



The genus *Dicksonia* (*Dicksoniaceae* - *Cyatheales*) in western Malesia

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Key words

biogeography
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Abstract We present an update of the taxonomy of the challenging genus *Dicksonia* in Malesia excluding New Guinea with its directly adjacent islands. The species *D. blumei* and *D. mollis* are maintained and additional distinguishing characters are given. As here defined their ranges do not overlap, with *D. blumei* present on Sumatra, Java and Bali, and *D. mollis* on Borneo and the Philippines. On Mindanao, *D. mollis* is sympatric with a newly recognized species, *D. amorosoana* sp. nov. On Sulawesi, there is only one species confirmed, *D. celebica* sp. nov. All these morphological separations are supported by molecular data. Also present in the area are *D. timorensis*, occurring only on Timor and more closely related to *D. antarctica* from southern Australia than to the rest of the Malesian taxa, and *D. ceramica* sp. nov., endemic to Seram Island and with strong affinity to the New Guinean *D. lanigera* and *D. hieronymi*. Lectotypes are chosen for *D. blumei* and *Balantium chrysotrichum*. Descriptions and a key for all species in the study area are provided.

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INTRODUCTION

Dicksonia is a well-known genus of tree ferns because it provides the most commonly cultivated tree fern, *D. antarctica* Labill. However, the taxonomy of the genus still contains many open questions. Most of the species are very similar to each other and their distinction is aided by their disjunct geographic distributions. For example, *D. antarctica*, *D. fibrosa* Colenso and *D. sellowiana* Hook. are superficially almost indistinguishable and their distinction relies on seemingly feeble differences in segment shape and small hairs; yet their respective geographic restriction to Australia, New Zealand and South America has been the strongest argument for their separation. Extensive field observations can add valuable distinguishing characters, like growth habit and ecological preferences, but these are rarely supplied with the unavoidably fragmentary herbarium specimens of tree ferns. Digital photographs have facilitated the documentation of the plants in the field and have greatly aided the recent discovery of new species (Adjie et al. 2012, Noben & Lehnert 2013), the first new descriptions for the genus in almost fifty years.

When FPC showed ML the field photographs of the plants he collected under the name *Cibotium* on Mindanao, it became clear that the plant was actually a species of *Dicksonia* hitherto unrecognized in the Philippines. This species differs from the only documented Philippine species, *D. mollis* Holttum, in having only soft, woolly hairs on the fronds. *Dicksonia mollis*, on the other hand, is characterized by stiff bristly hairs that bear irritating tips on the petioles and major frond axes, making its handling very unpleasant. At that time, in the absence of better comparative material for a sound taxonomic decision,

we addressed the new species preliminarily as '*D. cf. blumei*', because *D. blumei* (Kunze) T.Moore was the only other taxon known to occur within western Malesia. Given our incomplete knowledge at that time, we could not exclude the possibility that it represented just a local variety of that species.

In the meantime, the affinity of most of the taxa treated here has been tested phylogenetically (Noben et al. 2017). Among the Malesian species, the clear outlier is *D. timorensis* Adjie, which is most closely related to *D. antarctica* from south-eastern Australia and Tasmania, among a clade in which most species are adapted to cooler and more seasonal climates than the rest of the genus. All other Malesian samples are part of a different clade, in which most species belong to a relatively young radiation (Noben et al. 2017). Although with its soft hair being superficially more similar to the New Guinean *D. lanigera* Holttum, the Philippine sample identified as '*D. cf. blumei*' forms a separate subclade with samples from Sulawesi, which also could just be identified to '*D. cf. blumei*'. This monophyletic '*D. cf. blumei*' is characterized by a unique substitution pattern in the plastid genome (Noben et al. 2017, and references therein) that is found neither in *D. mollis* nor in *D. blumei*. The resolution in the crown group of the Malesian clade, which consists of *D. blumei* and all New Guinean *Dicksonia* species, is mostly weakly supported and needs further improvement before an evolutionary scenario between the island populations can be hypothesized (Noben et al. 2017). '*Dicksonia cf. blumei*' forms part of the well-supported paraphylum leading up to it, sitting between the stiffly hairy *D. herberti* W.Hill and *D. youngiae* C.Moore ex Baker from Australia and *D. mollis* from the Philippines and Borneo (Noben et al. 2017). We find the documented molecular differences a compelling support for separating '*D. cf. blumei*' from the already described species. There are considerable morphological differences between the two known populations, which would make treating them under one name taxonomically unsound. Consequently, we describe them here as two species, *D. amorosoana* from the Philippines (Mindanao) and *D. celebica* from Sulawesi.

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Table 1 Overview of the morphological differences between *Dicksonia* species in western Malesia. The colour of plant parts are less reliable due to natural variation and subjective impression, but show clear trends when a larger number of specimens is consulted.

	<i>D. mollis</i>	<i>D. blumei</i>	<i>D. celebica</i>	<i>D. amorosoana</i>	<i>D. ceramica</i>	<i>D. timorensis</i>
spores	'verrucose', with retate perispore	appearing smooth, granular perispore filling up areoles	'verrucose', with retate perispore	'verrucose', with retate perispore	'verrucose', with retate perispore	smooth, perispore evenly distributed
bristly hairs	on petiole	protruding from undercoat	non-irritant, with needle-tips	absent	absent	absent
undercoat	on petiole	visible between bristly hairs, relatively thin and pale, often yellowish	visible between bristly hairs, relatively thin (in most parts, thicker towards base) and pale, often yellowish to pale brown	not distinguishable between longer hairs, relatively thick, appearing pale reddish brown	not visible between longer hairs, relatively thick, appearing pale reddish brown	not visible between longer hairs, relatively thick, appearing whitish to pale brown
frond axes colour	abaxially	atropurpureous to blackish	medium brown to atropurpureous	medium brown to atropurpureous	atropurpureous to blackish	stramineous to brown
sori (in any given frond) subtended by sterile lobe	c. 25 %	c. 75 %	c. 75 %	c. 75 %	c. 25 %	not applicable
outer indusial valve	yellowish brown, or with yellowish margin if darker	often with darkened margin	yellowish brown	yellowish brown	yellowish brown	yellowish brown
inner indusial valve	often with darkened margin	medium brown	medium brown, often crinkled when dried	medium brown, often crinkled when dried	medium brown, often crinkled when dried	medium brown, often crinkled when dried

We further describe another species from Seram as new to science, *D. ceramica*, on morphological evidence alone. In order to help further field studies, we provide amended descriptions of *D. blumei* and *D. mollis* as well as a key to all *Dicksonia* species west of Lydekker's line (Simpson 1977); i.e., to all of Malesia except for New Guinea and its neighbouring islands. In this area, species are most easily determined by provenance (Map 1) but morphology is also reliable (Table 1).

In the descriptions we adhere to the terminology of Lellinger (2002), who applies the terms costa, costule and midvein differently than Holttum (1963), who called them pinna rachis, costa and costule, respectively. We adopt the term 'undercoat' of Holttum (1963) for a differentiated layer of usually shorter, softer hairs found on the petioles and thicker frond axes, through which the more obvious longer hairs protrude. It is of diagnostic importance whether the longer hairs are stiff and spreading, thus exposing the undercoat, or if they are soft and curved so that they obscure the undercoat. This pattern can change in one species from the lower petiole to the thinner frond axes. To simplify discussion of the morphology, we also call the indusium shape 'bivalved' and distinguish an 'inner' and 'outer' valve, which anatomically are a true indusium and a modified lobe of the laminar margin, respectively. Regarding the spore morphology, one type is dominating among the Malesian species, with the exospore weakly to strongly indented ('areolate' to 'foveate' sensu Lellinger 2002), creating a network of blunt anastomosing ridges ('retate' pattern sensu Lellinger 2002), on which a fragile layer of perispore is deposited. The perispore consists of small granules that are usually fused to sticks of short to moderate length ('granulate' to 'baculate' perispore sensu Lellinger 2002). The other common spore type of *Dicksonia* (in Malesia only found in two taxa) has the same type of perispore but in a continuous, even layer over a smooth exospore. As it is deposited last on the mature spore (Tryon & Lugardon 1991), the perispore may vary in quality between samples of viable spores. Sporangia of tree ferns seem to be fully functional well before the spores inside are fully formed and in dried specimens they often release clumps of collapsed spores, lacking any ornamentation (pers. obs.).

