

The fern genera *Dryopteris* and *Nothoperanema* (Dryopteridaceae) in Madagascar and neighbouring Indian Ocean islands, including Saint Paul

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KEY WORDS

Dryopteridaceae,
Dryopteris,
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Indian Ocean islands,
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Saint Paul.

ABSTRACT

Based on detailed morphological studies of a large number of herbarium specimens from various herbaria, a review of the fern genera *Dryopteris* and *Nothoperanema* in Madagascar and neighbouring Indian Ocean islands, including Saint Paul, is presented. Eleven species and a putative hybrid are recorded for the region, seven of these are considered endemic to the region.

RÉSUMÉ

Les fougères des genres Dryopteris et Nothoperanema (Dryopteridaceae) de Madagascar et des îles voisines de l'Océan Indien, incluant Saint Paul.

Une révision des genres de fougères *Dryopteris* et *Nothoperanema* de Madagascar et des îles voisines de l'océan Indien, y compris Saint Paul, est présentée. Elle s'appuie sur l'analyse morphologique détaillée d'un grand nombre de spécimens d'herbier provenant de différentes institutions. Onze espèces et un hybride présumé sont reconnus pour la région, dont sept sont considérées comme des endémiques de cette région.

MOTS CLÉS
Dryopteridaceae,
Dryopteris,
Nothoperanema,
îles de l'Océan Indien,
Madagascar,
Saint Paul.

INTRODUCTION

Dryopteris Adans. is a genus of about 230 species (Fraser-Jenkins 2006: 105) with a nearly worldwide distribution. *Dryopteris* is less common in the southern hemisphere and nearly absent from Australia and New Zealand. The chief centre of diversity is the Sino-Himalayan region and SW China, with minor centres of divergence in SE and E Asia, Oceania, Africa, Europe, and the Americas.

Nothoperanema (Tagawa) Ching is a genus of about five species occurring in northern India, southern China, Taiwan, South Africa and the Madagascar region. A single *Nothoperanema* species is known from the Indian Ocean region, extending to Africa.

Dryopteris and *Nothoperanema* species occur in diverse habitats ranging from forests in coastal regions to alpine habitats, but most species occur in subtropical montane environments. Eleven *Dryopteris* species and a putative hybrid occur on the Indian Ocean islands – Madagascar, Réunion, Mauritius, the Seychelles, the Comoro Island groups, and Saint Paul. Eight of these taxa (six species, a subspecies, and a putative hybrid) are endemic to the region, whilst the distribution of the other taxa extends to Africa.

MATERIAL AND METHODS

CITATIONS

Author citations follow Brummitt & Powell (1992) (<http://www.ipni.org/>). Herbarium acronyms follow *Index herbariorum*, ed. 8 (Holmgren *et al.* 1990).

MATERIAL

The review is based on herbarium collections studied at various herbaria visited, and material received on loan from B, BM, BOL, K, MO, P, NBG, NY, PRE, SAM, US and W. During December 2010, I also had the privilege to study several *Dryopteris* species in la Réunion.

METHODS

Indumentum, indusia and sporangia

The methodology and terminology used for studying and describing indumentum, indusium and sporangium features follow Roux (2000).

Distribution maps and specimen lists

Distribution maps of species within Madagascar were generated using ArcGIS 9.2. Georeferencing the collections studied was done using the gazetteers and <http://www.mobot.org/MOBOT/research/madagascar/gazetteer>.

MORPHOLOGY OF *DRYOPTERIS* AND *NOTHOPERANEMA* IN MADAGASCAR AND THE NEIGHBOURING INDIAN OCEAN ISLANDS

RHIZOME MORPHOLOGY

The rhizome in *Dryopteris* is either erect or decumbent. The erect rhizome type is generally short and unbranched with the fronds crowded in a caespitose manner at the apex. This rhizome type is cylindrical in outline and is sheathed by a mass of wiry roots, helically arranged persistent stipe bases that overlap and, at least in the younger parts, also with scales. It often forms a short and stout caudex with the growing point raised well above the substrate. Species with this rhizome type is uncommon in the region and is represented by *D. wallichiana* subsp. *madagascariensis* only.

The decumbent rhizome type is often longer than the erect rhizome type and it is generally irregularly branched, approximately cylindrical in outline, or slightly dorso-ventrally flattened. This is the most common rhizome type in the genus. The rhizome in *D. manniana*, however, remains unbranched with the apex often raised above the substrate. The diameter of the rhizome differs between species, but habitat and growing conditions also play a significant role in rhizome size. In the decumbent rhizome type, the fronds are generally more widely spaced, often exposing the “internodes”. Since the growth point is at or just below the substrate surface, the fronds are turned upwards. Scales form a dense covering over primarily the apical region of the rhizome, becoming increasingly more abraded in the older parts. *Nothoperanema* has a similar rhizome type.

FROND MORPHOLOGY

All the *Dryopteris* species within the study area are evergreen and the fronds remain alive for at least

two annual cycles. The persistent fronds are lost through decay or mechanical damage only. Frond length is greatest in *D. comorensis* where it can be up to 1.9 m long. The rhizome type determines the number of fronds borne by each plant, and species with the erect rhizome type always bear more fronds than those with a decumbent rhizome. In *D. wallichiana* subsp. *madagascariensis*, up to 25 fronds are borne by each plant, whereas in species with a decumbent rhizome type, the number of fronds rarely exceeds 12 (pers. obs.). Fronds in the relevant *Dryopteris* species and in *Nothoperanema* are considered monomorphic with no evident size differentiation between the sterile and fertile fronds. Frond venation is circinate.

STIPE

The value of stipe characters in fern taxonomy is discussed by Lin & De Vol (1977, 1978). They found that stipe features, especially their anatomy are more useful at the generic and family levels rather than at species level. The stipe in all the relevant *Dryopteris* species studied and *Nothoperanema* is firm and in *D. antarctica* the stipe bases form distinct trophopods. Trophopods are thickened persistent stipe bases that serve as food storage organs (Wagner & Johnson 1983). In species with erect rhizomes, the stipes grow directly upwards, whereas in species with decumbent rhizomes, they are initially strongly curved upwards. Their length ranges from 150 mm in *D. wallichiana* subsp. *madagascariensis* to 830 mm in *D. comorensis*. The latter species also appears to have the thickest stipes reaching up to 15 mm in diameter at the base. In most species, the stipe base is variously rounded abaxially, but distally it always becomes shallowly to deeply sulcate adaxially. In most taxa, the basal part of the stipe is brownish (castaneous) to black (ebeneous) and often lustrous (nitid), becoming paler higher up in dried material. In live plants, the distal part of the stipe generally remains green. In most species, the aerophore line is conspicuous throughout the entire stipe length, and generally somewhat paler in colour than the surrounding tissue. The stipe always bear scales, but their density shows considerable variation amongst the species. Glands and hairs also occur in some species.

In cross section, the stipe base is usually circular or transversely broadly ovate in outline. In the upper part of the stipe, however, the adaxial surface may be variously sulcate. The aerophore structure has been studied by Davies (1991). In *Dryopteris*, the aerophores consist of thin-walled parenchyma cells with large intercellular spaces, and they appear as a pale green line running dorso-laterally along the stipe length. Stomata occurring on the stipe are confined to the aerophore line. The number of meristemes at the stipe base varies from four to five, but rarely up to seven. In *Dryopteris*, the meristemes are arranged to form an open arc towards the adaxial stipe surface, with the two larger ones located adaxially at either end with the smaller ones between.

LAMINA

Most species in the study area have 2- to 3-pinnate fronds, but *D. wallichiana* subsp. *madagascariensis* has 1-pinnate-pinnatisect fronds. In *D. wardii*, the lamina can be up to 4-pinnate. Lamina outline shows significant variation between species, but within a species, the degree of variation is fairly restricted. Lamina length in the species studied is largest in *D. comorensis*, where it may be up to 1.1 m long.

The lamina is mostly anadromous at the base, but towards the lamina apex, it gradually becomes catadromous. The herbaceous pinnae and pinnules are borne opposite to alternately on the rachis and pinna-rachis. Proximally, the pinnae and pinnules are usually short-petiolate, but distally they become sessile and later adnate. In *D. wardii*, they can be up to 18 mm long and in *D. kilemensis*, up to 22 mm. The pinnae are mostly oblong-attenuate to narrowly oblong-attenuate in outline, but in some species, they may be ovate to narrowly triangular. In most species, one or more basal pinna pairs are inaequilaterally basiscopically developed. The degree to which they are developed shows considerable variation between and even within a species. The number of petiolated pinna pairs per lamina ranges from 8 in *D. bernieri* to 17 in *D. antarctica*, but in *D. wallichiana* subsp. *madagascariensis*, there may be as many as 47. In some species, the basal pinna pairs are slightly shorter than the pair above. In most species, the basal pinnae are usually widely

spaced with no or little overlap with the pinnae higher up. Towards the lamina apex, however, the pinnae frequently overlap with the pinna pair above. Pinna length ranges between 140 mm in *D. wallichiana* subsp. *madagascariensis* and 440 mm in *D. comorensis* and *D. wardii*.

Nothoperanema essentially has the same lamina architecture as species included in *Dryopteris* section *Marginatae*.

STOMATA

The distribution and the arrangement of subsidiary cells were considered of taxonomic value, especially at higher taxonomic level. Stoma frequency is often determined, but this has no taxonomic value as it is strongly influenced by the prevailing external conditions (Metcalfe & Chalk 1950).

Stomata in *Dryopteris* and *Nothoperanema* are confined to the abaxial surface of the lamina and positioned in the same plane as the epidermal cells, oriented with their longitudinal axis parallel or near-parallel to the lateral veins. Guard cell length is fairly variable within and between species, with the smallest stomata having been recorded in *D. kilemensis* and the largest in *D. manniana* (Table 1). Guard cell size has been widely used in determining or confirming ploidy levels in various plant groups (Goldblatt 1974; Barrington *et al.* 1986; Beck *et al.* 2003).

RACHIS

Morphologically and anatomically, the rachis of *Dryopteris* and *Nothoperanema* does not differ significantly from the stipe. The rachis is mostly straight throughout its length, but distally it may become slightly flexuose in some species. Adaxially, the rachis forms a V- or U-shaped sulcus along its entire length. The sulcus is open and admits the sulci of the pinna-rachises. However, the pinnule sulci of *Dryopteris* are not confluent with that of the pinna-rachis. The raised edges of the pinnule sulcus are basiscopically decurrent and join the edge of the pinnule lamina on the pinna-rachis as a lateral wing. In *Nothoperanema*, the pinnule rachises are convex and flanked by raised ridges that are interrupted where the costae branch from the pinnule-rachis. In *Dryopteris*, the dorso-lateral aerophore line is

generally visible with the naked eye and may be paler than the surrounding tissue.

PROLIFEROUS BUDS

Proliferous buds are outgrowths from the lamina axes, capable of developing into an independent plant. Under certain conditions, these organs also produce roots, whilst still raised well above the substrate. Proliferous buds appear to be genetically induced, but external stimuli may contribute to their formation. Few *Dryopteris* species produce proliferous buds and none of the *Nothoperanema* species are proliferous.

Scaled proliferous buds are mostly borne adaxially on the rachis near the frond apex in *D. manniana*, but they may also occur near the pinna apices. They largely occur in or near the pinnae "axils". One to three buds per frond appear to be the norm in *D. manniana*.

VENATION

Venation in *Dryopteris* and *Nothoperanema* is of the pectopteridis-type (Bower 1923: 97, fig. 93f). In this free venation type, a central vein extends into each segment. From this vein simple or branched, secondary veins develop acroscopically or basiscopically in a pinnate fashion, with the ultimate branches ending in the teeth near the margin. In live material, the venation pattern is most visible on the abaxial lamina surface. The veins of all the *Dryopteris* species in the study area and in *Nothoperanema* are always free and anadromous, becoming catadromous towards the pinna and pinnule apices. Most veins run into the teeth, where they terminate near the lamina margin. In *Nothoperanema*, the vein endings are enlarged and appear as hydathodes adaxially. In *D. antarctica* and *N. squamiseta*, the venation of fertile fronds differs slightly from that in sterile fronds. In these species, veins of the fertile pinnules mostly terminate in the soral receptacle, midway between the costa and the margin. However, variations do occur, with the fertile vein often extending for a short distance beyond the sorus.

INDUMENTUM

Indumentum in *Dryopteris* and *Nothoperanema* occurs in the form of glands, hairs and scales, and

TABLE 1. — Guard cell length and ploidy level in *Dryopteris* Adans. and *Nothoperanema* (Tagawa) Ching.

Taxon	Range and mean (µm)	Ploidy level
<i>D. antarctica</i>	(40-) 51 (-64)	4n
<i>D. aquilinooides</i>	(34-) 45 (-58)	?
<i>D. bernieri</i>	(32-) 47 (-56)	?
<i>D. bojeri</i>	(34-) 45 (-54)	?
<i>D. comorensis</i>	(34-) 40 (-46)	?
<i>D. kilemensis</i>	(30-) 39 (-50)	2n
<i>D. manniana</i>	(40-) 56 (-70)	4n
<i>D. penteri</i>	(34-) 53 (-72)	4n
<i>D. subcrenulata</i>	(46-) 52 (-58)	?
<i>D. wallichiana</i> subsp. <i>madagascariensis</i>	(50-) 54 (-60)	?
<i>D. wardii</i>	(38-) 48 (-58)	?
<i>D. hybrid</i> "La Réunion"	(40-) 50 (-58)	?
<i>N. squamiseta</i>	(40-) 48 (-56)	?

these are found on all parts of the plant. Although indumentum and especially the scales are considered diagnostic for many species, no study on the scale morphology in these genera is known to me.

Glands

The morphology of glands and their distribution in some *Dryopteris* species are discussed by Viane (1986). He identified two types of these unicellular structures; capitate glands and clavate glands. These gland types were also observed in several African and Madagascan *Dryopteris* species. Capitate glands occur in *D. bernieri* and *D. wardii*. These structures, which are 60-140 µm long, are most common in *D. bernieri*, where they occur on the stipe, rachis and lamina between the veins. Clavate glands 46-84 µm long occur along the veins in *D. bojeri*, *D. kilemensis* and *D. manniana*, but those in *D. antarctica* are much larger, measuring between 52 and 156 µm. In *Nothoperanema*, clavate glands are confined to the frond axes and veins and are 54-92 µm long (Fig. 31K). These cells rarely occur on a short basal cell. Similar glands up to 64 µm long occur on the indusium lamina. Oblong glands 60-260 µm long mostly occur along the lamina axes and veins in *D. penteri* (Fig. 20E), but in *D. aquilinooides*, they are confined to the scales (Fig. 6A-E). Glands as here defined do not always produce an exudate.

Hairs

Hairs are mostly pluricellular, uniseriate structures and chiefly occur along the frond axes and veins, but

often also on the lamina between the veins. Four hair types occur in the relevant *Dryopteris* species and another, not present in *Dryopteris*, occurs in *Nothoperanema*:

- 2-celled oblong hairs: hairs where the transverse wall separating the two cells is often somewhat oblique (Fig. 20D). These hairs have been observed in *D. penteri* only where they are confined to the lamina axes and veins;
- isocytic hairs (Viane 1986): all cells are similar and not rounded (Figs 6G; 9E; 15F, G). These hairs often bear one or more glands near the base. Cell length is extremely variable;
- clavate hairs (Viane 1986): the apical and/or some subapical cells are distinctly broader than the basal cells (Figs 12H; 18F). These hairs often bear one or more glands near the base (Figs 9D; 12G; 18E);
- moniliform hairs (Viane, 1986): at least the upper cells are rounded and the transverse cell walls are more or less constricted (Figs 4F; 26F, G). These hairs often bear one or more glands near the base. These hairs are primarily found in *D. antarctica*;
- nothoperanemoid hairs: these hairs are mostly seven to nine cells long, with the three to four basal cells much longer than the four or more distal cells. The basal cells gradually widen towards the four more or less cupiform distal cells. The hairs are up to 290 µm long and were observed in *N. squamiseta* only (Fig. 31I, J).

Scales

Scales are dermal appendages confined to the rhizome, frond axes and veins, but in *D. wallichiana* subsp. *madagascariensis*, small fibrils or hair-like scales occur along the lamina margin. Fibrils (= microscales [Daigobo 1972]) are multicellular hairs and hair-like scales with sinuate joints between the cells. They often are long-stalked and bear short outgrowths near the base. These scale-like structures are confined to the lobe margins of *D. wallichiana* subsp. *madagascariensis* only (Fig. 2F, G). In *Dryopteris* and *Nothoperanema*, scales never occur on the lamina surfaces between the veins. In both genera, scales are mostly one cell layer thick and flat, but in a few species, some of the frond scales are often bullate, and in *Nothoperanema*, they are mostly patent. Scales in *Dryopteris* are thin-walled, membranous, or chartaceous structures. In most species, they are concolorous, and depending on their age and location, they can be stramineous, ferruginous or castaneous. Young and immature scales are usually whitish.

Scale structure in *Dryopteris* shows extreme variation, but two basic types can be identified within the relevant *Dryopteris* species:

- the scales of species in sect. *Fibrillosae* are up to 17 mm long and 2.4 mm wide. They are chartaceous and castaneous, ferruginous or stramineous, but the larger (stipe) scales are often bicolorous. If bicolorous, then they are ferruginous to stramineous with (mostly central) castaneous streaks. The larger scales are subulate, broadly attached and cordate, whilst the margins are variously set with short and long, apically or basally directed, often branched outgrowths, which reduce in number and size towards scale apex. The scale apex terminates in an elliptic thin-walled cell or a subulate cell. Smaller scales are stalked, cordate to cordate-imbricate, and the margins proximally variously set with outgrowths similar to those on the rhizome scales. Short- or long-stalked filiform scales occur along the costa, veins, and lobe margins. These scales proximally bear short marginal outgrowths, but distally they are entire. The scale apex terminates in a subulate cell (Fig. 2C), an elliptic thin-walled cell, or the apical cell is undifferentiated. Similar scales occur in *Polystichum* Roth sect. *Lasiopolystichum* Daigobo (Daigobo 1972);

- scales of the other *Dryopteris* sections are generally less clearly defined and they also show a greater degree of variation in overall morphology. Scales of species in these sections are basifixed and generally larger than those in sect. *Fibrillosae*. They are chartaceous and stramineous to ferruginous in colour. The scales may be filiform, lanceolate, narrowly ovate or broadly ovate in outline and often bullate in sect. *Purpurascetes*. Pluricellular outgrowths of variable length generally occur along the scale margins, but often also on the scale laminae in *D. aquilinoidea*. In several species capitate, clavate or oblong glands occur along the scale margins and on the laminae. The scales generally terminate in a pluricellular filiform or flagelliform apex of which the terminal cell, like the marginal outgrowths may be clavate and thin-walled, or glandular (Figs 4A-E; 6B, C; 15C, D; 18A, D; 20A, B, F; 26A). In *D. antarctica*, the marginal outgrowths and scale apex terminates in a series of moniliform cells (Fig. 4A-E).

Scales in *Nothoperanema* are castaneous and firmly chartaceous to thinly crustaceous. In structure, they differ from any *Dryopteris* species in the region in that they are adnate, subulate and patent. Few-celled uniseriate hairs terminating in a clavate gland frequently occur along the scale margin with unicellular glands regularly occurring on the scale lamina margin and lamina. The scale apex terminates in a short uniseriate series of cells, the terminal cell being glandular (Fig. 31A', D', E', F').

SORI

Sori are borne abaxially on the lamina and are positioned medially, at or near the apex of an ultimate vein branch. Sori in the 1-pinnate-pinnatifid *Dryopteris* species are mostly borne on the anadromous secondary vein branches, but the bearing of sori on the catadromous secondary vein branches are not uncommon. The venation in *Dryopteris* species with more divided laminae generally does not show any differentiation between sterile and fertile fronds, but in *D. antarctica*, which belongs in sect. *Lophodium*, and *N. squamiseta*, the sori are borne at or near the apex of mostly shortened anadromous vein branches.

INDUSIUM

All the *Dryopteris* species in the study area, with the exception of *D. manniana*, are indusiate. The indusium is reniform and the wing is mostly one cell layer thick, but at the point of attachment, it is several cell layers thick. The margin is repand or entire. The anticlinal cell walls are sinuose to deeply lobed. In *Nothoperanema*, the transverse cell walls are straight to shallowly lobed. Indusia are persistent, but they may be lost as a result of mechanical damage. The structure is generally uniform in colour and whitish to almost translucent in live material, becoming pale to dark brown when dry. Clavate glands are often borne along the margin of some species, but in others glands also occur on the indusium lamina. The occurrence of many clavate glands on the indusium lamina is a characteristic of *N. squamiseta* (Fig. 31L, L'). In addition, a few short hairs near the point of attachment may also be present on the indusium lamina. *Dryopteris aquilinooides* and *D. wardii* are the only species where uniseriate hairs occur on the indusium lamina (Fig. 28B, C).

SPORANGIUM

Dryopteris and *Nothoperanema* sporangia are biconvex in facial view and circular to slightly obovate in outline in lateral view. The annulus is vertical and interrupted by the stalk. The number of indurated annulus (or bow) cells per sporangium is variable (Table 2), and a well-defined stomial region can be identified.

Cells of the stomial region are thin-walled. The two stomium cells themselves are distinct in being larger with slightly thicker walls. The average number of hypostomial cells per sporangium is three, but as few as two and as many as five are known. Similarly, the average number of epistomial cells per sporangium is three, but as few as one and as many as four have been observed.

The sporangium stalk is composed of three rows of cells for most of its length, but the base may be one or two cells thick. The length of the stalk and also its cellular structure vary considerably. The stalk is generally long and consists of slender cells, but it is often composed of short cupiform cells. The capsule generally breaks from the stalk through the tearing of the stalk cells, just below the capsule. Although the stalk is mostly simple, one or more clavate glands

frequently occur on it, or it may bear a pluricellular isocytic hair from near the base. In *D. wardii*, the hairs are composed of relatively long cells, with the apical cell pyriform and gland-like.

SPORES

A general descriptive overview of the spore surface, wall structure and spore diversity in *Dryopteris* and *Nothoperanema* is provided by Tryon & Lugardon (1990). Spores of the species dealt with here are ellipsoidal, monolete, brown, and the perispore folded to form low tubercles, narrow or broad compressed reticulate ridges that are densely echinulate, minutely rugulose, minutely scabrous, ruminant, or with narrow to broad reticulate ridges.

As with stomata, a correlation appears to exist between spore size and ploidal level within a group of related taxa. It was suggested that spore size can contribute in establishing hypotheses of evolutionary relationships within related polyploid complexes (Barrington *et al.* 1986). *Dryopteris bojeri* has the smallest spores and *D. antarctica* the largest (Table 3).

The number of spores per sporangium is mostly 64, except in *D. wallichiana* subsp. *madagascariensis*, where only 32 spores per sporangium are produced, suggesting it to be an obligate apomict.

Spores of the putative hybrid are aborted.

SYSTEMATICS

A review of the higher classification and relationships of *Dryopteris* is provided by Pryer *et al.* (1996, 2004), Smith *et al.* (2006), and Liu *et al.* (2007). Fraser-Jenkins (1986) provides the first subgeneric classification of the genus. In this classification, four subgenera were recognised with one or more sections within each of them. Two of these subgenera are represented in this treatment. This classification excludes *Nothoperanema* (Tagawa) Ching, which is treated as a segregate genus (Ching 1966: 25; Kramer *et al.* 1990: 109). Molecular studies by Geiger & Ranker (2005) and Li & Lu (2006) showed that *Dryopteris* is polyphyletic, with *Nothoperanema* nested in it. However, Liu *et al.* (2007) showed that *Nothoperanema* species group is closer to the peranemoid ferns than to the dryopteroid ferns, although within the same

TABLE 2. — Quantitative data for the number of indurated annulus cells per sporangium and stalk features in *Dryopteris* Adans. and *Nothoperanema* (Tagawa) Ching.

