GRANDE COMORE: *Humboldt 265* (B, P); *Boivin s.n.*, près du grand cratère (P); *Humboldt s.n.*, ole, 1000-1400 m (P); *Van Denken 22, 43*, Insula Angantiae monte ignivoms, 6000-9000 ft. (B); *Kersten 43*, Angasilia, vulkan, 6000-9000 ft. (B). — LA RÉUNION: *Cadet 1975*, Piton des Neiges, 3000 m (P).

VARIATION. — Morphological variation in *Polystichum wilsonii* is mostly restricted to the larger paleae present on the stipe and abaxially on the rachis. Variation is most apparent in the size, density, and colour of the paleae. The larger paleae are broad in plants growing in more exposed habitats and are also more closely spaced. No correlation could be drawn between habitat and paleae colour. The large paleae are generally stramineous and concolorous, but in some plants the larger stipe paleae are bicolorous with the proximal central part being densely impregnated and castaneous. In some plants these bicolorous paleae are restricted to the proximal part of the stipe whereas in others they may extend to the basal pinnae.

DISTRIBUTION AND ECOLOGY. — *Polystichum wilsonii* has a wide distribution ranging from Africa to the Uttar Pradesh Mountains in northern India to Bhutan, China (Szechuan) and Taiwan (Ilan, Taichung, Hsinchu). In the study area, *P. wilsonii* is known only from Grande Comore and La Réunion.

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