Vernacular names are proposed for all species in the fashion of the New Zealand species (Brownsey & Smith-Dodsworth 1989). *Dicksoniaceae* are commonly called 'hairy tree ferns', in juxtaposition to the 'scaly tree ferns' (*Cyatheaceae*). Given the variety of hair types, we propose a distinction of 'woolly', 'rough' and 'bristly' taxa within *Dicksonia*.

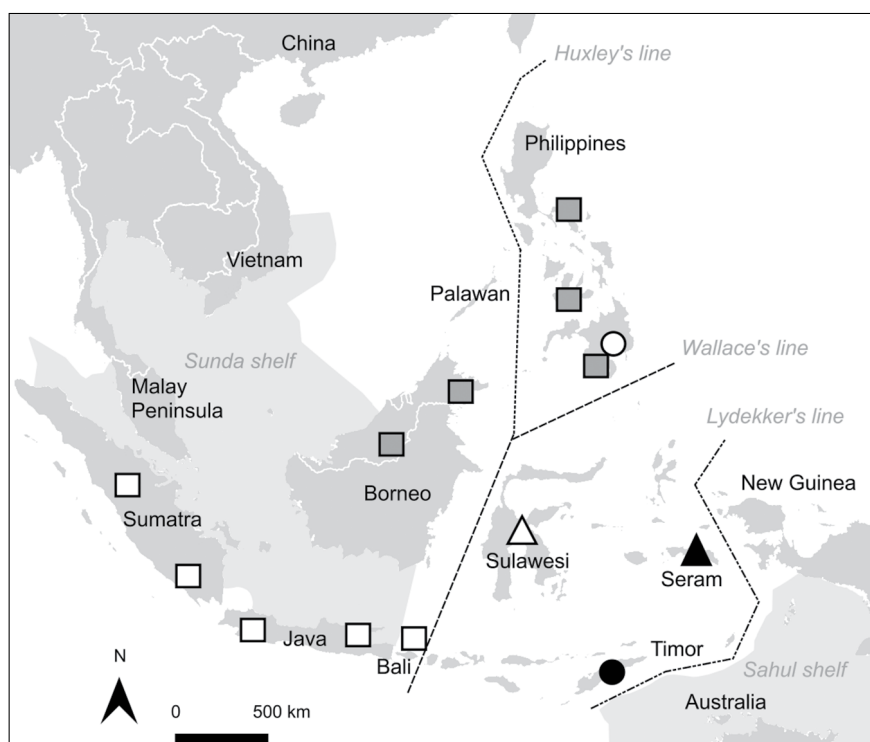
TAXONOMY

1. *Dicksonia amorosoana* Lehnert & Coritico, *sp. nov.* — Fig. 1, 2a; Map 1

A species with long matted woolly hairs on petioles and axes, these forming a uniform cover on the petiole; differing from *D. blumei* (Kunze) T.Moore in the areolate perispore of the spores (vs smooth and even in *D. blumei*) and the absence of stiff hairs protruding from the undercoat. *Dicksonia amorosoana* differs from *D. mollis* in lacking bristly irritating hairs on petioles and rachis (vs such hairs present in *D. mollis*) and having sori mostly subtended by a sterile lobe (vs sori usually without sterile lobe). — Type: *F.P. Coritico FPC 016* (holo PNH-255875; iso BONN (fragment), CMUH-00008374), Philippines, Mindanao, Davao Province, Mt Apo, Kidapawan, North Cotabato, Mandarangan trail to Lake Venado, N07°01'15" E125°16'30", 2106 m, 5 May 2012.

Etymology. The epithet honours Victor B. Amoroso, eminent Philippine pteridologist.

Tree fern, terrestrial. *Trunks* to 4 m tall, to 11 cm diam, with persistent petiole bases, frond scars not visible; adventitious buds not observed. *Fronds* to 210 cm long, held erect to ascending in a funnel-shaped crown. *Petioles* to 95 cm long (at least 1/3 of frond length), covered throughout with soft, reddish brown



Map 1 Distribution of *Dicksonia* in western Malesia: *D. amorosoana* (○), *D. blumei* (□), *D. celebica* (△), *D. ceramica* (▲), *D. mollis* (◻) and *D. timorensis* (●). Map by R. Cámara-Leret.



Fig. 1 *Dicksonia amorosoana* Lehnert & Coritico. a. Detail of petioles with shaggy hairs; b. segments of fertile pinnules, abaxially, showing matted catenate hairs on costa and costules grading into more spreading turgid hairs on midveins; c. sterile pinnules, adaxially. — Photos of the type collection (FPC 016) by F. Coritico.

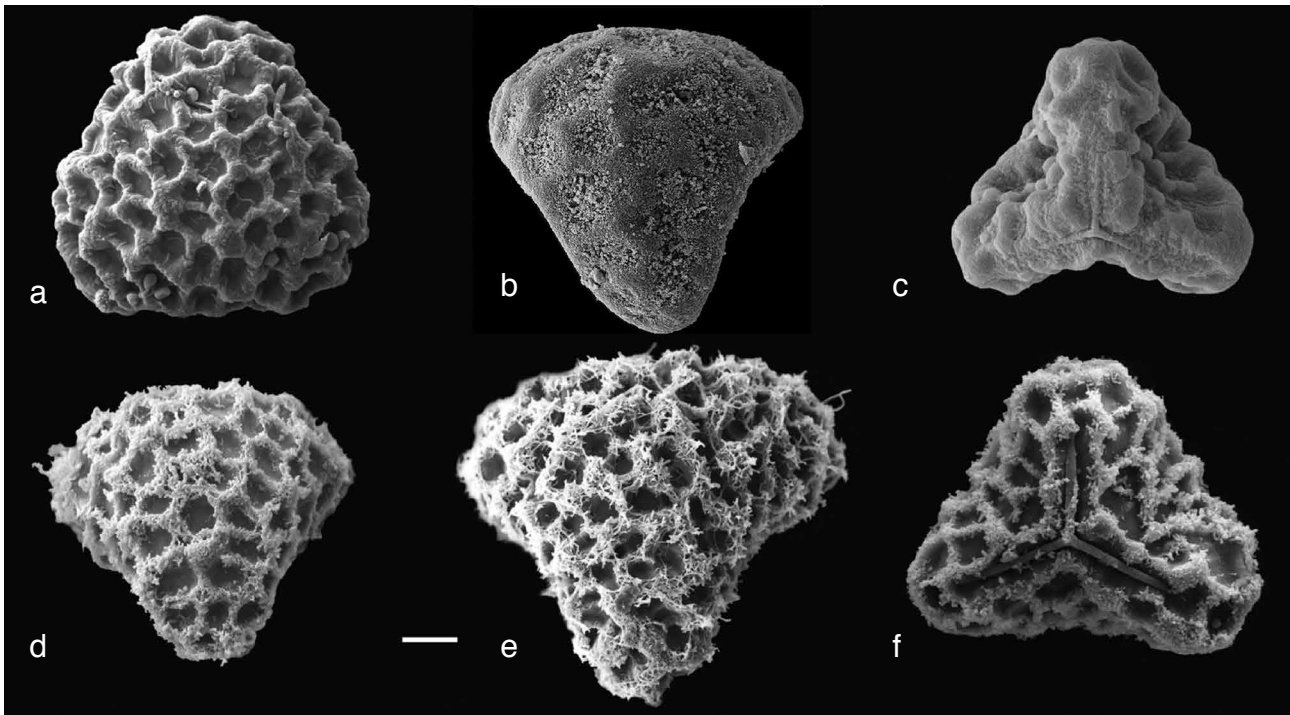


Fig. 2 Spores of Old World *Dicksonia*. a. *D. amorosoana*, distal view, perispore largely lacking, with some mould spore contamination (Philippines, Mindanao); b. *D. blumei*, distal view, granular perispore filling up retate structure of the exospore (Indonesia, Java); c. *D. celebica*, proximal view, young spore with perispore only beginning to form near the laesura (Sulawesi, Indonesia); d. *D. herberti*, distal view (Australia, Queensland); e. *D. mollis*, distal view (type; Philippines, Mindanao); f. *D. sciurus*, proximal view (Papua New Guinea) d and f are shown to illustrate the putative fully developed condition of the perispore in a and e, respectively (from: a. Coritico FPC 016, BONN; b. Chen 2040, TAIF; c. Brambach 2036, BONN; d. Kessler 14249, STU; e. Elmer 9874, MICH; f. Lehnert 2886, BONN). — Scale bar: 10 μ m.