Taxon	Range and mean	Sporangium stalk
<i>D. antarctica</i>	(11-) 16 (-21)	simple
<i>D. aquilinooides</i>	(11-) 14 (-19)	simple
<i>D. bernieri</i>	(12-) 14 (-17)	simple, glandular or haired
<i>D. bojeri</i>	(14-) 15 (-16)	simple, glandular or haired
<i>D. comorensis</i>	(13-) 15 (-18)	simple, glandular, or haired
<i>D. kilemensis</i>	(12-) 13 (-16)	simple, glandular, or haired
<i>D. manniana</i>	(11-) 14 (-18)	simple or haired
<i>D. pentheri</i>	(11-) 13 (-20)	simple, glandular, or haired
<i>D. subcrenulata</i>	14 (-15)	simple or haired
<i>D. wallichiana</i> subsp. <i>madagascariensis</i>	(13-) 14 (-17)	simple or with 1- or 2-celled glandular hairs
<i>D. wardii</i>	(13-) 14 (-17)	simple or haired
<i>D. hybrid</i> "La Réunion"	aborted	haired
<i>N. squamiseta</i>	(13-) 15 (-17)	simple or haired

TABLE 3. — Exospore size (minimum, mean and maximum) and spore number per sporangium in *Dryopteris* Adans. and *Nothoperanema* (Tagawa) Ching.

Taxon	Range and mean (mm)	Spores/Sporangium
<i>D. antarctica</i>	(44-) 50 (-58) × (32-) 35 (-42)	64
<i>D. aquilinooides</i>	(26-) 36 (-44) × (20-) 23 (-30)	64
<i>D. bernieri</i>	(36-) 42 (-52) × (24-) 29 (-36)	64
<i>D. bojeri</i>	(32-) 34 (-44) × (18-) 20 (-22)	64
<i>D. comorensis</i>	(34-) 37 (-44) × (20-) 23 (-26)	64
<i>D. kilemensis</i>	(32-) 36 (-42) × (20-) 22 (-26)	64
<i>D. manniana</i>	(40-) 44 (-58) × (26-) 30 (-32)	64
<i>D. pentheri</i>	(38-) 45 (-60) × (27-) 31 (-40)	64
<i>D. subcrenulata</i>	(32-) 35 (-38) × (22-) 22 (-24)	64
<i>D. wallichiana</i> subsp. <i>madagascariensis</i>	(36-) 41 (-36) × (26-) 28 (-34)	32
<i>D. wardii</i>	(22-) 47 (-52) × (24-) 26 (-30)	64
<i>N. squamiseta</i>	(32-) 35 (-36) × (18-) 20 (-22)	64

clade. Morphological studies by myself in *Nothoperanema* support this view (pers. obs.), and it is therefore treated as a genus distinct from *Dryopteris*.

CLASSIFICATION OF *DRYOPTERIS* SPECIES
AND *NOTHOPERANEMA* FROM MADAGASCAR
AND NEIGHBOURING INDIAN OCEAN ISLANDS,
INCLUDING SAINT PAUL

Genus *Dryopteris* Adans.

Subgenus *Dryopteris*

Section *Fibrillosae* Ching

D. wallichiana (Spreng.) Hyl. subsp. *madagascariensis* (C.Chr.) J.P.Roux

Section *Lophodium* (Newman) C.Chr. ex H.Itô

D. antarctica (Baker) C.Chr.

Section *Marginatae* Fraser-Jenk.

D. aquilinooides (Desv.) C.Chr.

D. bernieri Tardieu

D. bojeri (Baker) Kuntze

D. comorensis (Tardieu) Fraser-Jenk.

D. manniana (Hook.) C.Chr.

D. pentheri (Krasser) C.Chr.

D. subcrenulata (Baker) C.Chr.

Subgenus *Nephrocystis* (H.Itô) Fraser-Jenk.

Section *Purpurascetes* Fraser-Jenk.

D. kilemensis (Kuhn) Kuntze

Species incertae sedis

D. wardii (Baker) Kuntze

Hybrid

D. hybrid "La Réunion"

Genus *Nothoperanema* (Tagawa) Ching

N. squamiseta (Hook.) Ching

KEY TO THE DRYOPTEROID FERN GENERA IN MADAGASCAR
AND NEIGHBOURING INDIAN OCEAN ISLANDS, INCLUDING SAINT PAUL

- Frond scales often broadly attached, but never adnate and patent, scales and hairs not multistratose at the base *Dryopteris*
- Scales adnate to frond axes and patent, scales and hairs generally multistratose at the base ...
..... *Nothoperanema*

Genus *Dryopteris* Adans.

Familles des plantes 2: 20, 551 (Jul.-Aug. 1763), nom. cons. — Type: *Dryopteris filix-mas* (L.) Schott; *Polypodium filix-mas* L.

Nephrodium Michx., *Flora boreali-americana* 2: 266 (19 Mar. 1803). — Lectotype: *Nephrodium marginale* (L.) Michx.; *Polypodium marginale* L. (now *Dryopteris marginalis* (L.) A.Gray), designated by Pichi Sermolli (1977: 87-90).

Lophodium Newman, *The Phytologist* 4: 371, app. xvi (1851). — Lectotype: *Lophodium spinulosum* (O.F.Muell.) Newman (*Polypodium spinulosum* O.F.Muell.), designated by Christensen (1905: XXI), now *Dryopteris carthusiana* (Vill.) H.P.Fuchs.

Dichasium Fée, *Mémoires sur la famille des fougères* 5: 302, pl. 23B, fig. 1 (1852). — Type: *Aspidium parallelogramma* Kunze, *Linnaea* 13: 146 (1839); *Dichasium parallelogrammum* (Kunze) Fée (now *Dryopteris wallichiana* (Spreng.) Hyl.).

DESCRIPTION

Plants terrestrial or epilithic. Rhizome dictyostelic, short-decumbent and branched, or suberect to erect, then mostly unbranched. Fronds monomorphic or dimorphic, approximate or caespitose; stipe and rachis adaxially sulcate, rachis sulcus not open to the sulci of the lower order axes; lamina variously pinnately compound, mostly anadromous, be-

coming catadromous, the basal pinna pair often basiscopically developed; hypostomatic, stomata of the anomo-, polo-, and copolocytic types; venation of the pectopteridis-type, anadromous and/or catadromous, forked or pinnately branched, free vein branches ending in the teeth near the margin, not or rarely slightly abbreviated in fertile fronds. Indumentum composed of narrow and/or broad, sessile or short-stalked scales often bearing capitate, clavate, or oblong thin-walled glands along the scale margins and/or laminae, and clavate, oblong, or capitate glands, and short or long, simple or glandular, uniseriate hairs mostly abaxially along the lamina veins. Sori circular, medial, at or near the apex of abbreviated vein branches; receptacle nude; sporangium long-stalked, 3-seriate below the capsule, simple, glandular, or with an isocytic hair, capsule globose to obovoid in lateral view, with (11-)14(-21) indurated annulus cells and a well-defined stomium, epistomium (3-)4(-7)-celled, hypostomium (3-)4(-8)-celled; indusium reniform, entire or with clavate or capitate glands along the margin and/or indusium lamina rarely with hairs on lamina, or exindusiate. Spores 32 (apomicts) or 64 (sexual) per sporangium, ellipsoidal, monolete, with prominent narrow or broad folds and inflated tubercles, 20-70 µm long. Chromosome number based on 2n = 82.

KEY TO THE *DRYOPTERIS* SUBGENERA IN MADAGASCAR
AND NEIGHBOURING INDIAN OCEAN ISLANDS, INCLUDING SAINT PAUL

- Pinna-rachis with small ovate to broadly ovate scales subgen. *Nephrocystis*
- Pinna-rachis scales various, but never small and ovate to broadly ovate
..... subgen. *Dryopteris*

Subgenus *Dryopteris* Adans.

Dryopteris Adans., *Familles des Plantes* 2: 20, 551 (Jul.-Aug. 1763), subgen. *Dryopteris*.

Lastrea Bory subgen. *Arthrobotrys* C.Presl, *Tentamen pteridographiae*: 77 (1836). — Type: *Lastrea macrocarpa* (Wall.) C.Presl; *Arthrobotrys macrocarpa* Wall.

Dryopteris Adans. subgen. *Eudryopteris* C.Chr., *Index filicum*: 250 (2 Oct. 1905), XXI (10 Oct. 1906), pro parte, nom. inval. (McNeill *et al.* 2006: Art. 21.3). — Type: *Dryopteris filix-mas* (L.) Schott; *Polypodium filix-mas* L.

Dryopteris Adans. subgen. *Eudryopteris* C.Chr. in *Biologiske Arbejder tilegnede Eug. Warming*: 76 (3 Nov. 1911), nom. inval. (McNeill *et al.* 2006: Art. 21.3). — Type: *Dryopteris filix-mas* (L.) Schott; *Polypodium filix-mas* L.

KEY TO THE SECTIONS IN SUBGENUS *DRYOPTERIS*

1. Lamina 1-pinnate-pinnatisect, lobes with fibrils along the margin; axes scales subulate to filiform sect. *Fibrillosae*
- Lamina 2- to 4-pinnate, never with hairs or scales along the lobe margins; axes scales not subulate 2
2. Stipe scales more or less entire, apex and marginal outgrowths terminate in a uniseriate series of moniliform cells; fertile vein branches often somewhat abbreviated sect. *Lophodium*
- Stipe scales mostly with flagelliform marginal outgrowths, apex and marginal outgrowths terminate in a uniseriate series of oblong cells; fertile veins not abbreviated sect. *Marginatae*

Dryopteris Adans. section *Fibrillosae* Ching

Bulletin of the Fan Memorial Institute of Biology (Botany) 8: 366 (1938). — Type: *Dryopteris fibrillosa* (C.B. Clarke) Hand.-Mazz., non (Baker) C.Chr. (1905: 264); *Nephrodium filix-mas* (L.) Rich. var. *fibrillosa* C.B. Clarke (now *Dryopteris pulcherrima* Ching).

Aspidium Sw. subgen. *Dichasium* A. Braun in *Flora* 24: 710 (1841). — *Dichasium* (A. Braun) Fée, *Mémoires sur la famille des fougères* 5: 302 (1852). — *Dryopteris* Adans. subsect. *Dichasium* (A. Braun) H. Itô, in NAKAI & HONDA, *Nova flora japonica* 4: 6 ["1938"] (1939). — Type: *Dryopteris fibrillosa* (C.B. Clarke) Hand.-Mazz., non (Baker) C.Chr. (1905: 264), now *D. pulcherrima* Ching.

DESCRIPTION

Rhizome short and erect to suberect, up to 150 mm tall and closely set with roots, crowded and persistent stipe bases, and scales. Fronds are 1-pinnate to 1-pinnate-pinnatisect and more or less narrow-elliptic in outline. The pinna-lobes are markedly regular and rectangular to parallelogram-shaped with truncate apices. The lobe sides are mostly shallowly lobed, but the apices are strongly toothed. The scales are chartaceous to thinly crustaceous, broadly attached or short-stalked, subulate to filiform, and the margins variously set with short and long, apically or basally directed, often branched outgrowths which reduce in number and size towards the scale apex,

the apex terminates in a subulate cell or an elliptic thin-walled cell. Uniseriate hairs are absent. Sori occur medially or inframedially on predominantly anadromous vein branches, forming a single row on either side of the costa.

REMARKS

A section of about 21 species distributed throughout most of the range of the genus with the exception of North America, rare in Africa. Many of the species are thought to be derived from *D. wallichiana* or its relatives through hybridization with sexual diploids (Fraser-Jenkins 1986: 191). Species in the section show a high degree of chemical uniformity (Widén *et al.* 1996).

A single species belonging to section *Fibrillosae* occurs in the region.

Dryopteris wallichiana (Spreng.) Hyl.

Botaniska Notiser 3: 352 (1953). — *Aspidium wallichianum* Spreng., *Systema vegetabilium*, 16th ed., 4, 1: 104 (Jan. 1827), non C. Presl ex Kunze (1851: 291). — *Aspidium paleaceum* D. Don, *Prodromus florum nepalensis*: 4 (1825), nom. illeg. (McNeill *et al.* 2006: Art. 53.1), non Lag. ex Sw. (1806). — *Aspidium donianum* Spreng., *Systema vegetabilium*, 16th ed., 4, 1: 320 (1827), nom. superfl. (McNeill *et al.* 2006: Art. 53.1). — *Dryopteris doniana* (Spreng.) Ching, *Sunyatsenia* 6: 3 (1941), nom. illeg. —

Dryopteris paleacea Hand.-Mazz., *Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien* 58: 100 (1908), nom. nov. for *Aspidium wallichianum* Spreng., nom. superfl. — Type: Nepal, 1820, *N. Wallich* [340], (lecto-, B, designated by Fraser-Jenkins [1989: 353]; isolecto-, BM, G, K, L, P, W, often mixed collections).

Aspidium paleaceum Lag. ex Sw., *Synopsis filicum*: 52 (Mar.-Apr. 1806). — *Lastrea paleacea* (Lag. ex Sw.) T. Moore, *Index filicum* 2 (9): 99 (1858). — *Dryopteris paleacea* (Lag. ex Sw.) C. Chr., *American Fern Journal* 1 (5): 94 (7 Aug. 1911), nom. illeg. (McNeill *et al.* 2006: Art. 53.1), non Hand.-Mazz. (1908: 100). — Type: Peru, *M. Lagasca y Segura s.n.*, Herb. Swartz (holo-, S; iso-, GH, US).

Aspidium parallelogrammum Kunze, *Linnaea* 13: 146 (1839). — *Dichasium paralellogrammum* (Kunze) Fée, *Mémoires sur la famille des fougères* 5: 302, pl. 23B, fig. 1 (1852). — *Nephrodium filix-mas* (L.) Rich. var. *paralellogramma* (Kunze) Hook., *Species filicum* 4: 116 (1862). — *Dryopteris paralellogramma* (Kunze) Alston, *American Fern Journal* 47 (3): 92 (16 Oct. 1957). — Type: Regno Mexico, *Hegewisch s.n.* & *De Karwinski s.n.*, Herb. Lucae (KIEL, syntypes).

DESCRIPTION

Plants terrestrial. Rhizome short, erect to suberect, up to 150 mm tall and 22 mm in diameter, set with roots, crowded persistent stipe bases and scales, the scales castaneous, chartaceous to thinly crustaceous, broadly attached, subulate, up to 15 × 2 mm, cordate, the margins variously set with short and long, apically or basally directed, often branched outgrowths which reduce in number and size towards the scale apex, the scale apex terminates in an elliptic thin-walled cell. Fronds crowded, caespitose, erect to suberect, up to 1.2 m long; stipe proximally castaneous, stramineous higher up, firm, up to 230 mm long, adaxially shallowly sulcate, cicatricate, densely scaled, the smaller scales concolorous, ferruginous to stramineous, stalked, the larger scales mostly bicolorous, if bicolorous then ferruginous to stramineous with castaneous streaks, chartaceous, sessile, subulate, up to 17 × 2.4 mm, cordate to cordate-imbricate, the margins proximally variously set with outgrowths similar to those on the rhizome scales, the outgrowths reduce in number and size towards scale apex, the scale apex terminates in a subulate cell or an elliptic thin-walled cell; lamina 1-pinnate-pinnatisect,

anadromous, catadromous towards the apex, narrowly elliptic, up to 935 × 270 mm, with up to 47 petiolated pinna pairs, proximally with several pairs of slightly and gradually reducing pinnae; rachis stramineous, adaxially sulcate, the sulcus not open to the sulcus of the costae, cicatricate, moderately to densely scaled, the scales up to 13 × 0.8 mm, the smaller scales mostly concolorous, ferruginous to stramineous, short-stalked, the larger scales concolorous or bicolorous, if bicolorous then ferruginous with castaneous streaks, chartaceous, sessile, subulate, cordate to cordate-imbricate, the margins variously set with outgrowths similar to those on rhizome scales, the scale apex terminates in a subulate cell or an elliptic thin-walled cell; pinnae pinnatifid, near opposite to alternate, imbricate or not, the proximal pinnae generally more widely spaced, dark green and glossy adaxially, paler and matt abaxially, up to 140 × 28 mm, oblong-acuminate, petiolate, the petiole up to 2 mm long; costa narrowly winged, adaxially with narrow ridges on either side of the costa, extending between adjacent lateral veins, initially moderately set with ferruginous, filiform scales, abaxially moderately scaled, the scales ferruginous to stramineous, chartaceous, sessile to short-stalked, subulate, up to 6 × 1 mm, cordate to cordate-imbricate, the margins irregularly set with outgrowths similar to those on rhizome scales, the scale apex terminates in a subulate cell or an elliptic thin-walled cell; lobes firmly herbaceous, rectangular to parallelogram-shaped, up to 16 × 7 mm, the truncate apical margin dentate, the proximal acroscopic lobe often slightly longer than next, proximal basisopic lobe mostly basisopically auricled, shallowly lobed (in subsp. *madagascariensis*) adaxially glabrous, or sparsely set with filiform scales along the costa and veins, abaxially moderately scaled along the costule, veins and lobe margins, scales along the veins ferruginous to stramineous, chartaceous, subulate, up to 4 × 0.6 mm, short-stalked, cordate-imbricate, variously set with outgrowths similar to those on rhizome scales, the scale apex terminates in a subulate cell, an elliptic thin-walled cell, or the apical cell undifferentiated, scales along lobe margin, ferruginous, chartaceous, filiform, up to 5 × 0.1 mm, long-stalked, proximally with short marginal outgrowths, entire distally, the scale apex terminates in a subulate cell, an elliptic

thin-walled cell, or the apical cell undifferentiated. Venation evident adaxially and abaxially, lateral veins in lobes forked once or twice to form 2 or 3 veinlets ending near the margin, endings slightly enlarged. Stomata mostly of the polycytic types, (40-)53(-64) μm long. Sori 2-seriate on the lobes, circular, up to 1.5 mm in diameter, discrete at maturity, inframedial on unmodified, predominantly anadromous vein branches; indusium up to 1.5 mm in diameter, brown, firmly chartaceous, reniform or 2-lobed, entire. Sporangium stalk simple, or with a 1- or 2-celled glandular hair, capsule obovate, annulus with (13-)14(-17) indurated annulus cells, epistomium 4(-5)-celled, hypostomium 4(-6)-celled. 32 spores per sporangium, rugate, brown, endospore (40-)48(-54) μm long (Tryon & Lugardon 1990: 423, figs 159.4, 159.5).

REMARKS

Tryon & Tryon (1982: 504) treated *Dryopteris wallichiana* as a species confined to the palaeotropics, whilst *D. paleaceae* is considered as a sister species restricted to the neotropics. Others, however, consider them conspecific (Smith & Fraser-Jenkins 1982; Fraser-Jenkins 1986, 1989; Stolze 1981). *Dryopteris wallichiana* has a world-wide tropical and subtropical distribution with its centre of diversity in SW China and the eastern Himalayas (Fraser-Jenkins 1989). Fraser-Jenkins (2006: 109-110) recognises three subspecies in the *D. wallichiana* complex, one of them occurring in the study area. It has been shown to be a diploid apomict whilst *D. wallichiana* subsp. *reichsteinii* from Zimbabwe is a triploid apomict (Widén *et al.* 1996: 71). The phloroglucinol derivatives of the species have been studied by Widén *et al.* (1996).

Dryopteris wallichiana (Spreng.) Hyl.
subsp. *madagascariensis* (C.Chr.) J.P.Roux
(Figs 1; 2)

Synopsis of the Lycopodiophyta and Pteridophyta of Africa, Madagascar and Neighbouring Islands: 124 (Mar. 2009). — *Dryopteris paleacea* (Lag. ex Sw.) C.Chr. var. *madagascariensis* C.Chr., *Catalogue des plantes de Madagascar, Pteridophyta*: 27 (Feb. 1932), nom. illeg. (McNeill *et al.* 2006: Art. 32.1[d]). — *Dryopteris paleacea* (Lag. ex

Sw.) C.Chr. var. *madagascariensis* C.Chr., *Dansk Botanisk Arkiv* 7: 35, t. 11, figs 5-9 (Oct. 1932). — *Dryopteris reichsteinii* Fraser-Jenk., *Bulletin of the British Museum, Natural History (Botany)*: 14 (3): 191 (1986). — Type: Madagascar, Mt. Tsaratanana, 2400 m, IV.1924, *H. Perrier de la Bâthie 16454* (holo-, BM000801013; iso-, P00349500!, P00483234!, P00483235!).

OTHER MATERIAL EXAMINED. — **Madagascar**. Mont Tsaratanana, 2400 m, IV.1924, *Perrier de la Bâthie 16454* (BM000801013; P00349500; P00483234; P00483235).

Réunion. Habitat in insula Borboniae, *Desvaux s.n.* (P00349605). — Cilaos, str. du Cap Bouteille, 1740 m, 18.III.2009 (Herb. E. Grangaud).

DIAGNOSTIC FEATURES AND RELATIONSHIPS

Dryopteris wallichiana subsp. *madagascariensis* appears to be generally smaller than the other subspecies as the fronds grow up to 1.1 m long and up to 270 mm wide. The proximal basiscopic lobes are basiscopically auricled and frequently also shallowly lobed. The lamina scales terminate in a subulate cell (Fig. 2D, F), rather than an elliptic thin-walled cell. The larger stoma length, (40-)53(-64) μm , suggests it being a different cytotype than either subsp. *wallichiana* and subsp. *reichsteinii*.

DISTRIBUTION AND HABITAT

Dryopteris wallichiana subsp. *madagascariensis* appears to be rare in the Madagascan region. In Madagascar, it is known from the Tsaratanana Mountains only, where it occurs at 2400 m. At this altitude, the vegetation consists of evergreen forests with an understory consisting of small trees. More recently, the species was rediscovered in La Réunion, occurring at 1740 m in seasonally wet open montane forests (Fig. 5).

REMARKS

Christensen (1932a: 27) first mentioned the name *Dryopteris filix-mas* subsp. *madagascariensis* under *D. paleacea*, but the former was not validly published (McNeill *et al.* 2006: Art. 32.1[d]). It was, however, validly published later (Christensen 1932b: 35). Fraser-Jenkins (1986: 191) raised this variety to species level as *D. reichsteinii*. He later determined material from the eastern highlands of Zimbabwe to be a triploid apomict and



FIG. 1. — Holotype of *Dryopteris wallichiana* (Spreng.) Hyl. subsp. *madagascariensis* (C. Chr.) J.P.Roux at the Natural History Museum, London (BM000801013).

described this as *D. wallichiana* subsp. *reichsteinii* Fraser-Jenkins, 1996 (in Widen *et al.* 1996: 71). I found material from Madagascar to differ from both subsp. *wallichiana* and subsp. *reichsteinii*. For this reason, the name *Dryopteris wallichiana* subsp. *madagascariensis* was proposed, based on *D. paleacea* var. *madagascariensis* C.Chr.

A 1774 Commerson collection said to have come from “Île de France”, now Mauritius, is housed in the Lamarck Herbarium, Paris (P00307037 & P00307038). Poiret (1804) based *Polypodium umbilicatum* on this collection. It was later transferred to *Aspidium* Sw. (Desvaux 1811: 320, 321), and still later to *Nephrodium* Rich. as a variety of *N. marginale* Mich. (Desvaux 1827: 260). The name then appears to have been forgotten as it was not cited for nearly a century until Morton (1973: 265) commented on the type, tentatively ascribing it to *D. filix-mas* (L.) Schott, but suggested that it may be *D. paleacea* var. *madagascariensis*. The origin of the collection is clearly erroneous as the Commerson material is that of *D. filix-mas*, a species not occurring on Mauritius.

Dryopteris Adans. sect. *Lophodium*
(Newman) C.Chr. ex H.Itô

Nova flora japonica 4: 65 (1939). — *Lophodium* Newman in *New Phytologist* 4: 371, app. XVI (1851). — *Dryopteris* Adans. group *Lophodium* (Newman) C.Chr., *Index filicum*: XXI (1905). — Lectotype: *Lophodium spinulosum* (O.F.Muell.) Newman (*Polypodium spinulosum* O.F.Muell.), designated by Christensen (1905: XXI), now *Dryopteris carthusiana* (Vill.) H.P.Fuchs.

Aspidium Sw. group *Spinulosa* H.Christ, *Farnkräuter der Erde*: 261 (1897), nom. nud. (McNeill *et al.* 2006: Art. 32.1[d]). — Type: none indicated. Two species — *A. spinulosum* Sw. and *A. aemula* (Soland.) Sw. are listed. *Aspidium spinulosum* may be considered as the type.

REMARKS

A group of about 10 species chiefly occurring throughout the northern temperate regions of the world, Macaronesia, and northern Africa, with few species extending to the southern hemisphere.

Diagnostic features of the section are the short, erect or decumbent rhizome that is closely and

irregularly branched and which is set with roots and closely spaced trophopods. The lamina is up to 3-pinnate and the lobes are strongly dentate. The fertile vein branches are frequently shortened and end in the sori, or they extend for a distance beyond the sorus. Indumentum is composed of glands, moniliform hairs, and scales, the scale apex and marginal outgrowths generally end in a long moniliform series of cells. Fraser-Jenkins (1986: 195) noted that the minutely spinulose perispores may be unique for the section.

Dryopteris antarctica (Baker) C.Chr.
(Figs 3; 4)

Index filicum, Supplementum 1906-1912: 29 (20 Dec. 1913). — *Nephrodium antarcticum* Baker, *Journal of the Linnean Society, Botany* 14: 479, 480 (1875). — Type: Island of “Amsterdam” (Saint Paul), *G. Staunton s.n.* (holo-, BM!).

Dryopteris callolepis C.Chr., *Notizblatt des Botanischen Gartens und Museums zu Berlin-Dahlem* 9: 177 (1924). — Type: Kenya, “Mt. Aberdare: regio bambusina superior, ± 2800 m, 31 März 1922”, *R.E. & T.C.E. Fries 2554* (holo-, BM!).

Aspidium spinulosum sensu Pappe & Rawson, *Synopsis filicum Africae australis*: 38 (Jan.-Jul. 1858), non *Aspidium spinulosum* Sw. (1801: 38).

Aspidium spinulosum Sw. var. *dilatatum* sensu Kuhn, *Filices africanæ*: 142 (Oct. 1868), non *Aspidium dilatatum* (Hoffm.) Sm. (1804: 1125).

Dryopteris spinulosa (O.F.Müll. ex Roth) Kuntze subsp. *dilatata* sensu Bonap., *Notes ptéridologiques* 15: 16 (25 Feb. 1924), non *D. dilatata* (Hoffm.) A.Gray (1848: 631).

Nephrodium spinulosum sensu Peter, *Feddes Repertorium, Beiheft* 40 (1): 56 (1929).

Dryopteris austriaca (Jacq.) Woyn. subsp. *dilatatum* sensu Chiov., *Lavori dell’Istituto Botanico, Università di Modena* 6 (I/XI): 140 (1935), non *Dryopteris dilatata* (Hoffm.) A.Gray (1848: 631).

Dryopteris dilatata sensu Tardieu, *Flore de Madagascar et des Comores (plantes vasculaires), 5^e Famille. Polypodiacees (sensu lato) 5 (1) Dennstaedtiacees. (10) Aspidiacees*: 316 (May 1958), non (Hoffm.) A.Gray (1848: 631).

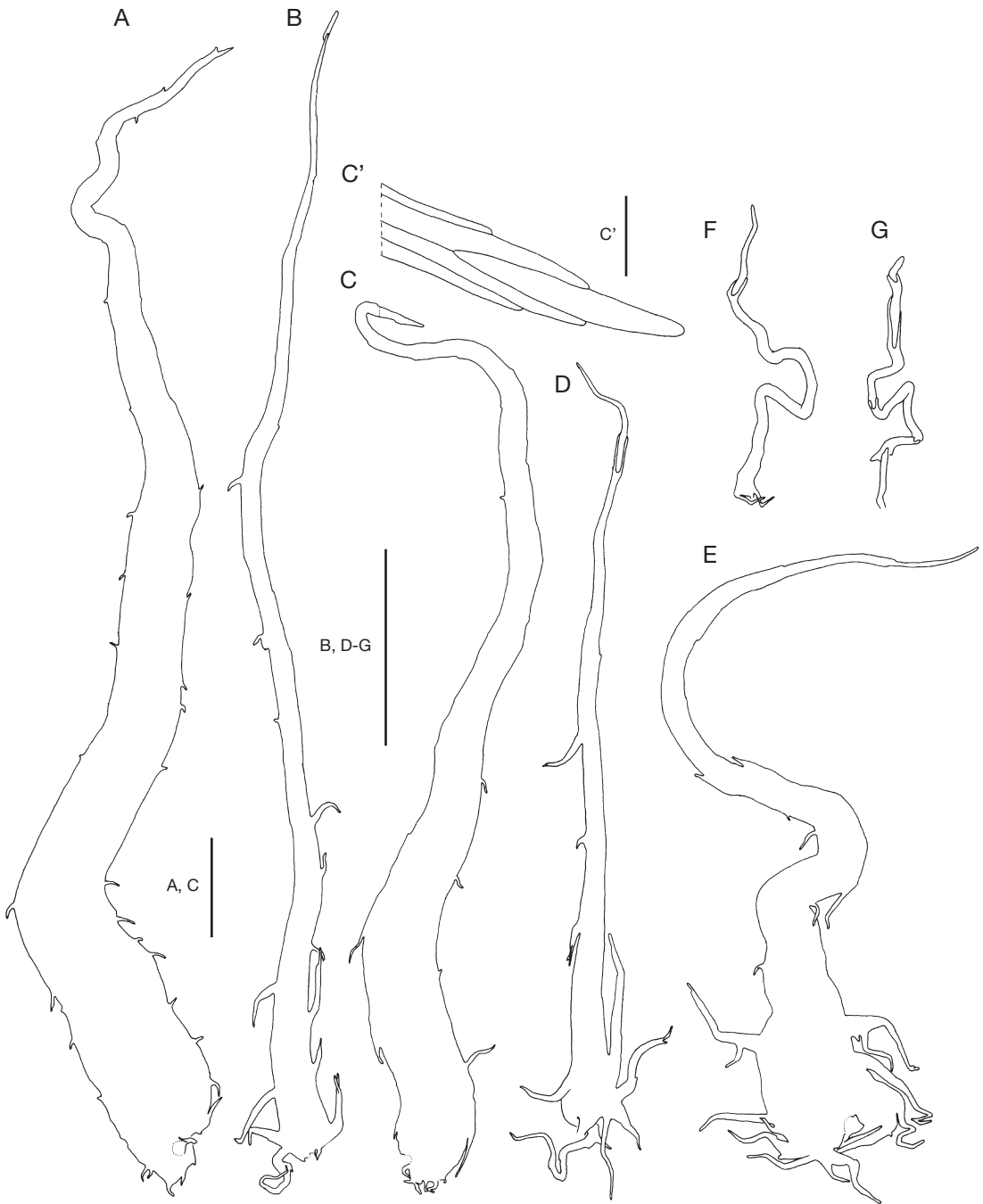


FIG. 2. — Scales of *Dryopteris wallichiana* (Spreng.) Hyl. subsp. *madagascariensis* (C.Chr.) J.P.Roux: **A, B**, stipe scales; **C, C', D**, rachis scales; **E**, scale from abaxial lamina surface; **F, G**, scales from lamina margin. *De la Bâthie 16454* (BM). Scale bars: A-G, 1 mm; C', 0.1 mm.

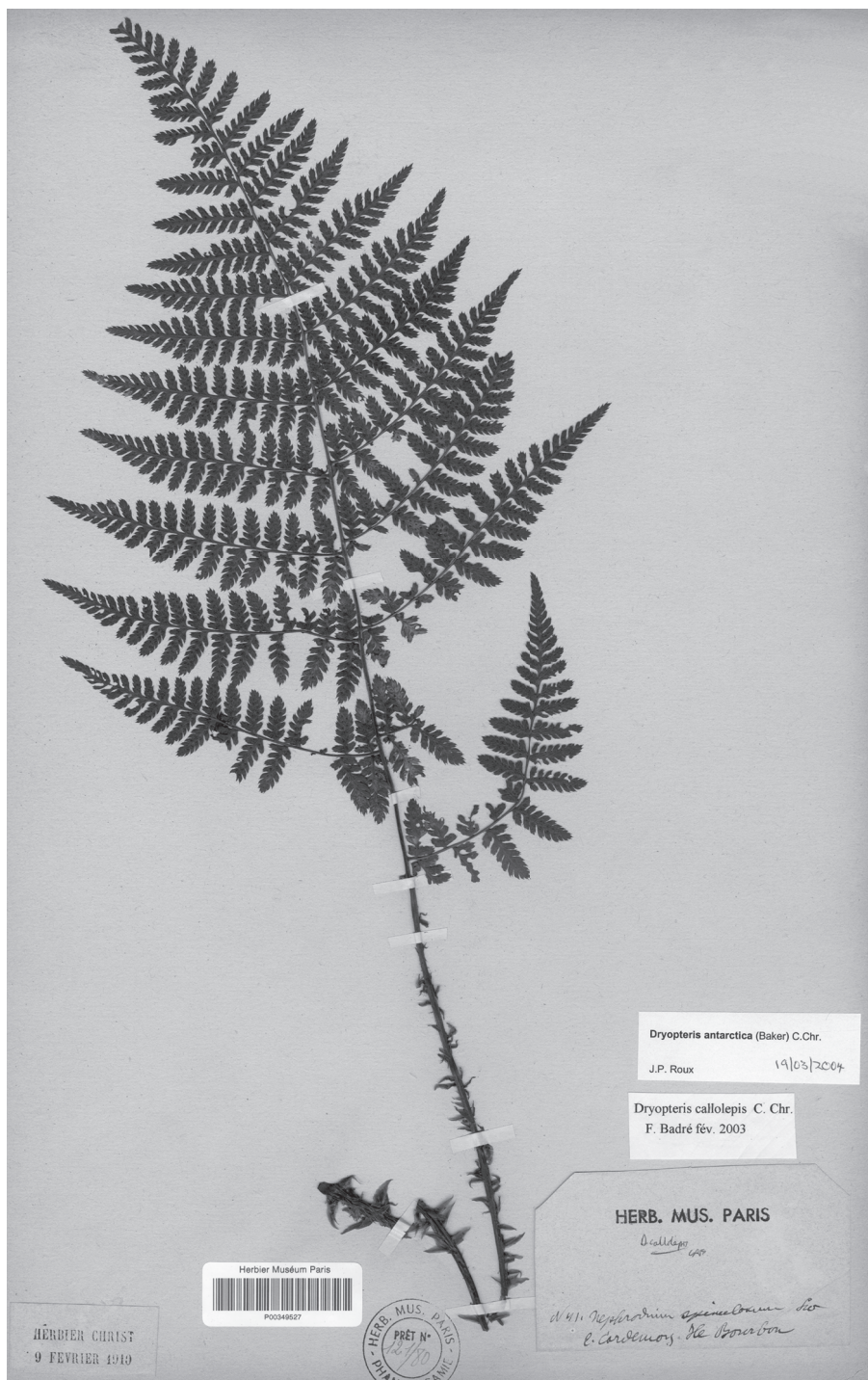


FIG. 3. — Specimen of *Dryopteris antarctica* (Baker) C.Chr., de Cordemoy 41 (P00349527). Photo: MNHN, Paris Herbarium, 2009.

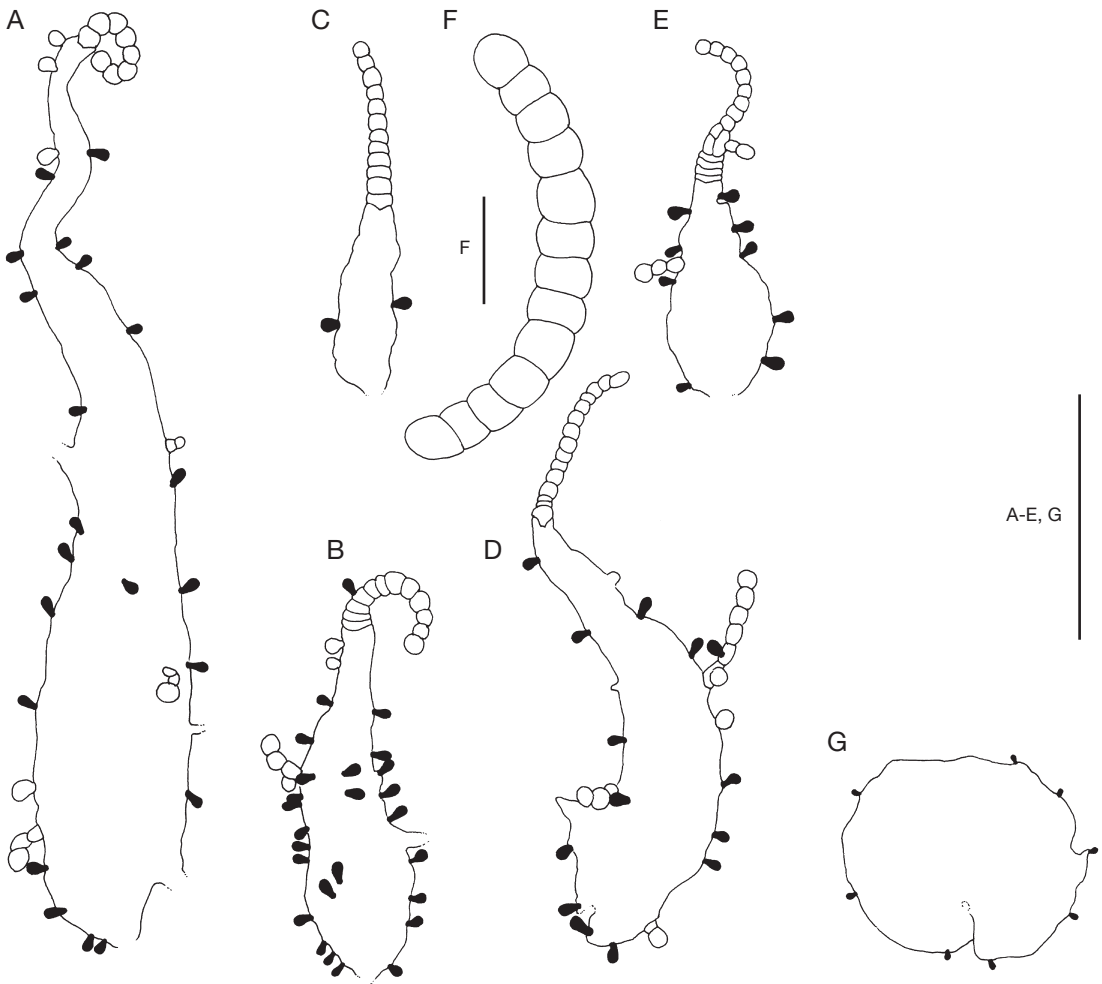


FIG. 4. — Indumentum and indusium of *Dryopteris antarctica* (Baker) C.Chr.: **A**, stipe scale; **B**, rachis scale; **C**, scale from pinna-rachis; **D**, **E**, scales from abaxial lamina surface; **F**, hair from abaxial lamina surface; **G**, indusium. *Stauton s.n.* (BM). Scale bars: A-E, G, 1 mm; F, 0.1 mm.

OTHER MATERIAL EXAMINED. — **Madagascar**. Massif de l'Andringitra (Iratsy): vallées de la Riambava et de l'Antsifotra et montagnes environnantes, reste de forêts, vers 2000 m, 27.XI-8.XII.1924, *Humbert 3760* (P00349521).

Mauritius. Des bois du centre de l'Île de France, *Bory de St Vincent s.n.* (P00349525).

Réunion. Fonds de la Rivière de l'est-Massif de la Fournaise, 1850 m, 02.IV.1971, *Cadet 3183* (P00349522). — Réunion (Île Bourbon), 1892, *Cordemoy 41* (P00349524, P00349527). — Île Bourbon, *Richard 669* (K). — À la plaine des Cafres, *Richard 37* (P00349528). — Dans les forêts élevées, Île Bourbon, *sine coll. 358* (P00349526). — À la plaine des Cafres, du côté du Volcan, *sine coll. 669* (P00349523).

Saint Paul. *Stauton s.n.* (BM). — Saint Paul, in humid situations all over the island, *Jelinek 123* (BM).

DESCRIPTION

Plants terrestrial or epilithic. Rhizome short, erect to suberect, closely branched, up to 5 mm in diameter, set with roots, crowded trophopods and scales, the scales ferruginous to castaneous, often bicolorous, chartaceous, sessile, lanceolate to narrowly ovate, up to 9 × 3 mm, cordate to cordate-imbriate, the margins entire or with scattered glands, the apex filiform, terminating in a moniliform series of cells.

Fronds crowded, caespitose, arching, up to 1.03 m long; stipe base castaneous, stramineous higher up, proximally adaxially flattened, shallowly sulcate distally, up to 460 mm long and 4.5 mm in diameter, moderately set with glands and spreading scales, the scales ferruginous, often slightly darker centrally, chartaceous, sessile, ovate to broadly ovate, up to 11×4.5 mm, truncate to cordate-imbricate, entire or with scattered glands, the apex terminates in a short series of moniliform cells; lamina herbaceous to thinly herbaceous, up to 3-pinnate, ovate, up to 600 mm long, anadromous, catadromous towards apex, with up to 17 petiolated pinna pairs; rachis greenish, adaxially sulcate, becoming narrowly winged towards apex, often set with glands and moderately to sparsely scaled, the scales ferruginous to stramineous, chartaceous, sessile or short-stalked, lanceolate to subulate, up to 4×2 mm, cuneate to cordate-imbricate, entire or with scattered glands, the apex terminates in a short uniseriate series of cells, the cells oblong or moniliform, scales on the adaxial surface of rachis linear to filiform, up to 5×0.4 mm; pinnae petiolate, the petiole up to 20 mm long, the basal pinnae inaequilaterally ovate, up to 2-pinnate, those higher up aequilaterally narrowly ovate to oblong-acuminate, up to 170×90 mm, basal pinna pair mostly longest, basiscopically developed, opposite to alternate, widely spaced at base, more closely spaced towards the apex and mostly somewhat imbricate, with up to 8 petiolated pinnule pairs; pinna-rachis adaxially shallowly sulcate, the sulcus confluent with that of the rachis, narrowly winged for most of its length, set with glands, also sparsely scaled, the scales stramineous, chartaceous, sessile or short-stalked, narrowly ovate to subulate, up to 3×0.6 mm, cuneate to cordate, entire to closely set with glands and globose to subglobose non-glandular cells along the margin and often also on surface, or with short moniliform hairs along the margin, the apex filiform, terminating in a short moniliform series of cells; pinnules petiolate, the petiole up to 2 mm long, symmetric or inaequilaterally narrowly ovate to oblong-obtuse, 1-pinnate, often acrosopically developed, acrosopic pinnule on basal pinnae up to 28×12 mm, basiscopic pinnule on basal pinnae up to 65×25 mm, not or slightly imbricate, with

up to 4 petiolated segment pairs; pinnule-rachis adaxially shallowly sulcate; segments broadly ovate to oblong-obtuse, up to 18×9 mm, basiscopically decurrent, spaced, never imbricate, lobed, the lobes strongly dentate, adaxially glabrous, or sparsely set with glands (52-)116(-156) mm long along the veins, often also with hairs and filiform scales near the base, abaxially sparsely to moderately set with glands similar to those on the adaxial surface, often also with hairs and (sparsely) scaled, the hairs moniliform with scattered glands, the scales stramineous, chartaceous, sessile or short-stalked, ovate to subulate, up to 1.8×0.7 mm, cuneate to truncate, entire or variously set with clavate glands and globose to subglobose non-glandular hairs along the margins, the scale apex filiform, terminating in a short or long series of moniliform cells. Venation pinnately branched in segments, vein branches forked or simple, often slightly abbreviated when fertile, evident, ending in the teeth near the margin, endings often slightly thickened. Stomata mostly of polocytic type, (40-)50(-64) mm long. Sori circular, at or near the apex of mostly shortened anadromous vein branch, discrete at maturity, up to 1.2 mm in diameter; sporangium stalk simple, capsule with (11-)16(-21) indurated annulus cells; indusium brown, firmly herbaceous, reniform, entire to erose, often glandular along margin, up to 1.2 mm in diameter. Spores ellipsoidal, monolete, perispore with compressed reticulate folds, densely echinulate, (44-)50(-58) \times (32-)35(-42) mm (Tryon & Lugardon 1990: 428, fig. 159.44, as "*D. callolepis*"). Chromosome number: $2n = 164 \pm 4$ (Vida *in* Widén *et al.* 1973: 2129).

DIAGNOSTIC FEATURE AND RELATIONSHIPS

Dryopteris antarctica is characterised by being restricted to high elevations, and the short, closely branched, erect to suberect rhizome generally enveloped by trophopods. Also characteristic are the firmly chartaceous, often bicolorous rhizome and stipe scales which appear entire, but which often bear glands along the margin. The scale apex and marginal outgrowths generally terminates in a short or long moniliform series of cells. The apical part of the lamina hairs terminates in a similar moniliform series of cells. The strongly dentate segments,

and the mostly shortened, fertile vein branches are further diagnostic features of the species.

Widén *et al.* (1999: 19) found *D. antarctica* to be very similar to *D. dilatata* (Hoffm.) A.Gray from Europe and Alaska in both morphology and chemistry. My observations on the scale morphology of the species support this suggestion.

VARIATION

Considering the wide and disjunct distribution of *Dryopteris antarctica*, the species shows little variation in overall morphology. Micromorphological variation includes the sporadic occurrence of glands along the indusium margin, and the often significant variation in the length of the glands (52-156 µm) occurring on the lamina. Stoma length of collections throughout the distribution range falls within the same size range (40-64 µm), which does not suggest different ploidy levels in the species. Variation has also been observed in the degree to which the lamina scales are set with glands. In collections from Saint Paul, the scale margins and laminae are closely set with clavate glands, whilst collections from the African continent are never as closely glandular. Non-glandular globose to subglobose cells have been observed on the scale laminae of collections from both Saint Paul and Africa. Morphologically, *D. callolepis* cannot be separated from *D. antarctica* and is therefore considered synonymous.

DISTRIBUTION AND HABITAT

Dryopteris antarctica is remarkably disjunct in its distribution, occurring on the isolated island of Saint Paul (37°52'S, 77°35'E) in the south Indian Ocean, and in Africa where it is confined to the Western Cape and the south-western corner of the Eastern Cape. The species also occurs at 1850 m on Réunion island, and at 2000 m on Massif d'Andingitra in southern Madagascar, and on Mauritius (Fig. 5).

REMARKS

Fraser-Jenkins (1986: 208) noted that *D. callolepis* is synonymous with *D. antarctica*. It was, however, again tentatively separated from *D. callolepis* for "geographical convenience and because of their distinct chemistry" (Widén *et al.* 1999: 19). The type of *D. antarctica* is in the Banks Herbarium at the British Museum of Natural History.

Dryopteris Adans. sect. *Marginatae* Fraser-Jenk.

Bulletin of the British Museum (Natural History), Botany 14 (3): 194 (1986). — Type: *Dryopteris marginata* (Wall. ex C.B. Clarke) H.Christ; *Aspidium marginatum* Wall. ex C.B. Clarke.

A group of about 26 species throughout southern and eastern Asia and Africa, with one species reaching Yemen (Fraser-Jenkins 1986: 194).

KEY TO THE *DRYOPTERIS* SPECIES IN SECTION *MARGINATAE* (EXCLUDING PUTATIVE HYBRID)

- 1. Lamina generally with one or more proliferous buds adaxially on the rachis near the lamina apex; sori exindusiate 5. *D. manniana*
 — Lamina never with proliferous buds along the lamina axes; sori indusiate 2
- 2. Lamina axes with or without hairs and scales, generally with some glands 3
 — Lamina axes with hairs and scales, but never with glands 4
- 3. Segments adaxially and abaxially closely set with capitate glands along and between the vein branches 2. *D. bernieri*
 — Segments without conspicuous glands between the vein branches 3. *D. bojeri*
- 4. Lamina with 2-celled hairs mostly along the axes and abaxially on the veins 6. *D. pentheri*
 — Lamina without 2-celled hairs occurring along the lamina axes and veins 5
- 5. Larger stipe base scales with oblong glands along the margins and on the scale laminae 1. *D. aquilinooides*

- Larger stipe base scales occasionally with glands along the margins, but never on the scale laminae 6
6. Plants with fronds up to 1.9 m long; lamina to 3-pinnate 4. *D. comorensis*
- Plants with fronds up to 1.2 m long; lamina to 2-pinnate-pinnatifid 7. *D. subcrenulata*

1. *Dryopteris aquilinoïdes* (Desv.) C.Chr.

(Fig. 6)

Index filicum: 252 (2 Oct. 1905). — *Nephrodium aquilinoïdes* Desv., *Mémoires de la Société linnéenne de Paris* 6 (2): 261, 262 (Jul. 1827). — *Aspidium aquilinoïdes* (Desv.) Mett. ex Kuhn, *Filices africanæ*: 126 (Oct. 1868). — Type: feuilles de 3 à 4 pieds dans les forêts, Île Bourbon, *J.M.C. Richard* 363 (holo-, P00349567!).