to golden, matted hairs, consisting of an outer layer of ciliform hairs to 3 cm long with elongate, turgid to collapsed cells and a dense undercoat of paler tortuous, catenate hairs to 5 mm long; largest hairs with indurated bases, hairs usually already matted and entangled in live plants, only a few protruding, leaving a faintly scabrous surface. *Laminae* to 120 by 112 cm, tripinnate-pinnatifid, base truncate to cuneate, apex gradually reduced, glossy dark green adaxially and light green abaxially, coriaceous; weakly dimorphic with fertile parts more deeply dissected, occurring throughout the lamina. *Frond axes* (rachises, costae and costules) abaxially covered with similar hairs as on petioles, with reddish, appressed hairs on rachis, costae and costules, becoming gradually shorter and more bicolorous towards costules, hairs with pale catenate bases and dark brown acicular tips; adaxially hairs sparser, thin and appressed on rachis and proximal costa parts, becoming shorter and more spreading towards costules, here uniformly whitish, curved, to 1.5 mm long. *Pinnae* subsessile to stalked to 4.5 cm, lanceolate with truncate bases and attenuate tips, alternate, patent, 8–10 pairs per frond, basal pinnae slightly shorter, more than 1/2 the length of longest pinna. *Sterile pinnae* to 65 by 25 cm; *fertile pinnae* 20–55 by 8–28 cm. *Sterile pinnules* to 14.0 by 3.2 cm, lanceolate, subsessile to shortly stalked to 1.3 mm, bases truncate to weakly cuneate, apices attenuate; *fertile pinnules* to 12.0 by 2.5 cm, elongate-lanceolate, subsessile to stalked to 1.3 mm, bases truncate to weakly cuneate, apices attenuate. *Sterile segments* to 15 by 5 mm, oblong to linear-lanceolate, deeply pinnatifid to pinnatisect, with rounded lobes, the obtuse apices with crenulate margins; *fertile segments* to 16 by 5 mm, oblong to linear-lanceolate, pinnatisect to basally pinnate, with acute triangular lobes, each bearing one sorus on the acroscopic arm of a branched vein, the sterile apical section rhomboid with serrate margins. Veins of segments adaxially glabrous, abaxially midveins with bicolorous hairs to 2 mm long, with hyaline catenate bases and dark brown acicular terminal cell,

lateral veins with few hairs to 1.5 mm long, spreading, hyaline, pale brown to whitish, thin-walled but usually turgid at base. *Sori* 1.0–1.6 mm wide, slightly kidney-shaped when closed, circular when open, mostly (c. 75 %) on end of branched vein, the sterile lobe sticking out weakly to strongly below the sorus, if sorus on simple vein (c. 25 %) then on a lobe that is as wide as or wider than the outer indusial valve; indusia bivalved, outer one greenish with a pale brown cartilaginous margin, inner one light brown with entire margins, both valves may turn darker brown with age or drying but retain a paler margin; paraphyses slightly longer than sporangia, abundant, with red brown clavate tip. Spores tetrahedral-globose, exospore foveate, perispore granulate to baculate, deposited in a retate pattern.

Distribution — Southern Philippines (Mindanao).

Habitat & Ecology — In upper montane forests at c. 2100–2200 m.

Vernacular name — ‘Amoroso’s woolly tree fern’, suggested herewith.

Additional specimens (paratypes). PHILIPPINES, Mindanao, Davao Province, Lake Linau, Mt Apo, 3 Nov. 1946, *Edaño s.n.* (UC-750887); Mt Apo, Kidapawan, North Cotabato, within the sampling plot # 9, near Lake Venado, N07°00'07" E125°16'05", 2299 m, 9 Apr. 2013, *Silverio FDS 089* (CMUH-00008401).

Notes — We could only investigate spores from the type, where we found little to no perispore deposited on the exospore. We attribute this to young age and assume that the aspect of fully developed spores will approach the condition seen in *D. herberti*, *D. mollis* or *D. sciurus* C. Chr. (Fig. 2f). With the *Cyatheales*, we often observe variation in the thickness of the perispore layer between different samples of one species, and in the case of the type of *D. mollis*, we even found spores without perispore (similar to Fig. 2a) mixed with spores that have it (Fig. 2e).

Dicksonia amorosoana is sympatric with *D. mollis* on Mindanao but usually occurs at higher elevations. It is very different from *D. mollis* and *D. blumei* in having all hairs soft and matted, and

of an even reddish brown colouration, on frond axes and the petiole. In *D. mollis* and *D. blumei*, the hairs on the thicker frond axes are differentiated into a pale, appressed thin undercoat and dark reddish brown to blackish spreading bristles, which in the case of *D. mollis* tend to have a fragile irritating tip. *Dicksonia amorosoana* is more similar to *D. mollis* than to *D. blumei* regarding the darkened parts of the indusia, the spore morphology and the thickness and orientation of the hairs on the costules.

Dicksonia lanigera from New Guinea is another species with a persistent thick shaggy hair cover on petioles and frond axes but is generally smaller than *D. amorosoana*, with short petioles and basally tapering laminae (petioles to 30 cm long, basal pinnae 1/4 or less of the longest pinnae in *D. lanigera* vs petioles to 95 cm long, basal pinnae more than 1/2 the length of longest pinna in *D. amorosoana*).

2. *Dicksonia blumei* (Kunze) T.Moore — Fig. 2b, 3a, 4a; Map 1

Dicksonia blumei (Kunze) T.Moore (1860) 190, not sensu Christensen (1934) 223. — *Balantium blumei* Kunze (1848) 214. — Type: *H. Zollinger* 1894 (holo? LZ destroyed; lecto B-20_0138231, here designated; iso LE-00007994 (image), P-01415028, UC-414484 (fragment)), Indonesia, Java, without locality, without date.

Balantium chrysotrichum Hassk. (1856) 53. — *Dicksonia chrysotricha* (Hassk.) T.Moore (1860) 190. — Type: *J.K. Hasskarl* s.n. (lecto L-1258965, here designated), Indonesia, Java, 'Bogor Botanic Garden, and certainly at Mt Gedeh and other places', 1855–1856.

Etymology. Named after Carl Ludwig Ritter von Blume (1796–1862), Dutch-German botanist and director of the Rijksherbarium in Leiden, who collected extensively on Java and neighbouring islands (1818–1827).

Tree fern, terrestrial. *Trunks* to 8(–10) m tall, to 12 cm diam, with old petiole bases, without skirt of old fronds. Adventitious buds not reported. *Fronds* to c. 400 cm long, ascending-arching, up to 12 per crown. *Petioles* 60–95 cm long, erect-ascending, dark brown, smooth to scabrous, basally densely covered with soft woolly hairs to 1.5 cm long, shiny golden to yellowish, grading distally into undercoat of matted ciliform to catenate, tortuous hairs to 1 mm long, with numerous protruding setiform hairs to 5 cm long, dark reddish brown, spreading, non-irritant, brittle, black bases usually sticking out from the undercoat. *Laminae* to c. 300 by 140 cm, tripinnate-pinnatifid, subcoriaceous to coriaceous, oblong-lanceolate, gradually reduced apically, widest pinnae at the middle, tapering towards the base; shiny dark green adaxially, paler green abaxially; weakly dimorphic with fertile parts more deeply dissected, may be fertile in any part but mostly in the centre. *Leaf axes* (rachises, costae and costules) mostly dark reddish brown, often becoming paler towards the costules, these yellowish brown, axes densely hairy, rachises adaxially with spreading reddish brown hairs, antrorsely curved yellowish white hairs, and dense grayish brown undercoat, abaxially with longer reddish brown hairs, spreading, fragile, indument of costae and costules gradually becoming shorter, softer and paler. *Pinnae* to 70 by 19 cm, oblong-lanceolate, subsessile to sessile, 10–14 pairs per frond, with attenuate tips, basal pinnae reflexed, more oblanceolate, c. 1/2(–1/3?) the length of largest pinnae. *Largest pinnules* (sterile ≈ fertile) 6.5–8.0 by 1.7 cm, triangular-lanceolate, with attenuate tips. *Sterile segments* to 12.0 by 4.5 mm, oblong to linear, ascending, sessile, proximal ones free, distal ones adnate, margins crenate to serrate, especially towards the acute tips; *fertile segments* to 12.0 by 4.0 mm, sessile, free to decurrently adnate, linear, contracted, with 2–4 pairs of sori on deltate lobes, segment tips sterile. *Veins* adaxially glabrous, abaxially only midvein weakly to strongly hairy, hairs whitish to partly reddish, flaccid, often catenate, to 2.5 mm long, lateral veins glabrous, mostly simple, only in proximal segments forked 1 or 2 times. *Sori* 1.8–2.0 mm diam, kidney-shaped when closed,

circular when open, mostly (c. 75 %) on end of branched vein, the sterile lobe sticking out weakly to strongly below the sorus, if sorus on simple vein (c. 25 %) then on a lobe that is as wide as or wider than the outer indusial valve; outer indusial valve with pale yellowish to brown cartilaginous margin and notably darkened, sometimes blackish rim, inner valve concolorous brown with subentire to erose margin, the rim not darkened. *Spores* tetrahedral-globose with prolonged, depressed lobes, to 57 µm diam, exospore retate, appearing smooth, areoles filled up by perispore, perispore papillate-granulate to baculate.

Distribution — Sumatra (up north to Karo Plateau; Holttum 1963), Java and Bali.

Habitat & Ecology — In wet montane forests, often abundant in the understory, at 1200–2500 m (and higher?).

Vernacular name — 'Blume's bristly tree fern', suggested herewith.

Additional specimens. INDONESIA, Bali, B. Pohen, Batukau National Reserve, S08°19'48" E115°04'48", 1700 m, 24 Mar. 1992, *Afriastini* 164B1 (K); 'Java Orientalis', Tengger Mts, Wonosari, 1200–1300 m, June 1909, *Mousset* s.n. [*Rosenstock exsicc.* 72] (STU, UC, W); Tankouban Prahou, *Wawra* 1191 (W); Java, Halimung National Park, 28 Oct. 2011, *Chen* 2040 (TAIF); Sumatra, SSE of Sibajak (c. N03°13'12" E98°31'12"), 1450 m, *Lörzing* 5959 (K); Sumatra, Gunung Singgalang (c. S00°24' E100°21'), 2134 m, 16 Jan. 1913, *Matthew* s.n. (K).

Notes — '*Dicksonia blumei* C.Chr.' is often given as a later homonym, but Christensen (1934) actually just discussed Bornean plants under the correctly referenced name *D. blumei* (Kunze) T.Moore, which he pointed out to be quite different from Javanese plants and more similar to Philippine populations. These Bornean and Philippine plants were later described as *D. mollis* (Holttum 1962).

In the discussion of *Balantium blumei*, Kunze (1848) cites two more collections: "From Java I received it first from collector Sporleder (with the added observation that the trunk is 15 feet tall). Junghuhn collected it on Mount Dieng (t. de Vr.)" [personal translation from Latin]. His description, however, is referenced solely by the collection of Zollinger ("S[pecimen]. l[egit]. Zollinger"), so it is interpreted to be based largely or entirely on this collection. "*Cibotium magnificum* de Vriese in litt." was cited as synonym (Kunze 1848) but seems to be unpublished and invalid.

In the description of *Balantium chrysotrichum*, Hasskarl (1856) specifically points out the soft hairs of the petiole and the trunk, which he reports to be used for the stopping of external and internal haemorrhages. He also mentions that some brown hairs are protruding from the woolly indument on the petiole, but without noting anything about them being irritating. The documented petiole characters are very useful for the distinction of *D. blumei* from *D. mollis*, which apparently always has irritant hairs and just a thin undercoat. Unfortunately, in most specimens the petioles are not or only fragmentarily preserved (i.e., bristly hairs broken off, or only upper petiole parts with less characteristic indument present), so more field observations are needed for validation.

Otherwise *D. blumei* and *D. mollis* have more or less the same general appearance in the field, with relatively thin trunks and long-stalked fronds with petioles and thicker frond axes covered in spreading dark brown to reddish brown hairs. In both species, the hairs inserted directly on the trunk differ strongly from those of the fronds, and are sometimes preserved in specimens as pale golden wool loosely attached to the petiole base.

Dicksonia blumei was also reported from Sulawesi (Holttum 1963); the respective specimen (*Sarasin* 2030) was not seen by us. Most likely it can be attributed to the very similar *D. celebica*.

Dicksonia blumei is currently the only *Dicksonia* known on Java, so an unspecified tetraploid plant from this island with $n = 130$