Nephrodium aquilinoïdes Desv. var. *angustatum* Desv., *Mémoires de la Société linnéenne de Paris* 6 (2): 262 (Jul. 1827.). — Type: Habitat in insula Borbonia, *sine coll. s.n.* (holo-, P00349566!).

Aspidium grande Fée, *Mémoires sur la famille des fougères* 5: 292, 295 (1852). — Type: Habitat in insula Borbonia, *De Montbrison s.n.* (?holo-, P00349529!).

OTHER MATERIAL EXAMINED. — **Mauritius.** Île Maurice, régions élevées, 1906, *Bijoux*, *F. 20* (P00349531). — Île Maurice, 2.XII.1909, *Royal Gardens Pamplemousses s.n.* (P00349570).

Réunion. Brûlé de St Denis, route forestière de la Roche écrite, env. 4 km après le village Le Brûlé, 31.X.1973, *Badré 738* (P00349538, P00349552). — Île de la Réunion, forêt hygrophile, Bonnet Carré, Cilaos, 1400 m, 15.XI.1973, *Badré 913* (P00349550, P00349551). — Fourré à *Philippia*, sentier de la mare à Joseph au coteau Kerveguen, cirque de Cilaos, 16.XI.1973, *Badré 938* (P00349555); *Badré 946* (P00349553, P00349554); *Badré 950* (P00349561, P00349562, P00349563); *Badré 956* (P00349564, P00349565). — Sentier vers la Roche écrite, forêt avant La plaine des Chicots, 25.XI.1973, *Badré 1019* (P00349539, P00349540, P00349541). — Plateau de Bébou, forêt d'altitude alt. 1300 m, 28.XI.1973, *Badré 1038* (P00349560). — Forêt d'altitude alt. 1300 m, 28.XI.1973, *Badré 1039* (P00349559). — Cirque de Salazie, sentier vers la Nouvelle, forêt hygrophile d'altitude, alt. 1300-1400 m, 29.XI.1973, *Badré 1056* (P00349568, P00349569). — Bourbon, *Barkly 23* (K, 2 sheets). — Réunion, *Baudouin 903* (P00349583). — St Denis, *Boivin 98* (P00349580). — Dans les bois élevés à Bourbon, *Boivin 668* (P00349581). — Île Bourbon, *Boivin 885* (B200052452, B200052454, B200052456, P00349530). — Sous-bois de formation arbustive-col de Bébou, 1400 m, 11.XI.1966, *Cadet 540* (P00349548, P00349549). — Île de la Réunion, *Cadet 638* (P0034954, P0034955, P0034956,

P0034957). — Humicole-végétation éricoïde à *Philippia* Plateau de Bébou, 1300 m, 16.XII.1970, *Cadet 2968* (P00349536, P00349537). — Sous-bois de la forêt à *Nastus*-plaine des Chicots, 1700 m, 13.III.1971, *Cadet 3149* (P00349534). — Sous-bois forêt hygrophile-col de Bébou, 1400 m, 15.I.1973, *Cadet 4026* (P00349535). — Petite plaine des Palmistes, *Cadet 4346* (P00349533, P00349556, P00349557, P00349558). — Île Bourbon, *De Montbrison s.n.* (P00349529). — Bébou, 16.XII.1970, *Friedmann 850* (P00349542, P00349543). — Île Bourbon, voyage de M. Gaudichaud sur *La Bonite*, 1836-37, *Gaudichaud s.n.* (P00349585). — Bourbon, *Johnstone s.n.* (BM000800980). — Bourbon, Salazie, *Lépervanche-Mézière s.n.* (P00349578). — Île Bourbon, *Richard 318* (P00349582). — Bourbon, *Richard s.n.* (B200052453). — Île Bourbon, *sine coll. s.n.* (P00349573). — Île Bourbon, *sine coll. s.n.* (P00349574). — Salazie, Bourbon, *sine coll. 40* (P00349572).

Sine Loco. 2.X.1882, *Bellouve 145* (P00349579, P00349586); *Desvoux s.n.* (P00349576); *Du Petit-Thouars s.n.* (P00349532); *Richard 307 & 308* (P00349584); *Richard 307* (BM000800983); *Richard 318* (P00349577).

DESCRIPTION

Plants terrestrial. Rhizome short-decumbent, up to 250 mm long and 25 mm in diameter, set with roots, closely spaced persistent stipe bases and scales, the scales ferruginous, thinly chartaceous, broadly attached, lanceolate, up to 35 × 10 mm, with clavate to oblong glands along the margin and scale laminae, often also with pluricellular, uniseriate hairs along the margins and on scale laminae. Fronds up to 1.4 m long, arching, anadromous, catadromous towards apex; stipe up to 800 mm long and 10 mm in diameter, mostly nitid to atrocastaneous, glossy, sulcate adaxially, proximally densely scaled, sparsely scaled to glabrous higher up; lamina up to 3-pinnate, broadly ovate to deltoid, up to 780 × 420 mm, with up to 15 petiolated pinna pairs; rachis castaneous, or stramineous with castaneous markings, glossy, sulcate adaxially, initially sparsely scaled, glabrous later, the scales castaneous, chartaceous, sessile, lanceolate-caudate, up to 5 × 2 mm, broadly cuneate, often with pluricellular, uniseriate hairs along the margin, generally also with oblong glands along margin and

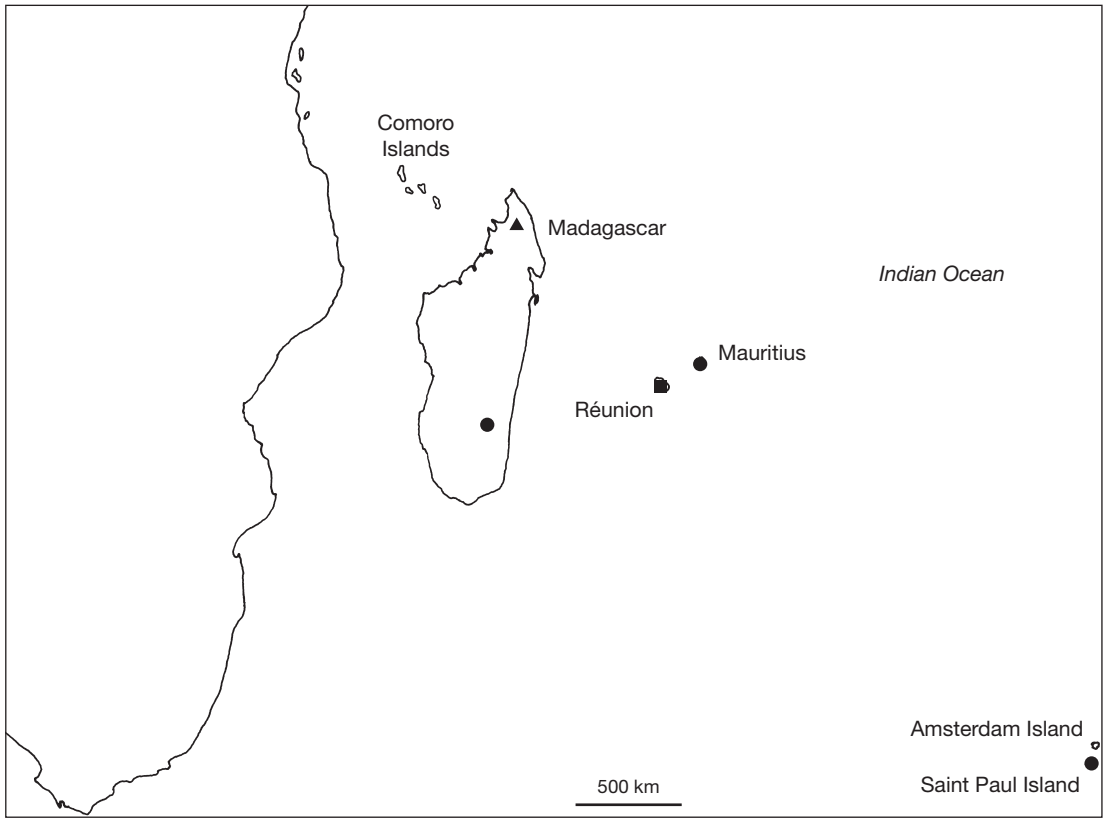


FIG. 5. — Distribution of *Dryopteris wallichiana* (Spreng.) Hyl. subsp. *madagascariensis* (C.Chr.) J.P.Roux (▲), and *Dryopteris antarctica* (Baker) C.Chr. (●). The solid square (■) indicates where both species occur.

scale laminae; pinnae near opposite to alternate, proximally widely spaced and slightly overlapping, more closely spaced distally, proximal 2 or 3 pinna pairs inaequilaterally ovate, up to 425 × 245 mm, pinnae higher up symmetric, narrowly ovate to oblong-acuminate, up to 2-pinnate, with up to 13 petiolated pinnule pairs, the petiole up to 20 mm long; pinna-rachis stramineous to ferruginous, adaxially sulcate, matt or glossy, glabrous or sparsely scaled, the scales similar to, but slightly smaller than those on the rachis; pinnules near opposite to alternate, proximally widely spaced, acroscopic pinnae on basal pinnae oblong-acuminate, narrowly ovate, or narrowly triangular, up to 110 × 32 mm, basiscopic pinnae on basal pinnae oblong-acuminate, narrowly ovate, or narrowly triangular, up to 145 × 50 mm, 1-pinnate, petiolate, the petiole up to 5 mm

long; pinnule-rachis adaxially sulcate, often flexuose and narrowly winged towards the apex, sparsely scaled, the scales ferruginous, chartaceous, sessile, ovate-caudate to subulate, up to 4 × 1.5 mm, often somewhat bullate, often with pluricellular, uniseriate outgrowths along the margin, also with oblong glands along the margins and laminae, the apex terminates in a long uniseriate series of oblong cells; segments firmly herbaceous to subcoriaceous, near opposite to alternate, widely spaced, narrowly ovate, oblong-acute, or oblong-obtuse, up to 30 × 13 mm, proximally petiolate, adnate and basiscopically decurrent towards the apex, petiole up to 1.5 mm long, lobed, the lobes oblong-obtuse, denticulate, glabrous adaxially, abaxially with rigid hairs and scales similar to, but smaller than those along the costules and veins. Stomata (34-)45(-58) μm long. Venation evident,

forked twice in proximal lobes, vein branches end in teeth near the margin. Sori medial to inframedial on predominantly anadromous vein branches, essentially 2-seriate on segments, up to 1.4 mm in diameter, discrete when mature; indusium firmly herbaceous, castaneous, entire to repand, strongly recurved, eglandular or rarely with a few glands on the laminae. Sporangium stalk simple, capsule with (11-)14(-19) indurated annulus cells, epistomium (3-)4(-6)-celled, hypostomium (3-)4(-6)-celled. Spores 64 per sporangium, brown, with narrow reticulate ridges, (26-)36(-44) × (20-)23(-30) μm.

DIAGNOSTIC FEATURES AND RELATIONSHIPS

Dryopteris aquilinoïdes is characterized by the large rhizome and stipe bases scales, the near glabrous dark brown stipe and glossy frond axes, and the small ovate-caudate scales occurring abaxially along the lamina axes and veins, which bear numerous oblong glands along the margins and laminae. The similar scale morphology of *D. aquilinoïdes* and *D. bernieri* may suggest an affinity.

DISTRIBUTION AND HABITAT

Dryopteris aquilinoïdes is restricted to Mauritius (20°17'S, 57°33'E) and Réunion island (21°18'S, 55°32'E) in the Indian Ocean (Fig. 7). The species appears to be rare on Mauritius, having been recorded from cloud forests (600-700 m) on Mt Le Pouce by Lorence (1978: 227). The species is more common on Réunion island, chiefly occurring in moist forests and heath scrub at elevations ranging between 1300 and 1400 m, extending up to 1700 m at plaine des Chicots.

REMARKS

Dryopteris aquilinoïdes is based on material from J.M.C. Richard collected in the early 1800's during his stay on Réunion island (« Bourbon »). Attached to the sheet is a label in the hand of Richard, which reads: "363 *Aspidium speciosum*? Feuilles de 3 à 4 pieds dans les forêts, Île Bourb." A sheet in the Berlin Herbarium (B200052453), collected by Richard on Réunion island is indicated as being an isotype of *D. aquilinoïdes*. The label, however, does not provide a collecting number, which places its authenticity as type in question. Although *D. aquilinoïdes* was

recognised by Kuhn (1868: 126) as distinct, it was not mentioned by Baker (1877). Baker most likely incorporated material belonging to this species into *Nephrodium filix-mas* (L.) Rich. var. *elongatum*, as did Cordemoy (1891: 76). Tardieu-Blot (1956a: 163) recognised *D. aquilinoïdes* as a distinct species, but erroneously included *D. bojeri* (Baker) Kuntze in it.

A. De Montbrison collection (P00349529) from "Île Bourbon", named *Aspidium grande*, is housed in the Paris Herbarium. The sheet contains two fragments, the larger bearing two pinnae and the smaller a pinna pair of *D. aquilinoïdes*. The label is in an unknown hand. There is no indication that the sheet forms part of the original De Montbrison collection.

Three sheets in the Berlin Herbarium (B200052452, B200052454 and B200052456), all of which are *Boivin 885* collections from Réunion island, has a label attached to them, which reads: "*A. politum* Kze Herb". All these sheets contain lamina portions of *D. aquilinoïdes* and have been indicated as types. *Aspidium politum* Kunze appears to be a manuscript name, as no reference could be located where the name was published. Desvaux (1827: 250), however, published the name *A. politum*, but it appears to represent a different species. The origin of Desvaux's plant is from Mauritius and not Réunion and he also gave no collector. Christensen (1905: 88) considers Desvaux's plant synonymous with *Rumohra adiantiformis* (G.Forst.) Ching.

2. *Dryopteris bernieri* Tardieu (Figs 8; 9)

Notulae Systematicae (Paris) 15 (2): 161 (Apr. 1956). — Type: Bourbon (Réunion), *Lépervanche-Mézière* 22 (holo-, P00349606!).

OTHER MATERIAL EXAMINED. — **Comoro Islands** (Anjouan). Johanna Island, III.1977, *Beusher s.n.* (K). **Réunion**. Bourbon, 1847, *Armange s.n.* (P00349616). — Bourbon, 1835, *Bernier 96* (P00349608). — Route forestière du pic Maïdo, falaise ombragée d'une ravine, 1750 m, 2.XI.1973, *Badré 773* (P00349619). — Palmiste rouge, vallée du Bras des Calumets, plantation d'*Eucalyptus*, 1000 m, 15.XI.1973, *Badré 902* (P00349617, P00349618). — Sentier de Cilaos vers l'îlet à Cordes, entre Cilaos et le bras Rouge, 17.XI.1973, *Badré 974* (P00349620, P00349621). — Île Bourbon, 15.II.1847,

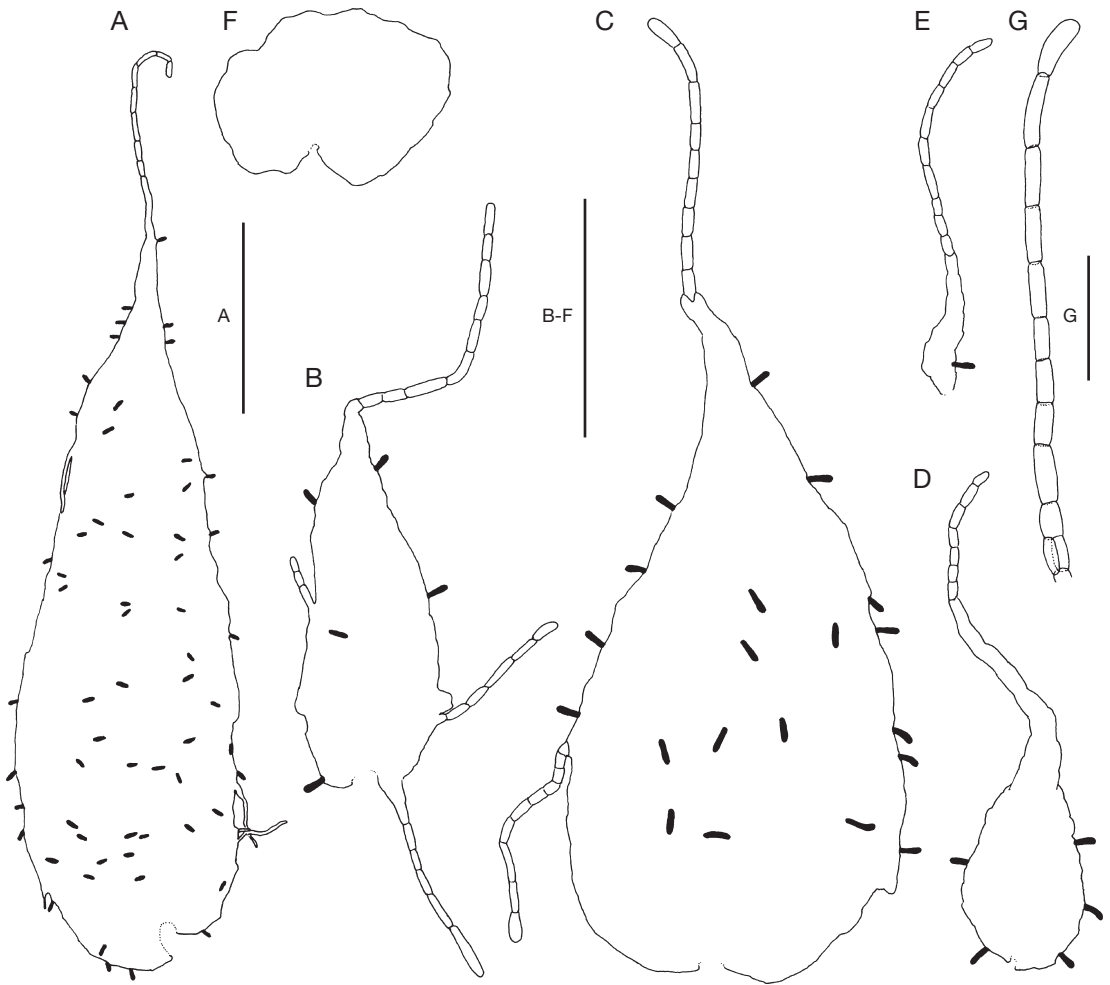


FIG. 6. — Indumentum and indusium of *Dryopteris aquilinoidea* (Desv.) C.Chr.: **A**, stipe scale; **B, C**, rachis scales; **D, E**, scales from abaxial lamina surface; **F**, indusium; **G**, hair from abaxial lamina surface. *Badré 1039* (P00349559). Scale bars: 1 mm.

Boivin s.n. (P00349609). — plaine des Cafres au pied du Piton de Villers, 7.VI.1851, *Boivin s.n.* (P00349612). — Oraison, VII.1851, *Boivin s.n.* (P00349611). — Île Bourbon, *Boivin s.n.* (P00349614). — Cilaos, près de la chapelle, 600 m, 12.I.1963, *Cadet 322* (P00349629). — Fissure profonde sommet du Rempart de Belle courbe, 2300 m, 12.IX.1968, *Cadet 1542* (P00349628). — Haute vallée de la rivière des Remparts, sous-bois sur falaise, 1600 m, 20.XI.1968, *Cadet 1713* (P00349626, P00349627). — La Réunion, sous-bois d'*Acacia* et d'*Hypericum*, bras Sec, cirque de Cilaos, 1300 m, 7.II.1969, *Cadet 1904* (P00349624). — La Réunion, terrestre, sous-bois de végétation arbustive, cirque de Cilaos, 1200 m, 16.II.1973, *Cadet 4115* (P00349622). — La Réunion, terrestre, sous-

bois de forêt sèche, cirque de Grand Bassin, vers 1000 m, 28.VI.1973, *Cadet 4375* (P00349623). — La Réunion, sous-bois de végétation arbustive pionnière, vallée du Bras Rouge, cirque de Cilaos au-dessous de l'Îlet du Salazes, 1300 m, 22.III.1974, *Cadet 4559* (P00349625). — Île Bourbon, *De Cordemoy s.n.* (BM000801043). — Île Bourbon, VII.1837, *Gaudichaud s.n.* (P00349615-A only). — Réunion, Cilaos Distr., road from Cilaos to Îlet à Cordes on steep earthbank, in deep shade, occasional, 1000 m, 20.IX.1984, *Jacobsen 5541* (FR). — Bourbon, *Johnstone 80* (BM000801026). — Bourbon, *Lépervanche-Mézière 22* (P00349606). — La Réunion, 1891, *Maigre s.n.* (P00349607). — Réunion, *Potier s.n.* (P00349610). — Sine Loco. *Lépervanche-Mézière s.n.* (P00349613).

DESCRIPTION

Plants terrestrial. Rhizome short-decumbent, up to 70 mm long and 16 mm in diameter, set with roots, closely spaced stipe bases and scales, the scales ferruginous, chartaceous, adnate, linear-acuminate, up to 35×4.5 mm, regularly set with capitate glands along the margins and laminae, the apex terminates in a short series of oblong cells. Fronds crowded, arching, up to 1.2 m long; stipe up to 510 mm long and 7 mm in diameter, proximally castaneous, stramineous higher up, adaxially shallowly sulcate, proximally densely set with scales similar to those on the rhizome, up to 45×4 mm, moderately to closely set with capitate glands, sparsely scaled higher up, the scales ferruginous to stramineous, sessile, ovate-caudate to narrowly lanceolate-caudate, up to 9×3 mm, cordate, the margins and laminae regularly set with capitate glands, often also with a few scattered pluricellular, mostly uniseriate hairs, which often is glandular, the scale apex terminates in a short series of oblong cells; lamina deltate to broadly ovate, up to 610×340 mm, to 2-pinnate-pinnatifid, pinnatifid towards the apex, with up to 8 petiolated pinna pairs; rachis ferruginous, sulcate adaxially, narrowly winged towards the apex, closely glandular, sparsely scaled, the scales sessile, narrowly lanceolate-caudate to subulate-caudate, up to 4×0.6 mm, cuneate, the margins and laminae regularly set with capitate glands, the apex terminates in a short series of oblong cells; pinnae opposite to alternate, mostly overlapping, petiolate at base, adnate and basiscopically decurrent with rachis winged towards lamina apex, petiole up to 13 mm long, basal pair longest and conspicuously basiscopically developed, up to 1-pinnate-pinnatifid, inaequilaterally ovate, up to 290×150 mm, pinnae higher up more symmetric, oblong-acuminate to linear-acuminate, with up to 6 petiolated pinnule pairs; pinna-rachis sulcate adaxially, narrowly winged towards the apex, closely glandular, sparsely scaled abaxially, the scales similar, but smaller than those on the rachis; pinnules petiolate, the petiole up to 2.5 mm long, opposite to alternate, pinnatifid, not or slightly overlapping, firmly herbaceous, dark green adaxially, paler abaxially, pinnatifid, acroscopic pinnule on basal pinnae linear-acuminate to ovate, up to 70×24 mm, basiscopic pinnule on basal pinnae linear-acuminate to narrowly ovate, up to 90×32 mm,

abaxially with isocytic hairs mostly along the veins, the hairs often with one or more glandular cells near the base; pinnule-rachis adaxially convex, narrowly winged, closely glandular adaxially and abaxially, the glands capitate, (60-)106(-140) μm long, and with scattered scales, the scales ferruginous, chartaceous, narrowly lanceolate-caudate to subulate-caudate, glandular along the margins and laminae; segments proximally sessile, adnate higher up, oblong-obtuse to ovate obtuse, up to 20×8 mm, larger segments often shallowly lobed, denticulate, adaxially and abaxially closely set with capitate glands along and between the veins. Venation obscure adaxially, evident abaxially, lateral veins in segments simple or once forked, ending in the teeth near the margin. Stomata mostly of the polocytic type, (32-)47(-56) μm long. Sori essentially 2-seriate on pinnules, inframedial on predominantly anadromous vein branches, up to 1.5 mm in diameter and discrete at maturity; indusium castaneous, firmly herbaceous, up to 1.7 mm in diameter, reniform, often strongly recurved, entire to shallowly repand, eglandular or glandular along the margin, often also on the lamina. Sporangium stalk simple, with several hairs and/or glands, capsule with (12-)14(-17) indurated annulus cells, epistomium (3-)4(-7)-celled, hypostomium (4-)6-celled. Spores brown, (36-)42(-52) \times (24-)29(-36) μm long.