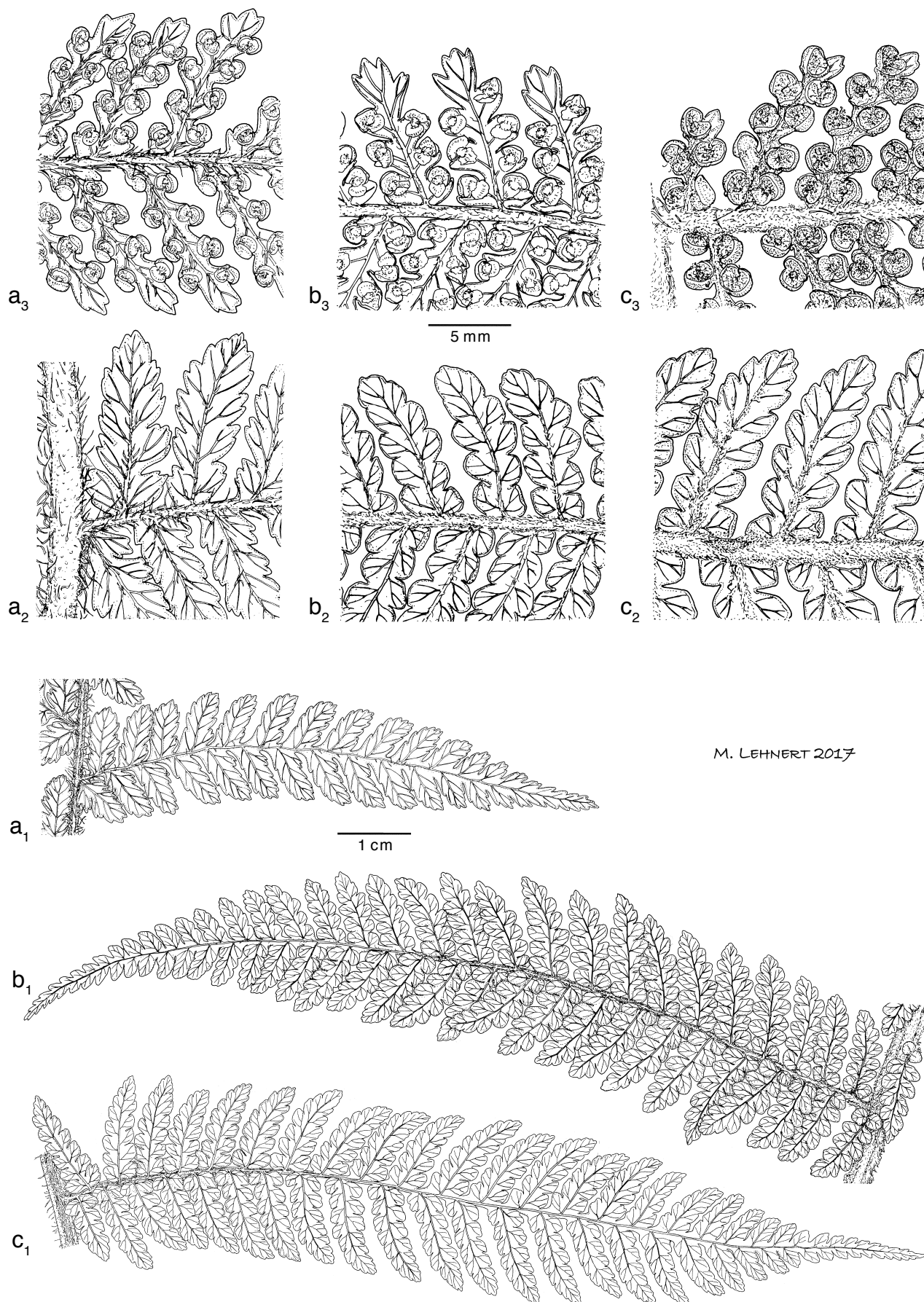


Fig. 3 Lamina details of Malesian *Dicksonia* species. a. *D. blumei*; b. *D. celebica*; c. *D. mollis*; a₁–c₁, sterile pinnules, adaxially (note: a₁ from distal part of pinna, b, and c, from proximal part of pinna); a₂–c₂, sterile segments, abaxially; a₃–c₃, fertile segments, abaxially (from: a. Chen 2040, TAIF; b. Brambach 944, BONN; c. Chen 3837, TAIF).

(Lovis 1978) most likely belongs to this species. The species is also unique within the Malesian clade (sensu Noben et al. 2017) in having smooth spores rather than the areolate to foveate spores with retate perispore ('verrucose' sensu Holttum 1963) that are typical of this clade. Our scanning electron microscopic images indicate that the areolate exospore pattern is obscured by a thick perispore layer (Fig. 2b).

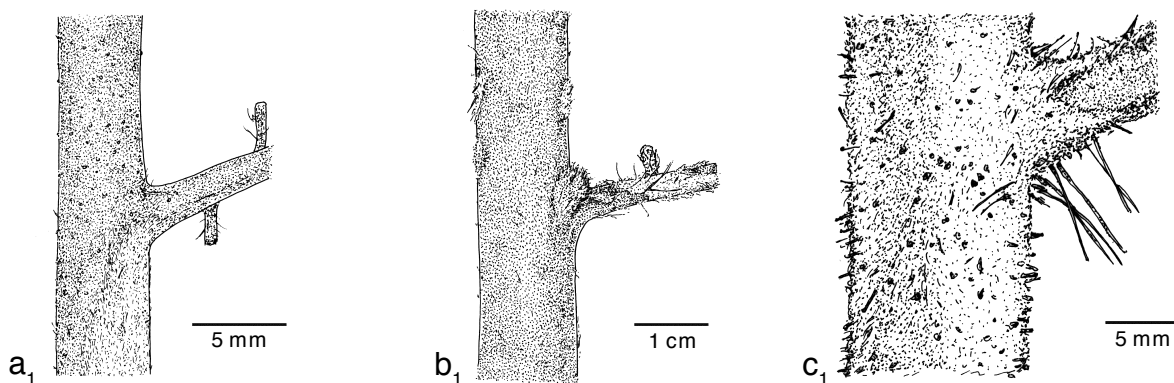
3. *Dicksonia celebica* Lehnert, sp. nov. — Fig. 2c, 3b, 4b; Map 1

This species differs from *Dicksonia amorosoana* in having a varying amount of thick, dark bristly hairs protruding from the predominantly soft and matted layer of hairs on the petioles. *Dicksonia celebica* is superficially most similar to *D. blumei* but has all hairs matted on the rachis (vs mostly spreading in *D. blumei*) and has spores with retate perispore (vs smooth). *Dicksonia celebica* differs from *D. mollis* in having a relatively voluminous reddish undercoat, and rachises and costae without bristly hairs (vs undercoat thinner, paler on petioles and rachis, and more darker bristly hairs that extend to the distal rachis and often onto the costae in *D. mollis*). — Type: *F. Brambach 0944* (holo BO; iso BONN, GOET), Indonesia, Sulawesi Tengah, tree-inventory plot 'Rorekautimbu', 8.7 km NNE of Sedoa, 800 m N of campsite Puncak Dingin following trail to peak of Rorekautimbu, S01.280° E120.308°, 2420 m, 18–30 July 2011.

Etymology. Refers to the type locality Sulawesi (Latin *celebicus* = from Sulawesi).

Tree fern, terrestrial. *Trunks* to 5.5 m tall, to 17 cm diam, with persistent petiole bases, frond scars not visible; adventitious buds not observed. *Fronds* to 310 cm long, held erect to ascending in a funnel-shaped crown. *Petioles* 70–110 cm long (at least 1/3 of frond length), covered throughout with soft, reddish

brown to golden, matted hairs, consisting of an outer layer of ciliform hairs to 3.5 cm long with elongate, turgid to collapsed cells and a dense undercoat of paler tortuous, catenate hairs to 5 mm long; largest hairs with indurated bases, most hairs already matted and entangled in live plants, few to copious bristly protruding hairs, leaving a faintly scabrous surface. *Laminae* to 200 by 130 cm, tripinnate-pinnatifid, base truncate to cuneate, apex gradually reduced, glossy dark green adaxially and light green abaxially, coriaceous, weakly dimorphic with fertile parts more deeply dissected, occurring throughout the lamina. *Frond axes* (rachises, costae and costules) abaxially covered with similar hairs as on petioles, with pale reddish, matted hairs on rachis, costae and costules, mostly catenate or with catenate bases and dark brown acicular tip, becoming gradually more turgid and spreading towards smaller costules and midveins, adaxially hairs sparser, thin and appressed on rachis and proximal costa parts, becoming shorter and more spreading towards costules, here uniformly whitish, curved, to 1.5 mm long. *Pinnae* to 65 by 25 cm; *fertile pinnae* 20–55 by 8–28 cm; subsessile to stalked to 4 cm, lanceolate with truncate bases and attenuate tips, alternate, patent, 8–10 pairs per frond, basal pinnae slightly to notably shorter, at least 1/2 the length of longest pinna. *Sterile pinnules* to 14.0 by 3.2 cm, lanceolate, subsessile to short-stalked to 1.3 mm, bases truncate to weakly cuneate, apices attenuate; *fertile pinnules* to 12.0 by 2.5 cm, elongate-lanceolate, subsessile to stalked to 5.0 mm, bases truncate to weakly cuneate, apices attenuate. *Sterile segments* to 15 by 5 mm, oblong to linear-lanceolate, deeply pinnatifid to pinnatisect, with rounded lobes, the obtuse apices with crenulate margins; *fertile segments* to 16 by 5 mm, oblong to linear-lanceolate, pinnatisect to basally pinnate, with acute



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Fig. 4 Petioles and axes of Malesian *Dicksonia*. a. *D. blumei*; b. *D. celebica*; c. *D. mollis*; first row (a₁–c₁) axils between rachis and costa, abaxially; second row (a₂–c₂) details of petioles, a₂ with hairs partially abraded, exposing the epidermis and the paler softer undercoat, c₂ with most hairs broken off on the right side (from: a. *Chen 2040*, TAI; b. *Brambach 944*, BONN; c. *Chen 3837*, TAI).

triangular lobes, each bearing one sorus on the acroscopic arm of a branched vein, the sterile apical section rhomboid with serrate margins. *Veins* of segments adaxially glabrous, abaxially midveins with bicolorous hairs to 2 mm long, with hyaline catenate bases and dark brown acicular terminal cell, lateral veins with few hairs to 1.5 mm long, spreading, hyaline, pale brown to whitish, thin-walled but usually turgid at base. *Sori* 1.0–1.6 mm wide, slightly kidney-shaped when closed, circular when open, mostly (c. 75 %) on end of branched vein, the sterile lobe sticking out weakly to strongly below the sorus, if sorus on simple vein (c. 25 %) then on a lobe that is as wide as or wider than the outer indusial valve; indusia bivalved, outer one greenish with a pale brown cartilaginous margin, inner one light brown with entire margins, often shrivelled in dried specimens, both valves may turn darker brown with age or drying but retain a paler margin; paraphyses slightly longer than sporangia, abundant, with pale to red brown clavate tips. *Spores* tetrahedral-globose, c. 40 µm diam, exospore foveate, perispore papillate-granulate to baculate, presumably deposited in a retate pattern.

Distribution — Indonesia (Sulawesi).

Habitat & Ecology — In upper montane forests, sometimes on exposed sandy ridges, at 1850–2900 m.

Vernacular name — ‘Sulawesi woolly tree fern’, suggested herewith.

Additional specimens (paratypes). INDONESIA, Sulawesi Tengah, Lore Lindu National Park, Nokilalaki, c. S01°14'12.1" E120°08'32.6", 1850 m, 28 Aug. 2007, Kluge 7542 (UC-1939486); tree-inventory plot ‘Rorekautimbu’, 78.7 km NNE of Sedoa, 800 m N of campsite Puncak Dingin following trail to peak of Rorekautimbu, S01.280° E120.308°, 2420 m, 18–30 July 2011, Brambach 0730 (BO, BONN, GOET); tree-inventory plot ‘Bulu Torenali’, 7.7 km NNE of Sedoa, 250 m ESE of campsite Puncak Dingin on mountain crest/plateau, S01.287° E120.312°, 2350 m, 21–24 Apr. 2012, Brambach 2036 (BO, BONN, GOET); Enrekang, ridge of Batu Bollong – Madjadja, NNW of Madjadja, 2900 m, 24 June 1937, Eyma 959 (A, K-000570425, L-959530233, SING n.v.).

Notes — The spores investigated with SEM (Fig. 2c) show hardly any perispore deposit but the collapsed spore walls indicate that the spore was probably young and not fully developed. See further comments under *D. amorosoana*.

To our knowledge, *D. celebica* is the only *Dicksonia* taxon present on Sulawesi. It is known so far only from north-central Sulawesi. Hidayat (2011) surveyed the fern diversity in the south-east of the island and found no *Dicksoniaceae*. *Dicksonia celebica* was already recognized as a dubitably distinct taxon by Holttum (1963), who discussed a specimen (Eyma 959) from Sulawesi that “agrees better with *D. mollis* than with New Guinean species (it is certainly not *D. blumei*)”. Hovenkamp & De Joncheere (1988) discussed a specimen from the type locality (‘Roroka Timbu’, Hennipman 5262, n.v.) of *D. celebica* under *D. cf. mollis*, which differed in having retate spores instead of the verrucose spores that proper *D. mollis* should have (Holttum 1962). We have looked at spores from the type of *D. mollis* and found that under a strong stereomicroscope, the spores may appear verrucose, but the SEM reveals a clear retate layer of perispore (Fig. 2e), surrounding clean areoles of the exospore that are usually strongly indented (foveate). We have screened spores of all Malesian species with light microscopes and most also with SEM, and found that species of the Malesian clade (sensu Noben et al. 2017) follow this pattern of spore ornamentation, with some variation in the size of the clean areoles in the retate perispore. The only exception is *D. blumei*, where the spores appear smooth because the areoles of the exospore are filled up by the copious perispore (Fig. 2b).

Superficially, *D. celebica* could be accommodated as a subspecies under either *D. blumei* (closer regarding the hairy indument

or *D. mollis* (matching the spore morphology), but we follow here the molecular evidence that shows *D. celebica* as the sister taxon to *D. amorosoana* (Noben et al. 2017, as ‘*D. cf. blumei*’), separated from the other two species.

4. *Dicksonia ceramica* Lehnert, sp. nov. — Fig. 5; Map 1

A species with only soft, woolly hairs, *Dicksonia ceramica* differs from *D. lanigera* from New Guinea in shedding most of the hairs on the abaxial surfaces of the rachis, costae and costules, exposing the shiny atropurpureous to blackish epidermis (vs hairs mostly persisting, epidermis dull brown, not shiny). — Type: Kato, Ueda & Mahjar C-1340 (holo K-000548897/-000548898; iso BO? n.v., L-1258681, TO n.v.), Indonesia, Seram, Manusela National Park, along trail between Hatuemetete (seaside) and Maraina (810 m) in Manusela Valley via Hoale Pass (1770 m) in Murkele Ridge, Kecamatan (District) Tehoru and Seram Utara, S03°10'–14' E129°35'–37', 18 Nov. 1983.

Etymology. Named after the type locality (Latin *ceramicus* = from Seram).

Tree fern, terrestrial. *Trunks* to 4 m tall, otherwise unknown; adventitious buds not reported. *Fronds* to 200 cm long. *Petioles* to 30 cm long (to 40 cm in sterile fronds), c. 1/6 of frond length, densely covered with reddish brown ciliform hairs to 4 cm long, mostly spreading but soft and often appressed, with undercoat of spreading pale, catenate hairs with dark brown acicular tips, 1–2 mm long; hairs if abraded leaving a smooth to faintly scabrous surface. *Laminae* to 170 by 80 cm, tripinnate-pinnatifid, coriaceous, shape unknown, weakly dimorphic with fertile parts more deeply dissected, occurring throughout the lamina. *Leaf axes* (rachises, costae and costules) shiny, dark castaneous to atropurpureous, appearing blackish in most parts, including most parts of costules, smooth to faintly scabrous, adaxially with antorsely curved hairs to 1.5 mm long, pale reddish brown to whitish, persistent but relatively sparse, abaxially probably first covered with similar but generally shorter hairy indument as on the petioles but soon glabrescent, remnants of longer turgid brown hairs to 15 mm long and much shorter undercoat hairs persist in axils, costules distally with some persisting turgid spreading hairs to 1.5 mm long, pale brown with whitish tips. *Pinnae* to 40 by 16 cm, subsessile to stalked 1 cm, lanceolate with attenuate tips and ± truncate bases, the basal pinnule pair may be covering the rachis adaxially; c. 8–10 pinna pairs per frond, most pinnae patent, basal pinna pairs c. 1/4 the length of longest pinnae, not reflexed. *Largest pinnules* (sterile ≈ fertile) to 9.5 by 2.5 cm, lanceolate, subsessile to short-stalked to 1 mm, ± 2 cm between costules with ± truncate bases and attenuate apices. *Sterile segments* to c. 13 by 5 mm, sessile, free to adnate, oblong, most weakly oblique, straight or distally curved, margins crenate to lobed, the tips obtuse to acute, separated by narrow sinuses to 1 mm wide; *fertile segments* to 13.0 by 4.5 mm, approximate, sessile, free to adnate, deeply lobed but laminar tissue not reduced to narrow strands along the veins, most lobes with simple veins, only few basal lobes with one sorus on acroscopic fork of a vein, subtended by a sterile lobe not reaching beyond the sorus; segment tips a coarsely serrate sterile lobe. *Veins* mostly glabrous except for persisting turgid spreading hairs to 1.5 mm long, pale brown with whitish tips on midveins adaxially. *Sori* 1.6–2.0 mm wide, slightly kidney-shaped when closed, circular when open; indusia bivalved, outer one pale brown with paler cartilaginous margin, inner one light brown with slightly erose margins, somewhat darkened; paraphyses longer than sporangia, thin, pale tortuous, fragile. *Spores* tetrahedral-globose, whitish to pale yellow, exospore areolate with weakly protruding ridges, presumably covered in papillate-granulate to baculate perispore (only light microscopic evidence), forming a retate pattern (‘verrucose’ sensu Holttum 1963).