DIAGNOSTIC FEATURES AND RELATIONSHIPS

Dryopteris bernieri can be separated from other *Dryopteris* species from Réunion by the axes being closely set with capitate glands, a feature that is absent from other *Dryopteris* species on the island. Similar glands also occur adaxially and abaxially along and between the veins on the lamina. The scales of *D. bernieri* are also regularly set with capitate glands along the margins and laminae.

Fraser-Jenkins (1986) does not list the species, but it is here placed in section *Marginatae* Fraser-Jenk. The occurrence and distribution of capitate glands on the lamina and the similar scale morphology suggest it being related to *D. glandulosopaleata* J.P.Roux from Africa. *Dryopteris bernieri* is separated from *D. glandulosopaleata* in them being geographically isolated, and in the stomata and spores of *D. bernieri* being significantly smaller than that of *D. glandulosopaleata*.

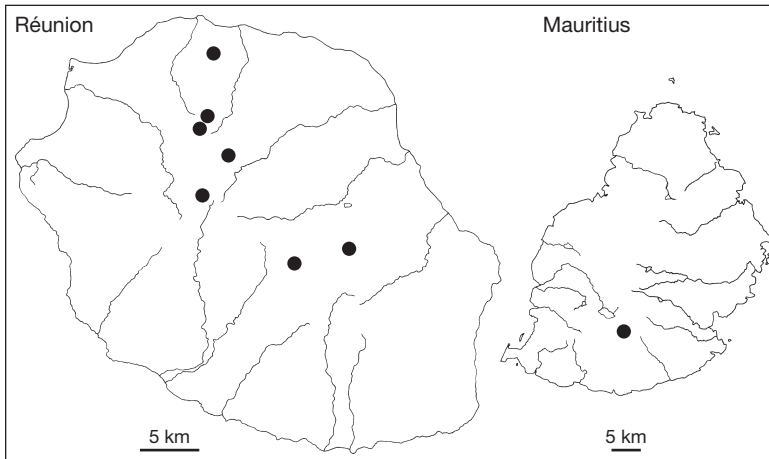


FIG. 7. — Distribution of *Dryopteris aquilinoïdes* (Desv.) C.Chr. in Mauritius and la Réunion.

DISTRIBUTION AND HABITAT

Dryopteris bernieri has a somewhat disjunct distribution occurring on Réunion, where it grows at elevations ranging between 600 and 2300 m on both Massif du Piton des Neiges and Massif de la Fournaise and on Anjouan (Johanna Island/Anjouan), Comoros (Fig. 10). Both massifs are the result of successive volcanic eruptions, but their subsequent erosion has resulted in the formation of radiating valleys with steep flanks. The species grows in deep shade in wet evergreen forests, on earth banks and screes along the steep sloped valleys, and in *Eucalyptus* plantations. Tardieu-Blot (1956a, 1958) noted that the species is also present in the “Comores” by citing a Boivin collection. I have not seen any collections of *D. bernieri* from that island group.

3. *Dryopteris bojeri* (Baker) Kuntze
(Figs 11; 12)

Revisio generum plantarum 2: 812 (5 Nov. 1891). — *Nephrodium bojeri* Baker, *Synopsis filicum* 7: 280 (4 Oct. 1867). — Type: Mauritius, *Bojer s.n.* (lecto-, K!, designated by Roux [2009: 121]; isolecto-, M0065885!).

Nephrodium amplum Bory, *Voyage aux Indes Orientales. Botanique* 2 (1): 62, 63 (24 May 1833). — Type: “à l’Île Maurice”, *Bélanger s.n.* (holo-, P00349575!).

Nephrodium filix-mas auct. non (L.) Rich., *Flora of Mauritius and the Seychelles*: 496 (1877), *pro parte*.

OTHER MATERIAL EXAMINED. — **Mauritius.** *Barkly & Lady Barkly s.n.* (BM000801021, BM000801022). — On rocky side of Piton at Ripailles, *Barkly & Lady Barkly s.n.* (BM000801027). — Île Maurice, IX-X.1849, *Boivin s.n.* (P00349594, P00349595). — Île de France, *Commerson s.n.* (P00349589). — Mauritius, Corps de Gardes, *Pike s.n.* (NY). — Bois de Moka à l’Île de France, *sine coll. s.n.* (P00349590, 2 sheets). **Sine Loco.** *Barkly & Lady Barkly s.n.* (BM000801028); *Boivin s.n.* (P00349591, P00349592, P00349593); *Boivin s.n.* (BM000801046); *Bojer s.n.* (K); *Bojer s.n.* (M0065885); *Duncan s.n.* (BM000801025); *Mc Gregor s.n.* (BM000801023, BM000801029); *sine coll. s.n.* (P00349571); *sine coll. s.n.* (P00349587); *sine coll. s.n.* (BM000801024).

DESCRIPTION

Plants terrestrial. Rhizome unknown. Fronds up to 1.2 m long; stipe stramineous, sulcate adaxially, up to c. 490 mm long and 6 mm in diameter, initially sparsely to moderately scaled, proximally densely scaled, subglabrous later, the scales ferruginous, chartaceous, linear-attenuate, up to 32 × 5 mm, adnate, variously set with glands and long uniseriate pluricellular filiform outgrowths along the margin, the apex filiform; lamina anadromous, catadromous towards apex, broadly ovate to deltoid, up to 580 × 620 mm, to 3-pinnate, with up to 13 petiolated pinna pairs, distal pinnae become sessile and eventually adnate and increasingly basiscopically decurrent; rachis stramineous, adaxially sulcate, narrowly winged near the apex, sparsely scaled, the scales stramine-



FIG. 8. — Specimen of *Dryopteris bernieri* Tardieu, Bewsher s.n. (K).

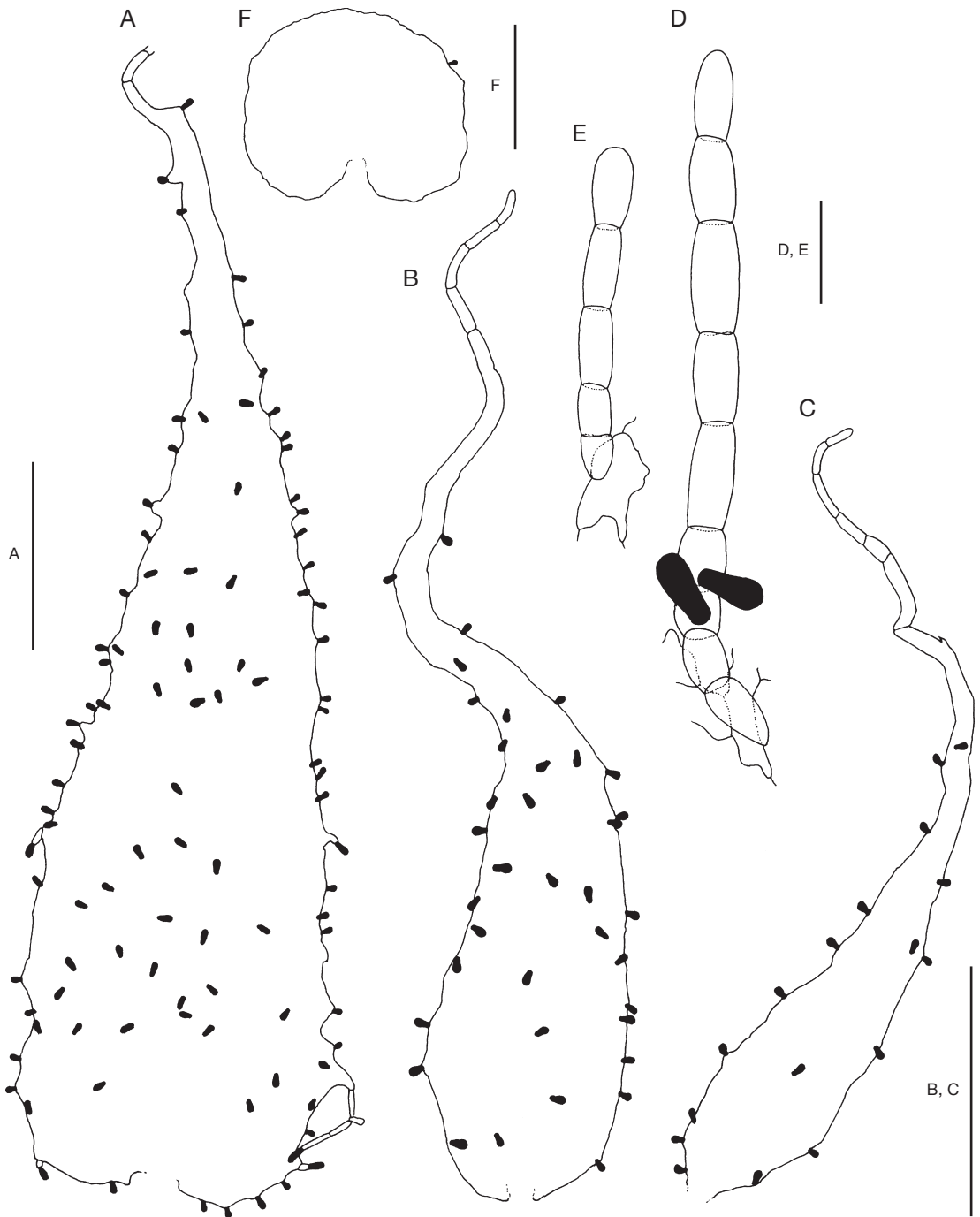


FIG. 9. — Indumentum and indusium of *Dryopteris bernieri* Tardieu: **A**, stipe scale; **B**, pinna-rachis scale; **C**, rachis scale; **D**, **E**, hairs from abaxial lamina surface; **F**, indusium. *Jacobsen 5541* (FR). Scale bars: **A-C**, **F**, 1 mm; **D**, **E**, 0.1 mm.

ous, thinly chartaceous, sessile, narrowly lanceolate to subulate, up to 4×1 mm, narrowly to broadly cuneate, often irregularly set with glands and long uniseriate pluricellular outgrowths, the apex terminates in a series of oblong cells; pinnae petiolate, the petiole up to 4 mm long, spaced or overlapping, near opposite to alternate, the basal pinna pair longest, to 2-pinnate, basal pinnae basiscopically developed, inaequilaterally lanceolate, up to 370×135 mm, pinnae towards the apex inaequilaterally oblong, with up to 10 petiolated pinnule pairs; pinna-rachis stramineous, adaxially sulcate, narrowly winged towards the apex, rarely sparsely glandular at the base, glands capitate, up to $62 \mu\text{m}$ long, sparsely scaled, the scales similar to those on the rachis; pinnules petiolate, the petiole up to 2 mm long, proximally spaced, slightly overlapping towards the pinna apex, the proximal basiscopic pinnule longest or not, acroscopic pinnule on basal pinnae ovate-acuminate to oblong-acuminate, up to 57×26 mm, pinnatifid, basiscopic pinnule on basal pinnae inaequilaterally lanceolate to oblong-acuminate, up to 105×34 mm, to 1-pinnate; pinnule-rachis stramineous, adaxially sulcate, pronounced abaxially, sparsely set with scales and hairs, the scales similar, but smaller than those on the pinna-rachis, the hairs isocytic; segments herbaceous, petiolate, the petiole up to 1 mm long, narrowly ovate to oblong-obtuse, up to 18×9 mm, glabrous adaxially, abaxially sparsely set with isocytic hairs along the costule and veins, hairs often long and long-celled, often glandular near the base, larger segments shallowly lobed, the lobes denticulate. Venation evident, lateral veins in pinnule lobes pinnately branched, vein branches end in the teeth near the margin. Stomata mostly of the polycytic type, $(34\text{--}45\text{--}54) \mu\text{m}$ long. Sori essentially 2-seriate on larger pinnule lobes, discrete, supramedial on predominantly anadromous vein branches, up to 1 mm in diameter at maturity; indusium dark brown, firmly herbaceous, reniform, entire or shallowly repand, strongly recurved. Sporangium stalk simple, glandular, or haired, capsule with $(14\text{--}15\text{--}16)$ indurated annulus cells, epistomium 4-celled, hypostomium 4-celled. Spores brown, 64 per sporangium, perispore folded to form pronounced reticulate ridges, exospore $(32\text{--}34\text{--}44) \times (18\text{--}20\text{--}22) \mu\text{m}$.

DIAGNOSTIC FEATURES AND RELATIONSHIPS

Diagnostic of the species are the scales, which bear numerous exceptionally long filiform outgrowths along their margins.

DISTRIBUTION AND HABITAT

Dryopteris bojeri is endemic to Mauritius and appear not to have been collected there recently (Fig. 13). Lorence (1978) does not list the species, but he may have identified it as *D. aquilinoïdes*. Nothing is known about the ecology of the species.

4. *Dryopteris comorensis* (Tardieu) Fraser-Jenk. (Figs 14; 15)

Thaiszia 4 (1): 34 (1994). — *Dryopteris inaequalis* (Schltld.) Kuntze var. *comorensis* Tardieu, *Notulae Systematicae* (Paris) 15 (2): 162 (Apr. 1956). — Type: Comores, environs de Niouadjou, *Humblot 254* (holo-, BM000801045!; iso-, K!, P00220415!).

OTHER MATERIAL EXAMINED. — **Comoro Islands.** Grande Comore, à 5 km au Sud-est de Niouadjou, 600 à 700 m d'alt., 23.XI.1975, *Coulon 277* (MO4374549). — Village de Kourani, 770 m, $11^{\circ}51'S$, $43^{\circ}25'E$, 15.II.1975, *Floret 950* (MO4374543, P00220424). — Centre-Sud, entre Kourani et Dombéni vers 500 m d'alt., 15.II.1975, *Floret 957* (P00220421). — Environs de Niouadjou, 400-500 m, IV.1911, *Humblot s.n.* (P00220417). — Comore Islands, 1884, *Humblot 254* (BM000801045, K, P). — Massif du Kartala, versant ouest, $11^{\circ}45'S$, $43^{\circ}19'E$, 1900 m, forêt dense humide de montagne, *Rakotondrainibe 6815* (P00312090, P00312091, P00312092).

Madagascar. Antsiranana, Parc national de la Montagne d'Ambre, environs du Lac Texier, rive NO. 1070 m, 27.VI.1992, *Rakotondrainibe 1739* (P00100256). — Antsiranana, Parc national de la Montagne d'Ambre, environs du lac Texier, rive NO, forêt primaire, cirque volcanique, 27.VI.1992, *Rakotondrainibe 1740* (P00100257, P00100258, P00100259).

DESCRIPTION

Plants terrestrial. Rhizome decumbent. Fronds crowded, suberect to arching, up to 1.9 m long; stipe proximally castaneous, stramineous higher up, sulcate adaxially, up to 830 mm long and 15 mm in diameter at the base, proximally densely scaled, moderately to sparsely scaled higher up, the scales ferruginous, chartaceous, rugose, linear-

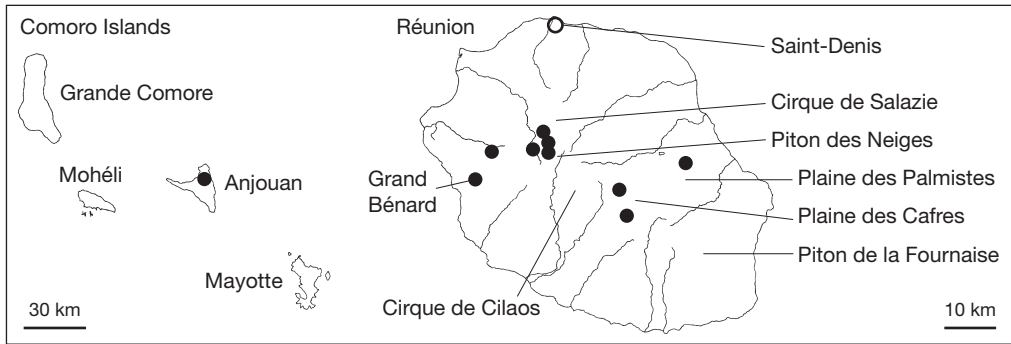


Fig. 10. — Distribution of *Dryopteris bernieri* Tardieu in la Réunion and Comoro Islands (●).

acuminate, up to 30 × 5 mm, adnate, the margins regularly set with capitate glands and twisted pluricellular, mostly pluriseriate outgrowths, the apex filiform, twisted, terminating in an oblong cell; lamina anadromous, catadromous towards the apex, broadly ovate to deltoid, up to 1.1 × 0.78 m, to 3-pinnate, with up to 15 petiolated pinna pairs, pinnae near the apex become sessile and increasingly basiscopically decurrent; rachis stramineous, adaxially sulcate, initially moderately scaled, sparsely scaled later, the scales similar to, but smaller than those on the stipe, up to 12 × 3 mm; pinnae petiolate, the petiole up to 45 mm long, spaced or overlapping, near opposite to alternate, basal pinna pair longest, to 2-pinnate, basiscopically developed, inaequilaterally lanceolate, up to 440 × 225 mm, pinnae towards the apex oblong-acuminate, with up to 10 petiolated pinnule pairs; pinna-rachis stramineous, adaxially sulcate, narrowly winged towards the apex, sparsely to moderately scaled, the scales stramineous, thinly chartaceous, sessile or short-stalked, lanceolate-caudate to narrowly lanceolate-caudate, up to 13 × 2.3 mm, narrowly to broadly cuneate, irregularly set with glands along the margins and laminae, the margins also with long and twisted pluricellular outgrowths, the apex terminates in a series of oblong cells; pinnules petiolate, the petiole up to 2 mm long, proximally widely spaced or overlapping, proximal basiscopic pinnule longest or not, acroscopic pinnule on basal pinnae oblong-acuminate, up to 87 × 27 mm, 1-pinnate, basiscopic pinnule

on basal pinnae oblong-acuminate, up to 135 × 45 mm, to 1-pinnate, with up to 6 petiolated segment pairs; pinnule-rachis stramineous, adaxially sulcate, pronounced abaxially, sparsely haired adaxially, sparsely to moderately scaled abaxially, the scales similar to those on the pinna-rachis, up to 5 × 1.4 mm; segments herbaceous, petiolate, the petiole up to 0.5 mm long, sessile and increasingly basiscopically decurrent along the costa towards the apex, narrowly lanceolate to oblong-acuminate, up to 27 × 10 mm, lobed, the lobes oblong-obtuse, up to 5 × 4 mm, shallowly denticulate, adaxially with a few hairs along the costule, abaxially sparsely to moderately set with hairs and scales along the costule and veins, the hairs isocytic, up to 2.5 mm long, the scales stramineous to ferruginous, thinly chartaceous, stalked, subulate-caudate, up to 2.5 × 0.6 mm, the apex terminates in a series of oblong cells. Venation evident, lateral veins in segment lobes pinnately branched, vein branches end in the teeth near the margin. Stomata mostly of the polocytic type, (34-)40(-46) µm long. Sori essentially 2-seriate on segments, discrete or touching at maturity, medial on predominantly anadromous vein branches, up to 1 mm in diameter at maturity; indusium ferruginous, firmly herbaceous, reniform, entire or shallowly repand, strongly recurved. Sporangium stalk simple, glandular, or haired, capsule with (13-)15(-18) indurated annulus cells, epistomium (3-)4(-6)-celled, hypostomium 4(-6)-celled. Spores brown, 64 per sporangium, exospore (34-)37(-44) × (20-)23(-26) µm.



FIG. 11. — Isosyntype of *Dryopteris bojeri* (Baker) Kuntze, *Bojer s.n.* (M0065885).

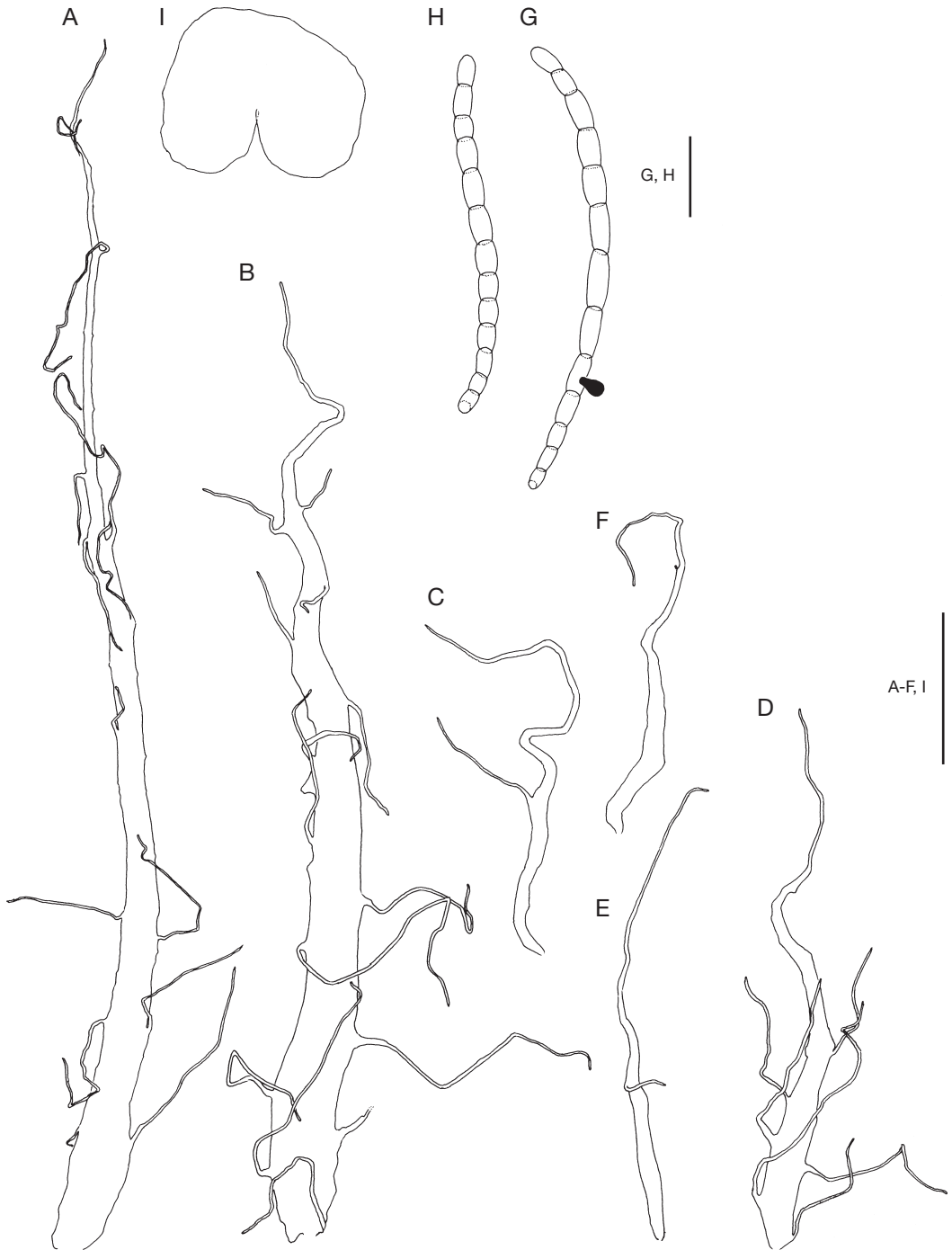


FIG. 12. — Indumentum and indusium of *Dryopteris bojeri* (Baker) Kuntze: **A**, stipe scale; **B**, rachis scale; **C**, **D**, pinna-rachis scale; **E**, **F**, scales from abaxial lamina surface; **G**, **H**, hairs from abaxial lamina surface; **I**, indusium. *Commerson s.n.* (P00349589). Scale bars: A-F, I, 1 mm; G, H, 0.2 mm.

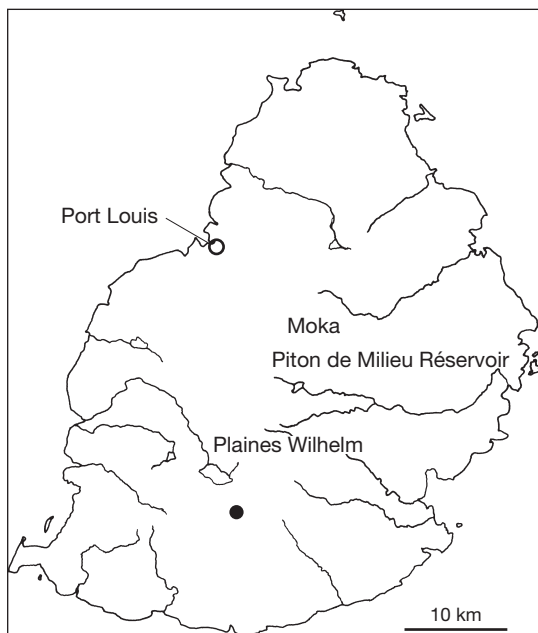


FIG. 13. — Distribution of *Dryopteris bojeri* (Baker) Kuntze in Mauritius.