Distribution — Restricted to the island of Seram, Indonesia.

Habitat & Ecology — At 980–1830 m in mossy montane forests on limestone (Kato 1990).

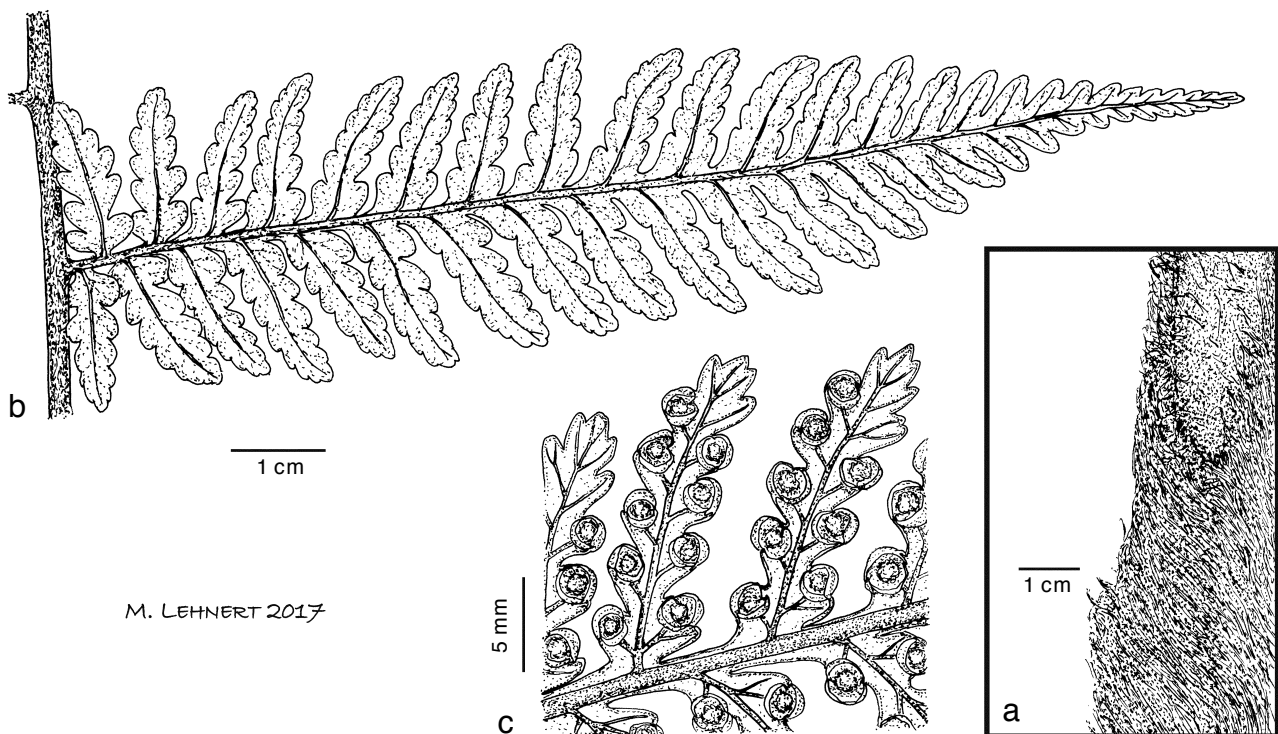


Fig. 5 *Dicksonia ceramica* Lehnert. a. Detail of petiole, hairs partially removed in upper part; b. pinnule adaxially; c. fertile segments abaxially (Kato, Ueda & Mahjar C-1340, holo K).

Vernacular name — ‘Seram woolly tree fern’, suggested herewith.

Additional specimens (paratypes). INDONESIA, Maluku, Seram, Manusela National Park, along a trail between Hatuemetete (sea level) and Hoale Pass (1770 m), southern slope of Murkele Ridge, Kecamatan (District) Tehoru and Seram Utara, S03°13–16' E129°36–37', 1770 m, 21 Feb. 1985, Kato, Ueda, Okamoto, Akiyama, Sunarno & Mahjar C-7492 (K-000548899, L-1258680); Kecamatan (District), Tehoru, along a trail from Hunisi to Muselleinan Pass (1280 m), S03°12–14' E129°45–48', 1280 m, 27 Aug. 1986, Kato, Ueda & Famani C-14048 (BO (image), TI n.v.).

Note — *Dicksonia ceramica* has been collected several times, and it is the only known species of the genus on Seram (Kato 1990). On one label, Kato indicated little variation occurring in the species on the island, and so, trusting Kato's taxonomic expertise, the two collections that we were not able to consult (Kato et al. C-13608 and C-13837, BO, TI) are considered most likely conspecific. *Dicksonia ceramica* was first determined and reported as *D. lanigera* based on its soft hairs, and it also resembles the New Guinean species *D. hieronymi* Brause in frond dissection (but *D. hieronymi* usually has a small sterile lobe subtending each sorus, whereas *D. ceramica* lacks this lobe). Unlike the other two mentioned species, *D. ceramica* loses most of its hair abaxially on the thinner frond axes, revealing their dark colour. In *D. lanigera*, the hairs are usually persisting and if removed the axes are not dark and shiny; in *D. hieronymi* it is mostly the same, but in some populations the epidermis of the axes may be dark and shiny. These plants of *D. hieronymi* still differ from in having the epidermis of the axes scabrous with spreading hairs (vs smooth epidermis, matted hairs in *D. ceramica*).

5. *Dicksonia mollis* Holttum — Fig. 2e, 3c, 4c, 6; Map 1

Dicksonia mollis Holttum (1962) 64. — Type: A.D.E. Elmer 9874 (holo K-000602588/-000602589; iso BM-000097867, L-0537138/-0537139, MICH-1190338, MO-2675154/-2675155, NY-00127912, P, U-0007357, US-00066376), Philippines, Negros Oriental, Dumaguete, Cuernos Mts, c. N09°15' E123°11', Apr. 1908.

Etymology. The name was chosen because of the softer, denser cover of pale hairs on the costules compared to the similar *Dicksonia blumei*; the choice appears rather ironic given that the species has prickly petiole hairs, a feature that *D. blumei* does not have.

Tree fern, terrestrial. **Trunks** to 6 m tall, c. 10–12 cm diam, with old petiole bases, old fronds soon falling, not forming skirt around apex; adventitious buds not reported. **Fronds** to 380 cm long, ascending-arching, few, c. 6–12 per crown. **Petioles** to 60 cm long, dark brown to blackish, rough with blackish bases of broken-off bristly setiform hairs to 4.5 cm long, dark reddish brown, undercoat of appressed whitish hairs 0.5–1.0 mm long, filiform to catenate, tortuous, undercoat usually not thicker towards petiole base (not counting golden woolly hairs of trunk that may adhere). **Laminae** to 320 by 130 cm, tripinnate-pinnatifid, coriaceous, ovate-elliptic, widest at the middle, apex gradually reduced, weakly dimorphic with fertile parts more deeply dissected, occurring throughout the lamina. **Leaf axes** (rachises, costae and costules) dark reddish brown to atropurpureous or blackish, usually paler towards costules, densely hairy, adaxially mainly with curved yellowish white hairs 1.5–2.0 mm long, also with some longer spreading reddish brown hairs, and dense pale undercoat, abaxially with longer spreading reddish brown setiform hairs to 20 mm long, fragile, their blackish bases sticking out of whitish undercoat of flaccid to catenate, tortuous hairs, indument of costae and costules gradually becoming shorter, softer and paler, whitish hairs on costules and midveins usually forming a voluminous cover, relatively few hairs also with reddish tips. **Pinnae** to 75 by 25 cm, sessile to short-stalked to 1.5 cm, oblong-lanceolate with attenuate tips, 10–14 pairs per frond, basal pinnae reflexed, c. 2/3 the length of largest pinnae, rarely smaller. **Sterile pinnules** to 14 by 2.5–3.0 cm, sessile, linear-lanceolate, bases truncate to cuneate, apices attenuate; **fertile pinnules** to 12.0 by 1.9 cm, sessile, linear-lanceolate, bases cuneate, apices attenuate. **Sterile segments** to 13.0 by 4.5 mm, oblong to linear, straight to weakly falcate, basal ones free, sessile, otherwise adnate, distal ones decurrent, most segments oblique, coarsely

crenate to lobed almost to the midvein, margins crenate to serrate, segment tips rather blunt, acute; *fertile segments* to 13.0 by 3.5 mm, linear, straight, sessile to adnate with constricted bases, with 5 or 6 pairs of sori, with reduced lamina, sinuses wider than in sterile segments, larger sinuses U-shaped, parallel-sided, segment tips mostly sterile, rhomboid with 2–4 blunt teeth. *Veins* adaxially glabrous except for sporadic hairs on the midveins, abaxially midveins weakly to densely covered with pale catenate hairs, few to absent on lateral veins. *Sori* 1.7–2.0 mm diam, oblong when closed, circular when open, mostly (c. 75 %) on simple veins in a lobe that is narrower than outer indusial valve, if sorus on branched vein (c. 25 %) then sterile lobe inconspicuous below sorus; indusia bivalved, outer valve with concolorous pale yellowish brown (rarely darker) cartilaginous margin with notably paler rim, inner valve brown with darkened, sometimes blackish, erose margin; paraphyses longer than sporangia, flaccid to catenate, whitish, with dark brown clavate terminal cell. *Spores* tetrahedral-globose, to 61 µm diam, exospore foveate, perispore papillate-granulate to baculate, deposited in a retate pattern ('verrucose' sensu Holttum 1963).

Distribution — Malaysia (northern Borneo), Indonesia (northern Borneo) and throughout the Philippines.

Habitat & Ecology — At 1500–2000(–2400) m in montane rain forests.

Vernacular name — 'Philippine bristly tree fern', 'porcupine tree fern', suggested herewith.

Additional specimens. MALAYSIA, Sabah, Mt Kinabalu, E116°32' N06°04', 1828–4100 m, 9 Apr. 1932, *Clemens & Clemens* 29055 (K, UC); Tenompok, 1500 m, 9 Mar. 1932, *Clemens & Clemens* 29734 (UC); Mt Trusmadi, 2000–2400 m, 10 Apr. 2015, *Chen* 4279 (TAIF). — PHILIPPINES, Luzon, Camarines Sur, Mt Isarog, Dec. 1928, *Edano s.n.* (UC); Mindanao, Davao, Todaya (Mt Apo), May 1909, *Elmer* 10640 (W); *ibid.*, Aug. 1909, *Elmer* 11452 (W); Negros, Balinsasayao twin lake to Guinsayawan, 7 Apr. 2014, *Chen* 3837 (TAIF). — INDONESIA, Kalimantan, Gunong Besar, c. S02.72 E115.62, 1300–1880 m, 18 Feb. 1979, *Murata, Kato & Moge* B3513 (K).

Notes — Holttum (1962) gives only a short description of *D. mollis*, stating just the differences to *D. blumei*. There are ample collections of both species in the major herbaria but almost all of them have no further information about the dimensions of the plants.

The spores of *D. mollis* are larger than those of the other Malaysian species, which is especially noticeable when compared side by side (Fig. 2). This could be an indication of polyploidy (Barrington et al. 1986) and it should be investigated, with a larger sampling than was possible here, in as much spore size varies within a population depending on plant age and nutrient supply.

6. *Dicksonia timorensis* Adjie — Map 1

Dicksonia timorensis (as '*timorensis*') Adjie (in Adjie et al. 2012) 360. — Type: *B. Adjie* BA653 (holo Herbarium of Bali Botanic Garden n.v.; iso BO n.v., K?), Indonesia, Nusa Tenggara Timur, Timor Island, Mutis Nature Reserve, Bukit Lelofui, 1760 m, cultivated in Bali Botanic Garden.



Fig. 6 *Dicksonia mollis* Holttum. a. Trunk apex, showing petioles with stiffly spreading hairs, exposing the thin matted yellowish undercoat; b. fertile pinnules, abaxially, showing thin cover of matted catenate hairs with some darker hairs protruding from costa, while on the costules there is a more uniformly pale brown cover of antorsely curved hairs. — Photos by F. Coritico.

Best described as a slender version of the well-known and widely-cultivated *D. antarctica*, differing mainly in the hemi-epiphytic habit. Also seems to retain more hair on the frond axes and not to develop a skirt of dead fronds below the crown. Spore diam c. 40–42 µm, exospore smooth, perispore granulate. See Adjie et al. (2012) for further details and illustrations.

Distribution — Endemic to western Timor, Indonesia.

Note — Our evaluation of this species relies solely on the original description and the accompanying photographs and illustrations (Adjie et al. 2012). The designated isotype at K was not found.

KEY TO THE WESTERN MALESIAN SPECIES OF *DICKSONIA*

1. Spreading thick bristly hairs abundant and evenly distributed on rachis and most parts of the petiole; hairs brittle, in specimens often only black indurated bases sticking out of the contrasting yellowish to pale brown undercoat of matted, flexuous to tortuous hairs (apparently translucent when wet); either outer or inner indusial valve with darkened margin, contrasting with paler remainder of the valve 2
1. Spreading thick hairs either not bristly or confined to petiole, if broken-off then bases inconspicuous within undercoat; indusial valves rather pale, stramineous to medium brown, if outer valve darkened then margin paler than the remainder of it 4
2. Paler undercoat comparatively thin for the complete length of the petiole, at least abaxially (adaxially woolly hairs from the trunk may be adhering); bristly hairs mostly irritating, ending in a ± straight tip; hairs on costules notably denser than on veins, mainly white, antrorsely curved, with few longer, red and ± straight hairs protruding. — Philippines, Borneo 5. *D. mollis*
2. Paler undercoat denser towards petiole base, abaxially becoming a thick golden woolly layer with bristly hairs protruding; bristly hairs not irritating, most ending in a flexuous tip; hairs gradually thinning from costae to midveins, on costules hairs mostly spreading, longer ones reddish, shorter ones white. — Sumatra, Java, Bali, Sulawesi 3
3. Outer indusial valve usually with dark brown margin; spores with evenly deposited perispore layer, appearing smooth at low magnification. — Sumatra, Java, Bali ... 2. *D. blumei*
3. Outer indusial valve usually with pale margin; spores with perispore deposited in retate pattern, appearing verrucose at low magnification. — Sulawesi 3. *D. celebica*
4. Hairs on petioles, rachises and costae forming a dark reddish brown shaggy coat, hairs curved and bent downwards in respect to the orientation of the frond; some indurated bases may persist if hairs are abraded on the axes; lamina not strongly tapering basally, petioles relatively long; costules of fully expanded fronds usually abaxially with persistent layer of reddish brown undercoat, obscuring the colour of the epidermis. — Philippines 1. *D. amorosoana*
4. Hairs on petioles dense, with reddish to dark orange spreading hairs and paler woolly undercoat, becoming gradually thinner and paler towards costae; lamina notably to strongly tapering basally, petioles relatively short; costules of fully expanded fronds abaxially usually with hairs sparse or absent, colour of the epidermis visible. — Seram, Timor 5
5. Plants terrestrial with ± straight trunks; epidermis of costae and costules abaxially with atropurpureous to blackish epidermis, contrasting strongly with the lamina; largest segments elongate with blunt tips; spores with retate perispore, appearing verrucose at low magnification. — Seram 4. *D. ceramica*

5. Plants starting as hemi-epiphytes on other tree ferns, trunk often bent where plant germinated on host; epidermis of costae and costules abaxially green in fresh material, yellowish to stramineous when dried, not contrasting strongly with the lamina; largest segments ovate-oblong with acute to short-acuminate tips; spores with evenly distributed perispore, appearing smooth at low magnification. — Timor .

..... 6. *D. timorensis*

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