DIAGNOSTIC FEATURES AND RELATIONSHIPS

Dryopteris comorensis is separated from other species in the Mascarene region by the rugose scales, which form a dense covering on the lower half of the stipe. These scales bear capitate glands and numerous long and twisted outgrowths along the margins. Although similar marginal outgrowths may occur in *D. pentheri*, that species does not occur on Grande Comore, neither does it bear unicellular oblong glands or 2-celled hairs along the lamina axes and veins. Scales along the pinna-rachis are often somewhat bullate. The stoma size is also smaller, (34-)40(-46) μm , which suggests it being diploid, rather than (34-)53(-72) μm as in *D. pentheri*, which is tetraploid.

Fraser-Jenkins (1986) failed to include the taxon in his classification. I see no evidence of this species being related to *Dryopteris inaequalis* (Schltdl.) Kuntze, as suggested by viewing it as a variety of this species (Tardieu-Blot 1956a: 162). I support Fraser-Jenkins (1994) in recognizing it as a distinct species.

DISTRIBUTION AND HABITAT

Dryopteris comorensis occurs on Grande Comore, also known as Ngazidja (11°45'S, 43°19'E), and on Montagne d'Ambre (c. 12°32'S, 49°10'E), in northern Madagascar (Fig. 16). The species is restricted to the evergreen rain forests and occurs at altitudes ranging between 400 to 1900 m on Mount Kartala. Both Mount Kartala and Montagne d'Ambre are of volcanic origin.

5. *Dryopteris manniana* (Hook.) C.Ch. (Figs 17; 18)

Index filicum: 276 (18 Nov. 1905). — *Polypodium manianum* Hook., *Species filicum* 4 (15/16): 253 (1863). — *Phegopteris manniana* (Hook.) Kuhn, *Filices africanae*: 123 (Oct. 1868). — Type: Fernando Po, on the peak, 2000 ft, 1860, *G. Mann s.n.* (holo-, K!; iso-, K!).

OTHER MATERIAL EXAMINED. — **Madagascar**. Ambatofitorahana, 1700 m, IX.1956, *Bosser 9787* (P00349514). — Centre, Forêt de Manjakatempo, versant E de l'Ankaratra, VII.1953, *Capuron 70RC* (P00349509). — Rahobeava, 960 m, 11.III.1951, *Cours 4292* (P00349513). — Madagascar, *Cowan s.n.* (BM000800961, A only, BM000800962), Ankafana, *Cowan s.n.* (BM000605571). — Madagascar, *Cowan s.n.* (BM000605576). — Prov. Imerina, VII.1880, *Hildebrandt 3529* (BM000800984). — Massif du Kalambatitra (Centre-Sud), Mont Kalambatitra et ses abords et mont Analatsitendrika, forêt ombrophile (sur latérite de gneiss), 1500-1750 m, XI.1933, *Humbert 11875* (P00349512). — Tanala, V.1880, *Kitching s.n.* (K, B only). — Antananarivo, Ankazobe, Manankazo, réserve spéciale d'Ambositantely, environ 8 km au Nord-Ouest d'Ankazobe, 18°10'S, 47°17'E, 1200-1650 m, *Rakotondrainibe 348* (P00349515).

DESCRIPTION

Plants terrestrial. Rhizome erect to short-decumbent, mostly unbranched, up to 8 mm in diameter, set with roots, closely spaced stipe bases, and scales, the scales brown to ferruginous, chartaceous, broadly attached, subulate, up to 22 × 3 mm, the margins closely set with short teeth, the apex filiform, terminating in an oblong cell. Fronds 4-7 per plant, caespitose, arching, up to 1.0 m long; stipe greenish to stramineous, shallowly sulcate adaxially, up to 480 mm long and 5 mm in diameter, proximally densely scaled, moderately scaled higher up, the scales stramineous to ferruginous, chartaceous, the



FIG. 14. — Specimen of *Dryopteris comorensis* (Tardieu) Fraser-Jenk., Rakotondrainibe 1739 (P00100256). Photo: MNHN, Paris Herbarium, 2009.

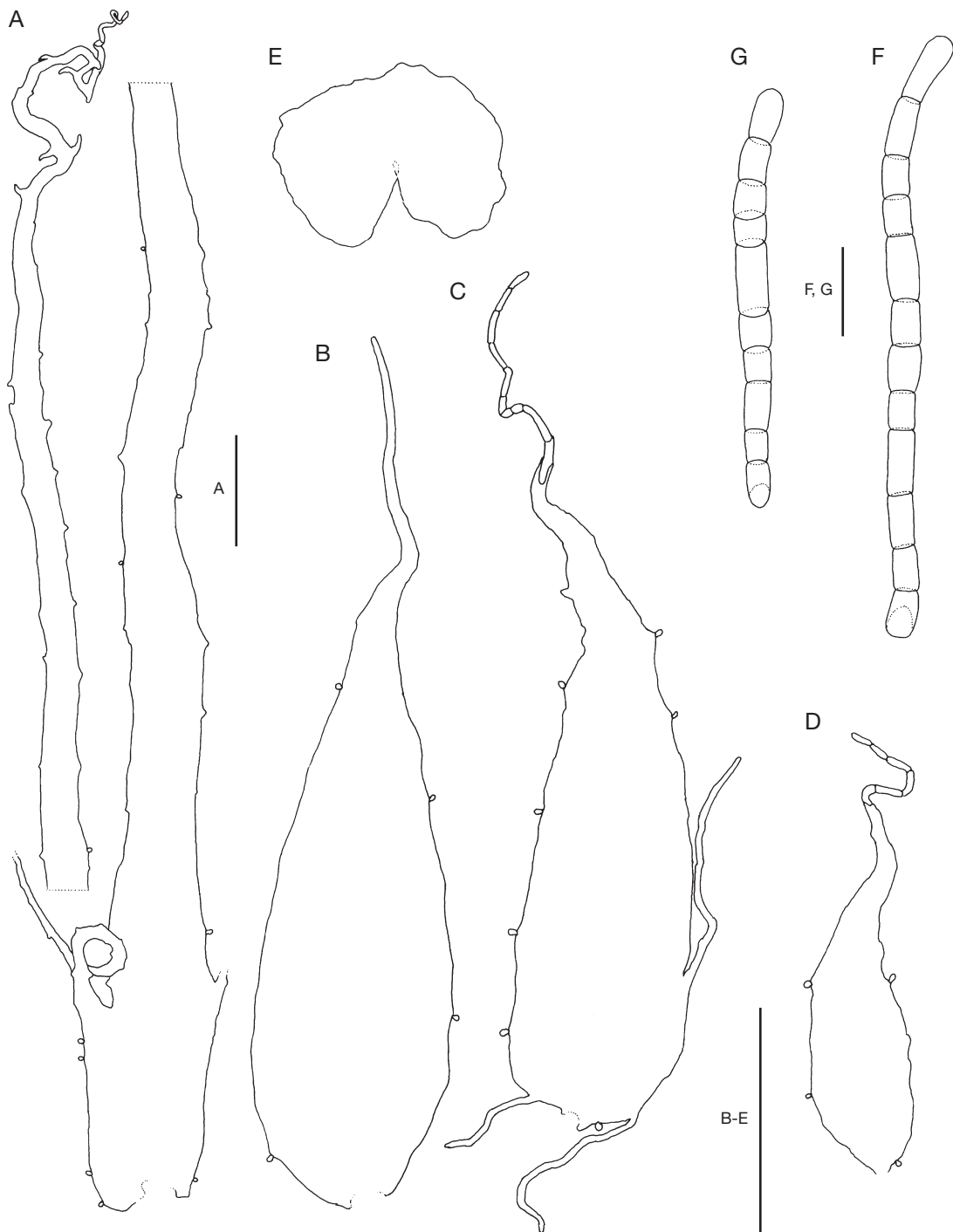


FIG. 15. — Indumentum and indusium of *Dryopteris comorensis* (Tardieu) Fraser-Jenk.: **A**, stipe scale; **B**, rachis scale; **C**, pinna-rachis scale; **D**, costa scale; **E**, indusium, **F**, **G**, hairs from abaxial lamina surface. Floret 957 (P00220421). Scale bars: A-E, 1 mm; F, G, 0.1 mm.

larger scales broadly attached, up to 15×4.5 mm, the smaller scales short-stalked, cordate to cuneate, the margins denticulate, basally frequently with one or more filiform outgrowths, often with scattered glands, the apex filiform, terminating in an oblong cell; lamina herbaceous, ovate, up to 525 mm long, to 2-pinnate-pinnatifid, anadromous, catadromous towards the apex, with up to 12 petiolated pinna pairs, proliferous, generally with one or more scaled buds adaxially along the rachis near the lamina apex, often also with buds on the pinna-rachis in larger fronds; rachis greenish to stramineous, adaxially sulcate, narrowly winged towards the apex, moderately scaled, the scales ferruginous to stramineous, chartaceous, sessile or short-stalked, filiform to lanceolate, up to 7×1.8 mm, cordate to narrowly cuneate, denticulate, basally frequently with one or more filiform outgrowths, higher up closely set with short teeth, the apex filiform, terminating in an oblong cell; pinnae petiolate, the petiole up to 18 mm long; basal pinna pair inaequilaterally ovate, narrowly ovate to oblong-acuminate towards the lamina apex, up to 250×95 mm, to 1-pinnate-pinnatifid; basal pinna pair mostly the longest, basiscopically developed, opposite to alternate, basally widely spaced, more closely spaced towards the lamina apex and often imbricate, with up to 3 pairs of petiolated pinnules; pinna-rachis adaxially shallowly sulcate, the sulcus confluent with that of the rachis, pronounced abaxially, narrowly winged for most of the length, abaxially sparsely to moderately scaled, the scales stramineous to ferruginous, chartaceous, sessile or short-stalked, filiform to narrowly oblong, up to 5×1 mm, cordate to narrowly cuneate, dentate, basally frequently with one or more filiform outgrowths, the apex filiform, terminating in an oblong cell; pinnules petiolate, the petiole up to 2 mm long, symmetric or inaequilaterally narrowly ovate to ovate, up to 50×17 mm, basiscopically decurrent, pinnatifid, acroscopic pinnule on the basal pinnae up to 56×23 mm, not or slightly imbricate, the lobes broadly oblong-obtuse, shallowly lobed, dentate, glabrous adaxially, abaxially rarely glandular, the glands $(56-)(62-)(72)$ μm long, sparsely set with hairs and scales along the veins, the hairs moniliform, often with a unicellular gland near the base, the scales stramineous, chartaceous,

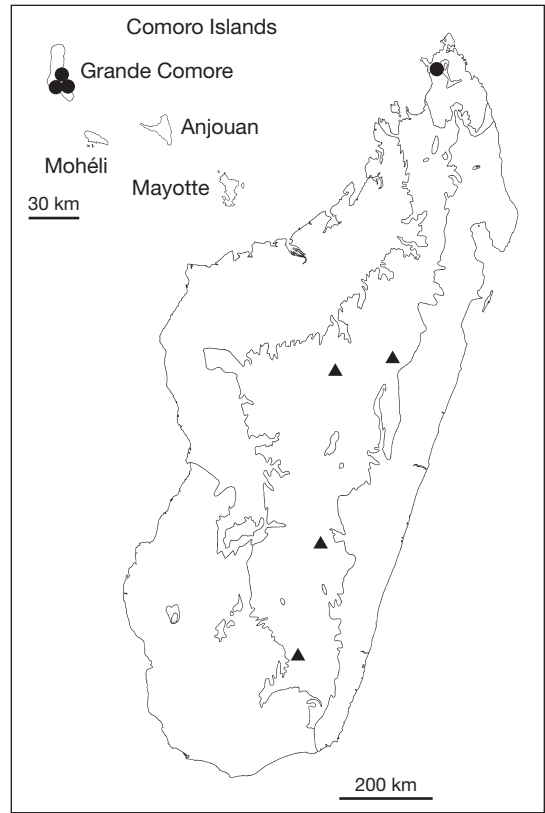


FIG. 16. — Distribution of *Dryopteris comorensis* (Tardieu) Fraser-Jenk. (●) and *D. manniana* (Hook.) C. Chr. (▲) in Madagascar and neighbouring Indian Ocean islands.

short-stalked, the stalk often glandular, filiform to linear, up to 2 mm long, repand to dentate, the apex filiform, terminating in an oblong cell. Venation anadromous, becoming catadromous towards the lamina and pinna apex, pinnately branched in the lobes, evident in the teeth near the margin, the endings mostly slightly enlarged. Stomata mostly of the polocytic type, $(40-)(56-)(70)$ mm long. Sori circular, inframedial on unmodified fertile vein branches, discrete at maturity, up to 1.5 mm in diameter; sporangium stalk simple or haired, capsule with $(11-)(14-)(18)$ indurated annulus cells; exindusiate. Spores ellipsoidal, monolete, perispore forming short and long ridges, ruminant, $(40-)(44-)(58) \times (26-)(30-)(32)$ mm. Chromosome number: $2n = c. 164$ (Vida *in* Widén *et al.* 1973).

DIAGNOSTIC FEATURES AND RELATIONSHIPS

Diagnostic of *Dryopteris manniana* is the scaled proliferous buds borne adaxially on the rachis, mostly near the lamina apex, the denticulate scales, and the exindusiate sori. A micromorphological feature separating it from other *Dryopteris* species is the stoma size, which supports it being tetraploid.

VARIATION

Morphologically, the species appears to be stable throughout its distribution, with little variation of significance having been observed.

DISTRIBUTION AND HABITAT

Dryopteris manniana is widespread in sub-Saharan Africa occurring in West-, East-, southern Africa, and in Madagascar. It chiefly occurs in moist montane forests, at elevations ranging from 1400 m in Kenya and Uganda to 2249 m along the Kikuyu Escarpment in Kenya. In Madagascar, it is known from elevations ranging between 960 and 1750 m (Fig. 16).

6. *Dryopteris pentheri* (Krasser) C.Chr. (Figs 19; 20)

Index filicum: 284 (18 Nov. 1905). — *Nephrodium pentheri* Krasser, *Annales des Kaiserlich-Königlichen Naturhistorischen Hofmuseums, Wien* 15: 5, 6 (1900). — Type: South Africa, Van Reenens Pass, 4.III.1895, *F. Krook s.n.*, sub *Penther Plantae Austro-Africanæ* 36 (lecto-, W8042! designated by Pichi Sermolli [1984: 329]; isolecto-, BM!), .

Dryopteris inaequalis sensu Tardieu, *Flore de Madagascar et des Comores (Plantes Vasculaires), 5^e Famille. Polypodiacées (sensu lato) 5 (1) Dennstaedtiacées. (10) Aspidiacées*: 315 (May 1958), *pro parte*, non (Schltdl.) Kuntze (1891: 813).

MATERIAL EXAMINED. — **Madagascar.** Route d'Anjozorobe, près d'Analabe, XII.1958, *Bosser 12329* (MO4405417). — Route d'Arivonimamo, 1958, *Bosser 12344* (MO4405414). — Andramasina, XII.1958, *Bosser 12446* (MO4405413). — Route de Manankaraly, III.1957, *Bosser 12871* (MO4405415). — Ankaratra, V.1962, *Bosser 16183* (MO4405425). — P.K. 39 route du sud, ravin humide, III.1953, *Bosser 6203* (MO4405416). — Imerina, 1881, *Cowan s.n.* (BM000800959, BM000800960, BM000800981, BM000800985, BM000800998,

BM000801020, BM000801031, BM000801044). — Fianarantsoa, 1879, *Cowan s.n.* (BM000801030). — Prov. Tananarive, vicinity of Station forestière Antsampanrano, disturbed prairie, 1750 m, 23.I.1975, *Croat 29124* (MO3295933). — Prov. Fianarantsoa, forest and forest edge along Route 7, 113-116 km N of Fianarantsoa, 1580-1590 m, 28.I.1975, *Croat 29928* (MO3295935). — Massif de l'Ankaratra, flanc oriental du Tsiafajavona, reste de forêt, 1700-2000 m, 15.VII.1928, *Decary, Humbert & Swingle 4568* (BM000801032). — Interior, near waterfall Ramainandro, *Elliot 1965* (K). — Ambohitombo forest, 19.I.1895, *Forsyth Major 180* (BM000800986, K). — Prov. Imerina, IV.1884, *Hildebrandt 3529* (K, M, US815398). — Madagascar, V.1880, *Kitching s.n.* (K, A only). — Ilafy, Tananarive, 6.I.1970, *Onreadt 70M66* (US3005426). — Moramanga, c. 900 m, Regenwald, *Schlieben 8109* (M). — La Mandraka, c. 1000 m, Regenwald, 7.XII.1959, *Schlieben 8137* (BM, K, M, 2 sheets, PRE, US3001350). — Bord de l'eau à l'ombre Tsimbazaza, 14.VII.1885, *sine coll. s.n.* (P00349496). — Madagascar, *sine coll. 68* (NY, US719837). — Madagascar, *sine coll. 87* (NY, US719841). — Province du Vakinankaratra, Distr. d'Antsirabe, fentes des rochers sur la pente interne du cratère du Tritriva vers 1800 m d'alt., 16.XI.1972, *Viguiet & Humbert 1294* (P00349498).

Réunion. Fissures aux environs du Piton Maito, Grand Bénard, 2200 m, 22.XI.1968, *Cadet 1751* (P00349598). — Sous-bois de la forêt hygrophile, forêt de la Mare à Joseph Cilaos, 1400 m, 7.II.1969, *Cadet 1904* (P00349599, P00349600). — Clairière dans la forêt du Grand Matarum Cilaos, 1600 m, 23.III.1974, *Cadet 4582* (P00349596, P00349597). — Cilaos Distr., footpath from Cilaos thermal baths to Bras Rouge cataract, on earth bank with *Polystichum ammfolium*, 1100 m, 4.X.1984, *Jacobsen 5608* (FR).

DESCRIPTION

Plants terrestrial or epilithic. Rhizome short-decumbent, sparsely branched, up to 20 mm in diameter, set with roots, closely spaced stipe bases, and scales, the scales stramineous to ferruginous, chartaceous, broadly attached, linear, oblong or narrowly ovate, up to 37 × 6 mm, truncate, the margins irregularly set with long, twisted, pluricellular filiform outgrowths, the apex filiform, twisted. Fronds caespitose, erect to arching, up to 1.8 m long; stipe proximally castaneous, brown to stramineous higher up, proximally adaxially flattened, shallowly sulcate higher up, up to 485 mm long and 10 mm in diameter, proximally densely scaled, the scales higher up fugaceous, stramineous to ferruginous, chartaceous, the larger scales up to



Fig. 17. — Specimen of *Dryopteris manniana* (Hook.) C.Chr., Humbert 11875 (P00349512). Photo: MNHN, Paris Herbarium, 2009.

40 × 7 mm, broadly attached, the smaller scales sessile or short-stalked, narrowly lanceolate to filiform, cordate to cuneate, the margins irregularly set with long, twisted, pluricellular filiform outgrowths and often also with scattered glands, the apex filiform; lamina herbaceous to firmly herbaceous, ovate to ovate-triangular, up to 780 mm long, 2-pinnate to 3-pinnate, anadromous, catadromous towards the apex, with up to 16 petiolated pinna pairs; rachis stramineous, adaxially shallowly sulcate, becoming narrowly winged towards the apex, initially moderately scaled, the scales fugaceous, broadly attached or short-stalked, narrowly lanceolate to linear, up to 7 × 2 mm, cuneate, the margins irregularly set with long filiform outgrowths, often also with scattered glands, the apex filiform, twisted; pinnae petiolate, the petiole up to 18 mm (rarely to 38 mm) long, the basal pinna pair inaequilaterally ovate to narrowly ovate, narrowly lanceolate to oblong-acuminate towards the lamina apex, to 2-pinnate, basal pair the longest, mostly basiscopically developed, up to 315 × 185 mm, opposite to alternate, basally widely spaced, often somewhat imbricate higher up, with up to 9 petiolated pinnule pairs; pinna-rachis adaxially shallowly sulcate, the sulcus confluent with that of the rachis, pronounced abaxially, narrowly winged distally, abaxially moderately to sparsely set with scales and hairs, the scales and hairs stramineous to ferruginous, the scales chartaceous to membranous, broadly attached or short-stalked, narrowly to broadly cuneate, up to 5 × 1.6 mm, the margins irregularly set with long pluricellular, filiform outgrowths, the apex filiform, twisted, up to 5 × 1.6 mm, the hairs are of three types: 1) unicellular oblong glands, 2) bicellular hairs with straight or oblique transverse walls, and 3) pluricellular simple or branched, mostly isocytic hairs often bearing a single glandular cell near the base; pinnules petiolate, petiole up to 3 mm long, aequilaterally to inaequilaterally lanceolate to oblong-acuminate, basiscopically decurrent, 1-pinnate to lobed, acroscopic pinnule on the basal pinnae up to 90 × 35 mm, basiscopical pinnule on the basal pinnae up to 112 × 42 mm, widely spaced or imbricate; pinnule-rachis adaxially shallowly sulcate, pronounced abaxially, narrowly winged, the wing continuous with that of the pinna-rachis, variously

set with scales, isocytic- and 2-celled hairs; segments widely spaced to imbricate, ovate to oblong-obtuse, up to 22 × 9 mm, basiscopically decurrent, lobed, the lobes serrate, adaxially glabrous, with oblong glands along and between the veins, or with a few pluricellular mostly isocytic hairs along the costule, abaxially sparsely set with unicellular oblong glands (60-)137(-260) mm long, 2-celled hairs, and isocytic and/or moniliform hairs, those near the segment base often with a glandular cell near the base, and filiform scales, the scales short-stalked, the stalk often with one or more glandular cells, hairs and scales mostly occur along the costule and veins. Venation anadromous, becoming catadromous towards the lamina and pinna apex, pinnately branched in the segments, vein branches pinnately branched, forked or simple near the apex, evident, ending in the teeth near the margin, endings slightly enlarged and often conspicuous adaxially. Stomata of the anomo- and polocytic types, (34-)53(-72) mm long. Sori circular, medial on predominantly anadromous vein branches, discrete, up to 1.8 mm in diameter at maturity, essentially uniseriate; sporangium stalk simple, or with one or more glandular cells, but mostly with a long multicellular, uniseriate hair, capsule with (11-)13(-20) indurated annulus cells, epistomium (3-)6(-8)-celled, hypostomium (3-)6(-8)-celled; indusium persistent, pale brown, firmly herbaceous, reniform, entire, repand, or erose, (rarely glandular along margin), often strongly revolute, to 1.8 mm in diameter. Spores ellipsoidal, monolete, perispore folded into tubercles or reticulate ridges, finely rugose to ruminate, (38-)45(-60) × (27-)31(-40) mm (Tryon & Lugardon 1990: 426, fig. 159.21). Chromosome number: 2n = c. 164 (Vida *in* Widén *et al.* 1973: 2129).

REMARKS

The spores of *Viguier & Humbert 1731* (P00349497) are highly abnormal and may be indicative of it being a hybrid. Other features of the specimen – stoma size and the presence of 2-celled hairs – are typical of *D. pentheri*.

DIAGNOSTIC FEATURES AND RELATIONSHIPS

Dryopteris pentheri is an extremely variable species difficult to separate from other species using

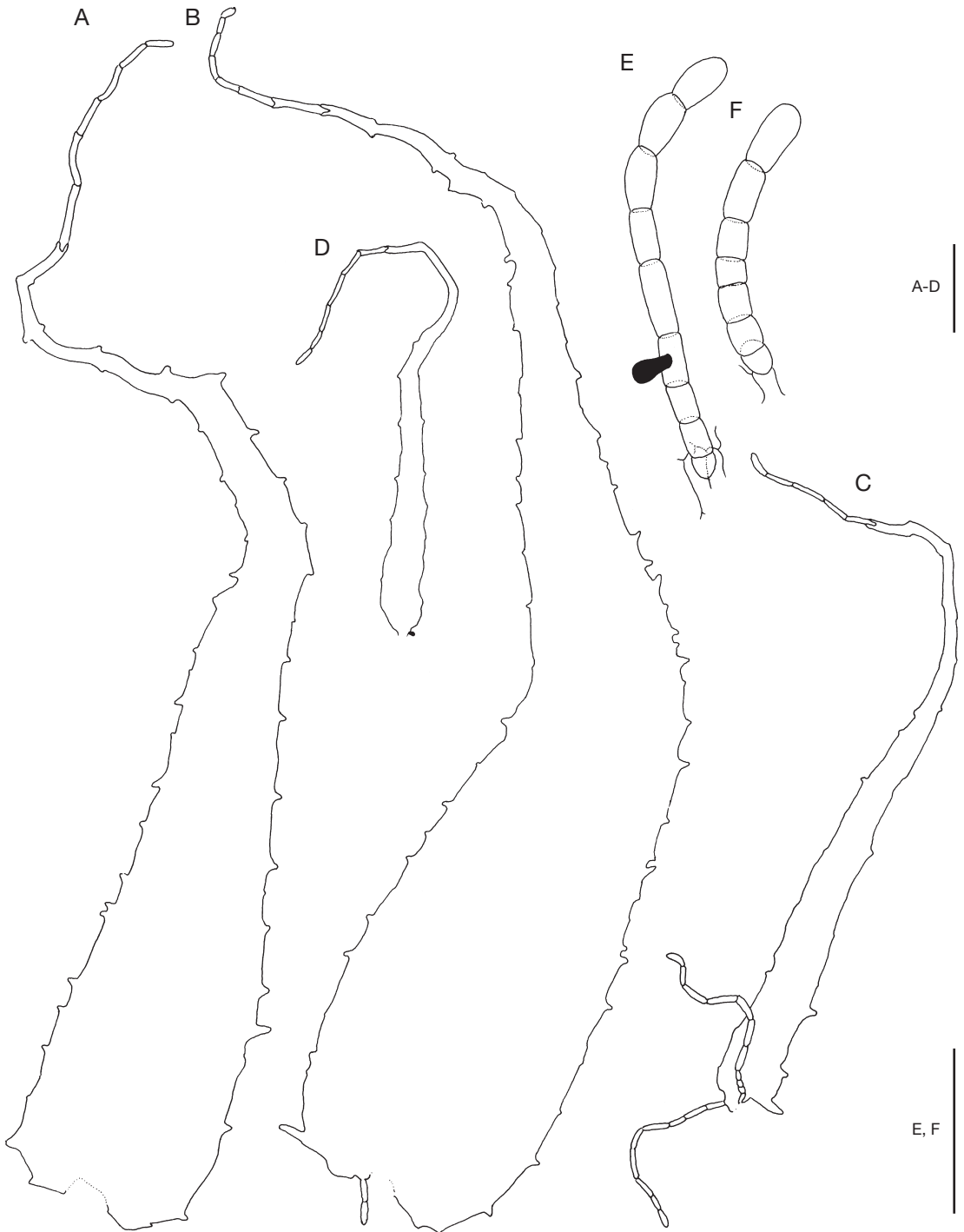


FIG. 18. — Indumentum of *Dryopteris manniana* (Hook.) C.Chr.: **A**, stipe scale; **B**, rachis scale; **C**, pinna-rachis scale; **D-F**, scale and hairs from abaxial lamina surface. *Roux 2857* (NBG). Scale bars: A-D, 0.5 mm; E, F, 0.1 mm.

macromorphological features. Micromorphological features separating it from other *Dryopteris* species in the region are the oblong glands (Fig. 19E) and 2-celled hairs (Fig. 19D), occurring along the frond axes and veins, and the larger stomata (Table 1).

VARIATION

Dryopteris pentheri is extremely variable in gross morphology and attempts by several authors to separate this species based on macromorphological characters have failed. Micromorphological characters and cytological observations are more reliable in separating *D. pentheri* from other taxa. Micromorphological features of significance are the presence of bicellular hairs, unicellular gland length, as well as stoma and spore size. These features, however, all show some variation. Bicellular hairs occurring abaxially on the lamina were observed on the costa, costules or veins in 64.5% of the collections studied. These hairs mostly occur centrally on an epidermal cell, but rarely also near the distal end of a cell. The periclinal wall of the epidermal cells bearing the hairs is flat or the hairs are positioned on a low but prominent bulge. The transverse wall between the two hair cells may be straight or oblique. Unicellular glandular hairs were observed in 96.8% of the collections studied. These oblong hairs, 60–260 μm long, are positioned on the epidermal cells in a similar fashion as bicellular hairs. Pluricellular hairs 6 to 21 cells long occur adaxially and abaxially on or near the costae, costules and veins. They are of the isocytic or moniliform type and are positioned centrally on or near the distal margin of an epidermal cell. They often bear a single (rarely 2) glandular cell near the base. The indusium also shows significant variation in size and margin sculpture. In a few cases, glands have been observed along the indusium margin.

DISTRIBUTION AND HABITAT

Dryopteris pentheri is widespread in the eastern and western mountainous regions of sub-Saharan Africa, Madagascar and Réunion (Fig. 20). Although predominantly confined to moist forests, the species occurs in open habitats at higher elevations. In these habitats, the plants are mostly confined to boulder bases and rock crevices on ridges and

montane streams. In grassland habitats, the species is exposed to regular burning, but this appears to have little effect on the subterranean rhizome. In Madagascar, it is confined to the central mountainous regions, at elevations ranging between 1580 and 2000 m, but on Réunion, it occurs in moist montane forests and in seasonally wet forests from 1100 to 2200 m, where the plants often become seasonally dormant.

7. *Dryopteris subcrenulata* (Baker) C.Chr. (Figs 22; 23)

Index filicum: 295 (18 Nov. 1905). — *Nephrodium subcrenulatum* Baker, *Journal of the Linnean Society, Botany* 16: 202 (1877). — *Aspidium subcrenulatum* (Baker) Kuhn, *Von der Decken's Reisen in Ost-Afrika in 1851-1861* 3 (3): 65 (Aug.-Sep. 1879). — Type: Madagascar, Antananarivo, *H. Gilpin s.n.* (holo-, K000351090!, K000351091!).

Dryopteris mangindranensis Tardieu, *Notulae Systematicae* (Paris) 15 (2): 161, 162 (Apr. 1956). — Type: Madagascar, montagnes au Nord de Mangindrano, jusqu'aux sommets d'Ambohimirahavavy, 1900-2500 m, *Humbert 25054* (holo-, P00483232!; iso-, K000351050!).

OTHER MATERIAL EXAMINED. — **Madagascar.** Ambohimombo forest, 27.XI.1894, *Forsyth Major 193* (K). — Montagnes au Nord du Mangindrano (haute Maevarano), jusqu'au sommet d'Ambohimirahavavy (partage des eaux Mahavavy-Androranga: Centre-Nord): haute Bemafo (affluent de l'Androranga), forêt ombrophile sur latérite de gneiss, 1900 m, *Humbert & Capuron 25054* (P00349516). — Montagnes au Nord de Mangindrano (haute Maevarano) jusqu'aux sommets d'Ambohimirahavavy (partage des eaux Mahavavy-Androranga: Centre-Nord), 1800-2000 m, 19.I-12.II.1951, *Humbert & Capuron 25055* (P00349518). — Massif de Marivorahona au sud-ouest de Manambato (haute Mahavavy du nord, district d'Ambilobe), forêt ombrophile sur gneiss, 1750-2000 m, 18-26.III.1951, *Humbert & Capuron 25810* (P00349519). — Tampoketsa au N d'Ankazobe (Centre), forêt d'Ambohitantely et reste de forêts aux alentours, vers 1600 m, 1933, *Humbert 11127* (P00349502). — Massif du Kalambatitra (Centre-Sud), Mont Beanjavidy: forêt ombrophile, 1500-1730 m, XI.1933, *Humbert 12064* (P00349520). — Mt Tsaratanana, 2000 m, *Humbert 16165* (P00349510). — Bassin supérieur du Sambirano, forêt ombrophile sur sol siliceux, 1700 m, XI-XII.1937, *Humbert 18656* (P00349511). — Mt Tsaratanana, 2000 m, IV.1923, *Perrier de la Bathie 16458* (P00349517). — Massif



FIG. 19. — Specimen of *Dryopteris pentheri* (Krasser) C.Chr., Croat 29928 (MO3295935).

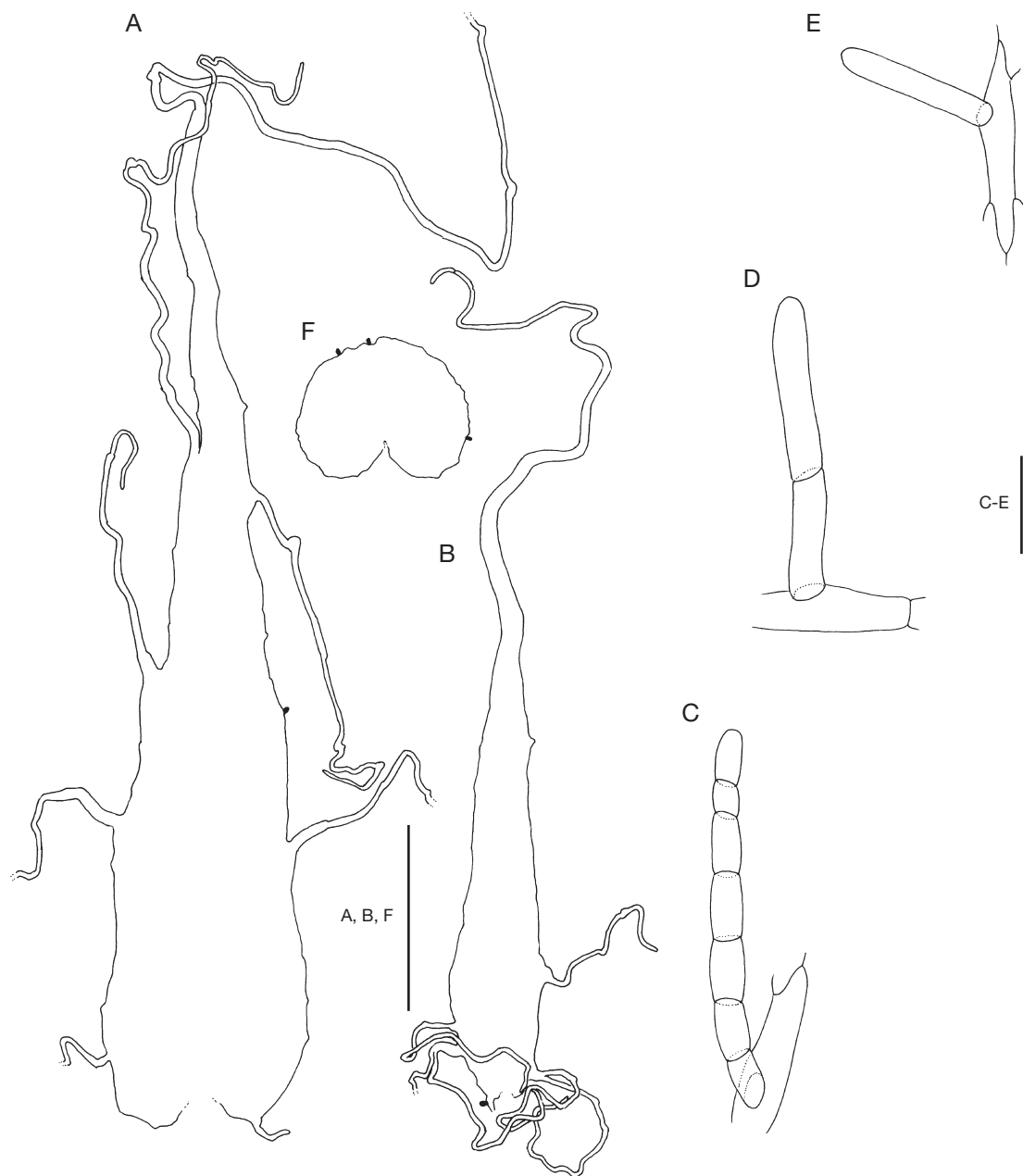


FIG. 20. — Indumentum and indusium of *Dryopteris pentheri* (Krasser) C.Chr.: **A**, stipe scale; **B**, rachis scale; **C**, isocytic hair from abaxial lamin surface; **D**, 2-celled hair; **E**, unicellular oblong hair; **F**, indusium. *Schelppe 6018* (BOL). Scale bars: A, B, F, 0.5 mm; C-E, 0.1 mm.

de Manongarivo, bois vers 800 m, III.1909, *Perrier de la Bathie* 7445 (P00349501). — Antananarivo, 4/76, *Pool s.n.* (K). — Antsiranana, Andapa, RNI

12 du Marojejy, au bord d'un affluent de la rivière Manantenina, à 10 km au Nord-Ouest du village de Manantenina, 820 m, 20.X.1996, *Rakotondrainibe*

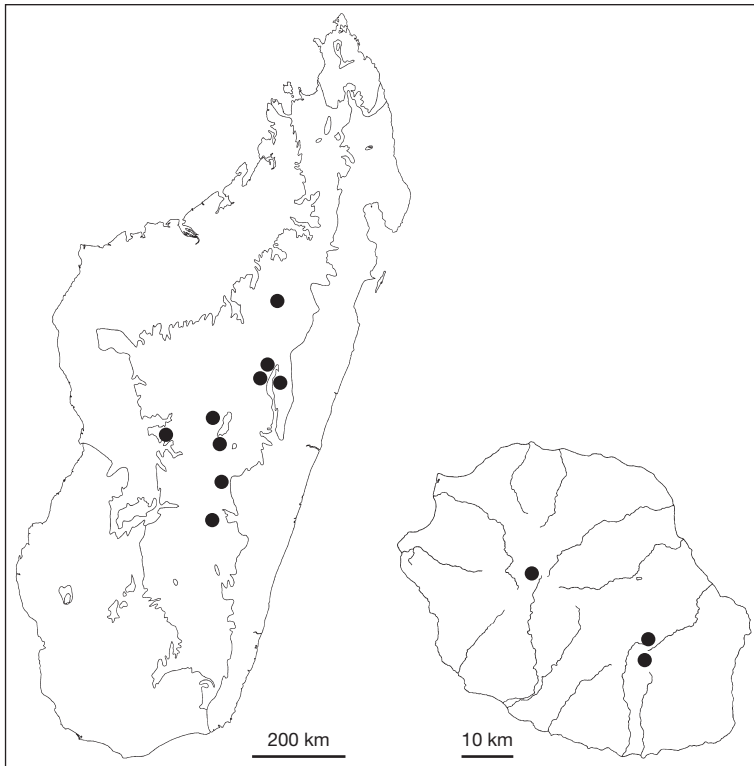


FIG. 21. — Distribution of *Dryopteris pentheri* (Krasser) C.Chr. in Madagascar and la Réunion.

3429 (P00084909, P00084910). — Toamasina, near Andisabe, forest of Mantadia, beyond the graphite mine, 900 m, 3.XI.1994, *Van der Werff, McPherson & Rapanarivo 13626* (PRE).

DESCRIPTION

Plants terrestrial. Rhizome short-decumbent to suberect, up to 110 mm long and 15 mm in diameter, set with roots, closely spaced stipe bases and scales, the scales ferruginous, thinly chartaceous, broadly attached, lanceolate to subulate, up to 15 × 3.5 mm, proximally entire, denticulate towards the apex, often with scattered glands and/or one or more pluricellular, mostly recurved outgrowths along the margin, the smaller scales often with more marginal outgrowths, the apex filiform, terminating in a uniseriate series of oblong cells. Fronds caespitose, suberect to arching, up to 7 per plant, up to 1.2 m long; stipe up to 640 mm long

and 8 mm in diameter, proximally castaneous, stramineous higher up, sulcate adaxially, initially densely scaled, the scales fugaceous, castaneous, chartaceous, the larger scales broadly attached, ovate to lanceolate, up to 15 × 3.4 mm, cordate to broadly cuneate, denticulate, often irregularly glandular along the margins, and/or with one or more mostly recurved pluricellular outgrowths, the apex filiform, terminating in a series of oblong cells, the smaller scales short-stalked, the stalk often glandular, subulate, narrowly cuneate, denticulate, the apex terminating in a short series of oblong cells; lamina ovate to broadly ovate, 1-pinnate-pinnatifid to 2-pinnate, up to 710 × 420 mm, with up to 16 petiolated pinna pairs, the basal pinnae widely spaced, becoming increasingly more closely spaced distally, never overlapping; rachis stramineous, sulcate adaxially, narrowly winged towards the apex, sparsely scaled, the scales stramineous

to ferruginous, chartaceous, short-stalked, linear to subulate, up to 11×2 mm, entire, irregularly denticulate, often with scattered glands along the margins and with numerous filiform outgrowths, the apex terminates in a short series of oblong cells; pinnae petiolate, the petiole up to 4 mm long, near opposite to alternate, becoming increasingly basiscopically decurrent along the rachis and more broadly attached towards the lamina apex, falcate, herbaceous, one to two basal pinna pairs inaequilaterally oblong-acuminate to narrowly lanceolate, pinnatifid to 1-pinnate, symmetrically oblong-acuminate towards the lamina apex, becoming less deeply lobed towards lamina and pinna apices, basal pinnae longest or not, up to 260×62 mm, with up to 8 petiolated pinnule pairs; pinna-rachis shallowly sulcate adaxially, glabrous, pronounced abaxially, narrowly winged for most of the length, sparsely scaled, the smaller scales stramineous to ferruginous, chartaceous, short-stalked, the stalk often glandular, filiform, up to 5×1.4 mm, denticulate or with several filiform marginal outgrowths, the apex terminates in a short series of oblong cells, the larger scales sessile, cordate to cordate-imbricate; pinnules sessile or petiole up to 1 mm long, acroscopic pinnule on basal pinnae oblong-obtuse to oblong acute, up to 28×13 mm, basicopic pinnule on basal pinnae up to 24×10 mm, shallowly to deeply lobed, the lobes entire to shallowly crenulated to obtusely denticulate, oblong-obtuse, mostly widening acroscopically and basicopically towards the lamina apex, up to 8×5 mm, glabrous adaxially, or with a few isocytic hairs near the costa, abaxially with isocytic hairs up to 0.8 mm long along and near the veins, hairs often glandular near the base. Venation evident, lateral veins in pinnules pinnately branched, forked or simple, vein branches end near the margin. Stomata mostly of the polocytic type, (34-)50(-58) mm long. Sori 2-seriate on lobes, medial to suprmedial on predominantly anadromous vein branches, up to 1.4 mm in diameter; sporangium stalk simple or haired, capsule with 14(-15) indurated annulus cells, epistomium 4(-5)-celled, hypostomium 4(-5)-celled. Indusium castaneous, firmly chartaceous, reniform, entire, up to 1.5 mm in diameter, margins strongly recurved,

entire. Spores 64 per sporangium, brown, with short reticulate ridges and bulges, (32-)38(-42) \times (22-)23(-24) mm.

DIAGNOSTIC FEATURES AND RELATIONSHIPS

Characteristic of the species is the narrow rhizome and frond scales, which are denticulate and which often bear a few very long filiform outgrowths along the margins. The outgrowths are mostly uniseriate and are composed of several long cells. The joints between these cells are sinuate.

DISTRIBUTION AND HABITAT

A species confined to Madagascar, where it occurs in moist evergreen forests, at elevations ranging between 800 and 2000 m (Fig. 24).

Dryopteris Adans.

subgen. *Nephrocystis* (H.Itô) Fraser-Jenk.

Bulletin of the British Museum (Natural History), Botany 14 (3): 197 (30 Jan. 1986). — *Dryopteris* Adans. sect. *Nephrocystis* H.Itô, *The Botanical Magazine* (Tokyo) 49: 437 (Jul. 1935). — Type: *Dryopteris hayatae* Tagawa (now *D. subexaltata* (H.Christ) C.Chr.; *Aspidium subexaltatum* H.Christ).

Section *Purpurascences* Fraser-Jenk.

Bulletin of the British Museum (Natural History), Botany 14 (3): 197 (30 Jan. 1986). — Type: *Dryopteris purpurascences* (Blume) H.Christ; *Aspidium purpurascens* Blume.

A group of about 13 species in south-east Asia, the Australasian and Pacific Ocean islands, extending to Hawaii, Africa and the Madagascan region. A single species belonging to this section occurs in the defined region.

Plants with a short, but stout erect rhizome. The frond axes are generally sparsely scaled, the lamina to 4-pinnate-pinnatifid bearing broadly ovate (often bullate) scales abaxially along the costae of the segments. The scales are entire, or they bear a few scattered glands along the margins. The scale apex is filiform and terminates in an oblong or spheroidal cell.



FIG. 22. — Specimen of *Dryopteris subcrenulata* (Baker) C.Chr., Humbert & Capuron 25055 (P00349518). Photo: MNHN, Paris Herbarium, 2009.

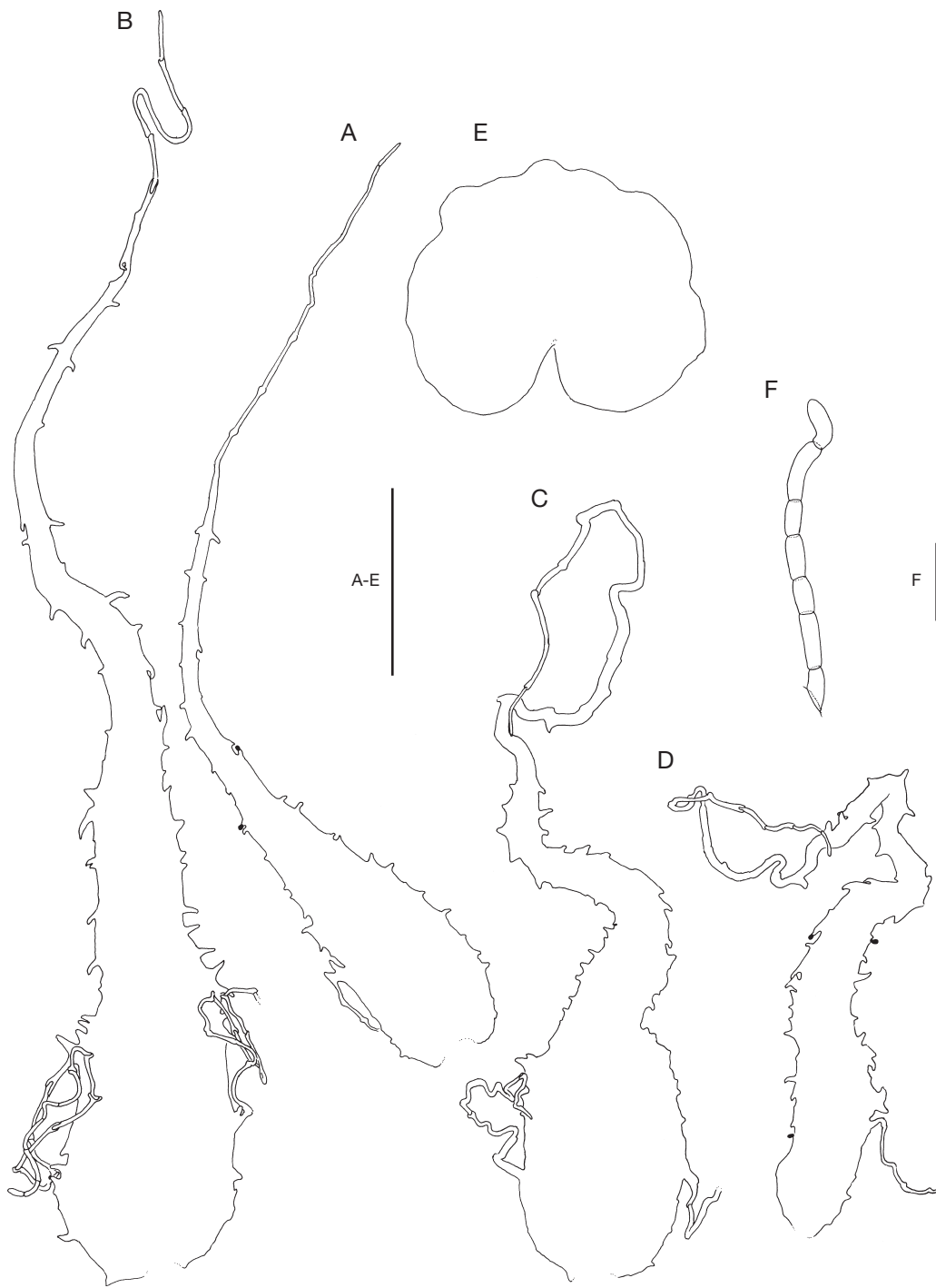


FIG. 23. — Indumentum and indusium of *Dryopteris subcrenulata* (Baker) C.Chr.: **A**, stipe scale; **B**, rachis scale; **C**, pinna-rachis scale; **D**, pinule-rachis scale; **E**, indusium; **F**, hair from abaxial lamina surface. *Humbert 18656* (P00349511). Scale bars: A-E, 1 mm; F, 0.1 mm.

Dryopteris kilemensis (Kuhn) Kuntze
(Figs 25; 26)

Revisio generum plantarum 2: 813 (5 Nov. 1891), as "*kilemensis*". — *Aspidium kilemense* Kuhn, *Filices africanae*: 24 (Oct. 1868), as "*kilmense*". — *Nephrodium kilemense* (Kuhn) Baker, *Synopsis filicum*, ed. 2: 498 (Oct. 1874), as "*kilmense*". — Type: In Kilma ad radices montis Kilimandjaro regionis Dschagga, 3-4000 ped., 1864, *Kersten* 46 (holo-, B20 0051628!; iso-, B20 0058467!).

Nephrodium lastii Baker, *Annals of Botany* 5: 324 (1891). — *Aspidium lastii* (Baker) Hieron., *Die Pflanzenwelt Ost-Afrikas und der Nachbargebiete* 1, C: 85 (Jun. 1895). — *Dryopteris lastii* (Baker) C.Chr., *Index filicum*: 274 (18 Nov. 1905). — Type: Mozambique, Namuli, Makua Country, 1887, *J.T. Last s.n.* (holo-, Kl, 2 sheets).

Dryopteris platylepis Rosenst., *Feddes Repertorium* 4: 4, 5 (1907). — Type: Africa orient. germ. (Tanzania), Kilimanjaro, 4000 m, in humidis sylvae primaevae, 1906, *P. Daubenberger* 37 (holo-, M!; iso-, M!).

Dryopteris remotipinnulata Bonap., *Notes ptéridologiques* 16: 178, 179 (14 Apr. 1925). — Type: Madagascar, Massif de Manongarivo, vers 1700 mètres d'altitude, bois humide, rocailles, mai 1909, *H. Perrier de la Bâthie* 7619 (holo-, P00349503!; iso-, P00483237!, P00483238!).

Dryopteris cordipinnula C.Chr., *Catalogue des plantes de Madagascar. Pteridophyta*: 27 (Feb. 1932), nom. nud. (McNeill *et al.* [2006] Art. 32.1(d)); Christensen, *Dansk Botanisk Arkiv* 7: 55, 56, t. 11, figs 10-12 (Oct. 1932). — Type: Madagascar, Mandraka, Aug. 1906, *d'Alleizette* 111 (holo-, BM!); Imerina: Betsitra, près Andsoforobé (*sic*), Oct. 1906, *d'Alleizette* 170 (para-, BM).

OTHER MATERIAL EXAMINED. — **Réunion.** Insul. Borboniae, 1845, *Garnier* 52 (BM).

Madagascar. Ankafana, 1880, *Cowan s.n.* (BM000800963, BM000800964, BM000800965). — Mandraka, VIII.1906, *d'Alleizette* 111 (BM). — Massif du Kalambatitra (Centre-Sud), Mont Analatsitendrika, forêt ombrophile (sur latérite de gneiss), 1650-1800 m, XI.1933, *Humbert* 11948 (P00349504, P00349505). — Massif du Kalambatitra (Centre-Sud), mont Beanjavidy, forêt ombrophile, alt. 1500-1700 m, XI.1933, *Humbert* 12067 (P00349506). — Montagnes entre le haut Sambirano et le haut Maivarano (entre Mangindrano et Ampanompia), forêt ombrophile sur latérite de gneiss, 1400-1800 m, XI.1937, *Humbert* 18143 (P00349507). — Partie occidentale du massif de Marojejy (Nord-est) de la vallée de l'Ambatoharanana au bassin supérieur de l'Antsahaberoka, forêt ombrophile sur argile latéritique de gneiss et granite, c. 1400 m, 9.XI-2.

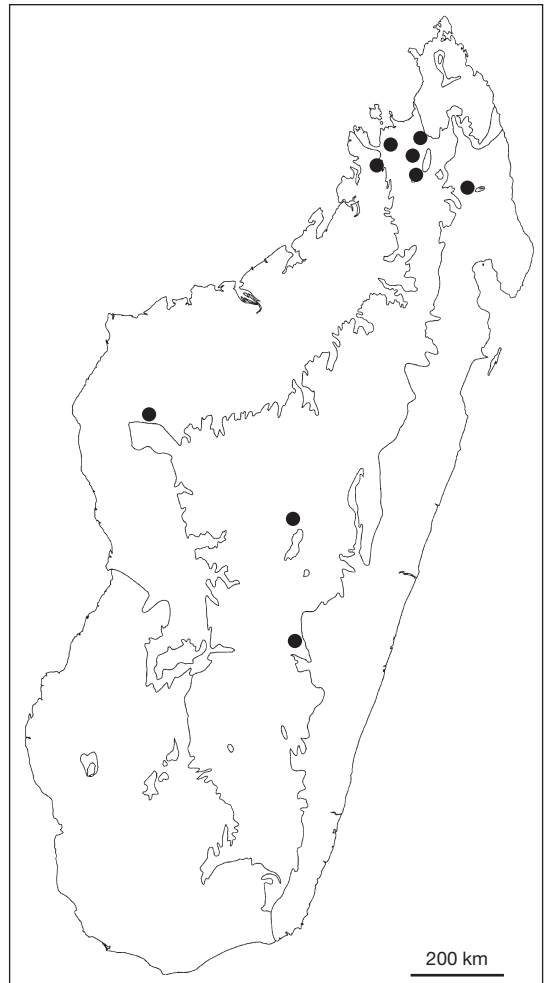


FIG. 24. — Distribution of *Dryopteris subcrenulata* (Baker) C.Chr. in Madagascar.

XII.1959, *Humbert & Saboureaux* 31602 (P00349508). — Fianarantsoa, Ranomafana-Ifanadiana, PN de Ranomafana, forêt de Vatoharanana, à 4 km au sud-ouest du village de Ranomafana, 980 m, 3.X.2000, *Rakotonrainibe* 5820 (P00181240, P00181241, P00181242). — Fianarantsoa, Ivohibe, dans la RNI d'Andringitra, au nord-ouest d'Ambarongy, au sud-ouest du campement no. 3, 1210 m, 28.XI-1.XII.1994, *Rakotavao* 267 (P00116711).

DESCRIPTION

Plants terrestrial. Rhizome short-decumbent or short and erect, up to 15 mm in diameter, set with roots, crowded stipe bases, and scales, the

scales ferruginous, chartaceous, broadly attached, subulate to narrowly lanceolate, up to 30×4 mm, entire, or with a few scattered filiform outgrowths near the apex, the apex short-filiform, terminating in an oblong cell. Fronds caespitose, arching, up to 1.5 m long; stipe base castaneous, stramineous higher up, sulcate adaxially, up to 815 mm long and 9 mm in diameter, proximally densely scaled, subglabrous higher up, the scales ferruginous to castaneous, chartaceous and often rugate, or thinly crustaceous, broadly attached or sessile, filiform to broadly ovate, up to 40×9 mm, truncate to cordate, entire, or with a few scattered filiform outgrowths near the base or apex, occasionally with a few scattered glands (these frequently also occur on the scale laminae), and short uniseriate hairs, the scale apex filiform, terminating in a short uniseriate series of cells, the apical cell oblong or spheroidal, higher up often with glands; lamina herbaceous, broadly ovate, to 4-pinnate-pinnatifid, anadromous, catadromous towards the apex, up to 625 mm long, with up to 14 pairs of petiolated pinna pairs; rachis stramineous, adaxially shallowly sulcate, becoming narrowly winged towards the apex, sparsely scaled, the scales castaneous to ferruginous, chartaceous, to thinly crustaceous, broadly attached or sessile, filiform to broadly ovate, up to 6×3 mm, truncate to cordate, the margins regularly set with glands or with a few uniseriate hairs near the base, the apex filiform, terminating in a short uniseriate series of cells, the apical cell oblong or spheroidal; pinnae petiolate, the petiole up to 22 mm long, the basal pair inaequilaterally ovate, ovate to lanceolate towards the lamina apex, to 3-pinnate-pinnatifid, the basal pair the longest, basicopically developed, up to 345×230 mm, opposite to alternate, basally widely spaced, more closely spaced apically, often imbricate, with up to 12 petiolated pinnule pairs; pinna-rachis adaxially shallowly sulcate, the sulcus confluent with that of the rachis, often closely set with unicellular glandular hairs and scales, abaxially sparsely scaled, the scales ferruginous to stramineous, chartaceous, sessile, ovate to broadly ovate, up to 4.5×2.7 mm, cordate, entire or regularly set with glands, the apex filiform; pinnules petiolate, the petiole up to 9 mm long, ovate, to 2-pinnate-pinnatifid,

the acroscopic pinnule on the basal pinnae up to 105×29 mm, the basicopic pinnule on the basal pinnae up to 150×70 mm, opposite to alternate, spaced or slightly imbricate, with up to 9 petiolated segment pairs; pinnule-rachis adaxially sulcate, sparsely scaled, the scales similar to, but smaller than those on the pinna-rachis; segments petiolate, the petiole up to 1 mm long, ovate, to 1-pinnate-pinnatifid, with up to 3 pairs petiolated ultimate segments, spaced, the basicopic segment on the basal pinnae up to 44×20 mm, the acroscopic pinnule on the basal pinnae up to 28×14 mm; costa adaxially sulcate, winged, ridged adaxially, abaxially sparsely scaled, the scales similar to, but smaller than those on the pinna-rachis; ultimate segments oblong-obtuse, firmly herbaceous, the basicopic ultimate segment on the basal segment up to 11×6 mm, the acroscopic ultimate segment on the basal segment up to 9×6 mm, deeply lobed, the lobes serrate to obtusely dentate, glabrous adaxially, abaxially glabrous or often with glands along the veins, (46-)66(-84) mm long, with isocytic to moniliform hairs and scales, the scales often bullate, sessile, broadly ovate, up to 1.5×0.7 mm, truncate to cordate, entire or with a few scattered glands, the apex filiform, terminating in an oblong or spheroidal cell. Venation anadromous, becoming catadromous towards the lamina and pinna apex, pinnately branched in the segments, the vein branches pinnately branched, forked or simple near the apex, evident, ending in the teeth near the margin. Stomata mostly of the polocytic type, (30-)39(-50) mm long. Sori circular, infra-medial on the anadromous vein branches, discrete at maturity, up to 1 mm in diameter; sporangium stalk simple, glandular, or rarely with a pluricellular uniseriate hair, capsule with (12-)13(-16) indurated annulus cells, epistomium (4-)5(-6)-celled, hypostomium (4-)6(-7)-celled; indusium brown, firmly herbaceous, reniform, entire or glandular along the margin (rarely also on the laminae), up to 1 mm in diameter. Spores ellipsoidal, monoete, the perispore with low tubercles and/or long reticulate ridges, minutely rugulose to minutely scabrous, (32-)36(-42) \times (20-)22(-26) mm (Tryon & Lugardon 1990: 426, fig. 159.19). Chromosome number: $2n = c. 82$ (Vida *in* Widén *et al.* 1973: 2129).

REMARK

The correct spelling of the specific epithet is discussed by Pichi Sermolli (1985: 158).

DIAGNOSTIC FEATURES AND RELATIONSHIPS

Dryopteris kilemensis can be separated from all other African *Dryopteris* species by its large structure, fronds up to 1.5 m long, and the finely dissected lamina, which may be up to 4-pinnate-pinnatifid. The sessile, broadly ovate, often bullate scales with the apex terminating in a short uniseriate range of cells are also characteristic.

VARIATION

Dryopteris kilemensis shows little variation in gross morphology, but micromorphological variation was detected in scale morphology, the presence of glands on the lamina, the presence of glands or pluricellular hairs on the sporangium stalk, and the distribution of glands on the indusium lamina.

Scale texture appears to be influenced by environmental conditions, as plants occurring in less favourable conditions have scales that are thinly crustaceous rather than chartaceous. The rhizome and frond scales of these plants are generally also broader than those of plants from moist forest habitats. Glands and pluricellular hairs along the scale margins also show variation in frequency.

A direct correlation cannot be drawn between habit and the presence of glands occurring on the lamina. Whilst some collections from higher elevations bear these structures, others do not. Similarly, glandular collections from moist forests were also observed.

The sporangium stalk of *D. kilemensis* is generally simple, but in some the sporangia bear a single gland on the stalk. In others, a long simple pluricellular hair is borne near the stalk base. No collections were observed where both glands and pluricellular hairs occur.

Generally, the indusium of *D. kilemensis* is simple, or it may bear a number of glands along the margin. The occurrence of glands on the indusium lamina is, however, less frequent and have only been observed in a few collections from Africa.

DISTRIBUTION AND HABITAT

Dryopteris kilemensis is confined to the central and eastern parts of tropical Africa and Madagascar

where it occurs in forests at 980 to 1800 m (Fig. 27). Although reported from Réunion, it has not been collected on that island recently.

SPECIES INCERTAE SEDIS

Fraser-Jenkins (1986: 198) places *Dryopteris wardii* in subgenus *Nephrocystis* sect. *Purpurascentes*, a position I cannot support. The unique features the species exhibits (see Diagnostic features and relationships) cast a doubt over its inclusion in *Dryopteris*, but due to the lack of a better placement, it is here tentatively retained in this genus. A molecular and detailed morphological studies based on live material are required to ascertain the correct placement of *D. wardii*.

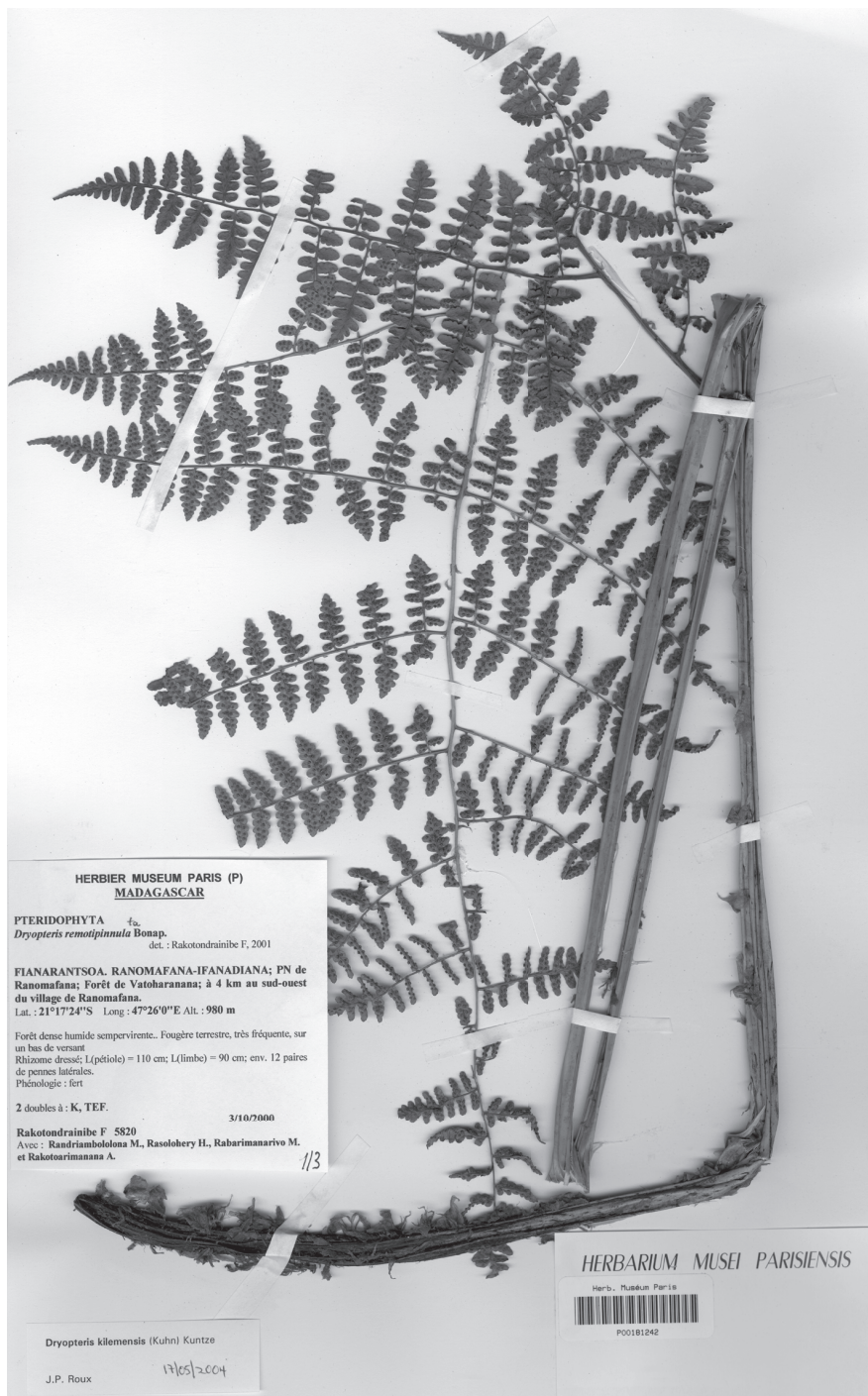
Dryopteris wardii (Baker) Kuntze
(Fig. 28)

Revisio generum plantarum 2: 814 (5 Nov. 1891). — *Nephrodium wardii* Baker, *Synopsis filicum*, ed. 2: 500 (Oct. 1874). — *Polystichopsis wardii* (Baker) Tardieu, *Notulae Systematicae* (Paris) 15 (2): 176 (Apr. 1956). — *Araioptegia wardii* (Baker) Tardieu, *Adansonia* 5 (4): 493 (1965). — Type: Seychelles, *Ward s.n.* (lecto-, BM000801014!, here designated); Seychelles, *Neville s.n.* (syn-, BM000801015!, K000228190!); *Horne 177* (syn-, K000228193!).

OTHER MATERIAL EXAMINED. — Seychelles. Mahé, 1853, *Rawson 196* (BM000801017). — Mahé, 1800 ft., *Ward s.n.* (BM000801014). — Seychelles, *Barkly s.n.* (BM000801015). — Seychelles (excl. *Horne s.n.*), *sine coll. s.n.* (BM000801016). — Silhouette, 2.VIII.1908, *Gardiner s.n.* (BM000801018).

DESCRIPTION

Plants terrestrial. Rhizome “horizontal, *c.* 20 mm thick” (Christensen 1912: 413). Fronds anadromous, up to *c.* 820 mm long; stipe castaneous, adaxially sulcate along the entire length, up to 320 mm long and 6 mm in diameter, proximally densely scaled, sparsely scaled to glabrous higher up, the scales ferruginous, chartaceous, broadly attached, narrowly lanceolate to subulate, up to 14 × 2 mm, entire to denticulate, irregularly glandular along the margins, the apex terminates in a



HERBIER MUSEUM PARIS (P)
MADAGASCAR

PTERIDOPHYTA f.
Dryopteris remotipinnula Bonap.
det.: Rakotondrainibe F, 2001

FIANARANTSOA, RANOMAFANA-IFANADIANA; PN de
Ranomafana; Forêt de Vatoharanana; à 4 km au sud-ouest
du village de Ranomafana.
Lat.: 21°17'24" S Long.: 47°26'0" E Alt.: 980 m

Forêt dense humide sempervirente.. Fougère terrestre, très fréquente, sur
un bas de versant
Rhizome dressé; L (pétiole) = 110 cm; L (limbe) = 90 cm; env. 12 paires
de pennes latérales.
Phénologie : fert

2 doubles à : K, TEF. 3/10/2000

Rakotondrainibe F 5820
Avec : Randriambololona M., Rasolohery H., Rabarimanarivo M.
et Rakotoarimana A. 113

Dryopteris kilemensis (Kuhn) Kuntze
J.P. Roux 17/05/2004

HERBARIUM MUSEI PARIENSIS
Herb. Muséum Paris
P00181242

FIG. 25. — Specimen of *Dryopteris kilemensis* (Kuhn) Kuntze, Rakotondrainibe 5820 (P00181242). Photo: MNHN, Paris Herbarium, 2009.

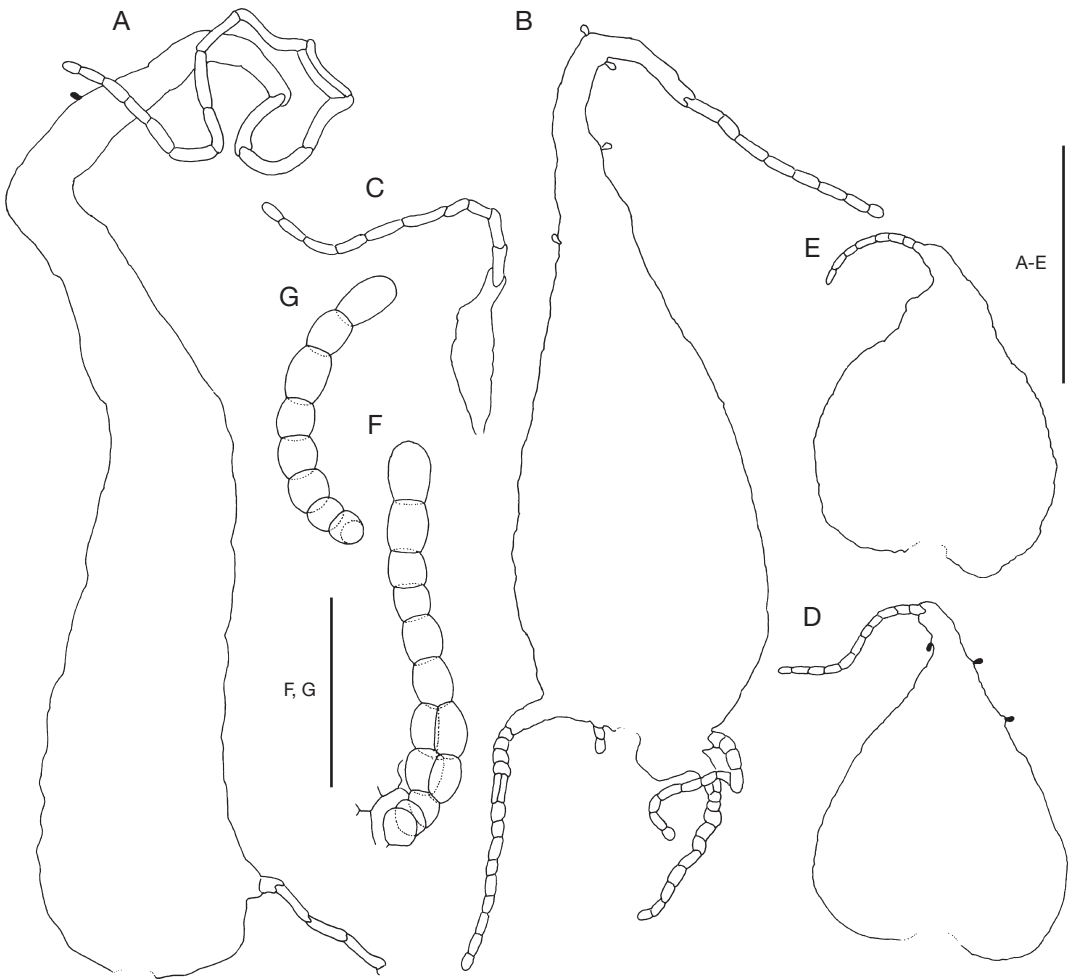


FIG. 26. — Indumentum of *Dryopteris kilimensis* (Kuhn) Kuntze: **A, C**, stipe scales; **B**, rachis scale; **D**, pinna-rachis scale; **E**, scale from abaxial lamina surface; **F, G**, hairs from abaxial lamina surface. Roux 2927 (NBG).2009. Scale bars: A-E, 1 mm; F, G, 0.2 mm.

short series of oblong cells; lamina anadromous, broadly ovate, up to 500 mm long (clearly longer, but material incomplete) and 900 mm wide, to 4-pinnate, with up to 9 (perhaps more) petiolated pinna pairs; rachis castaneous, adaxially shallowly sulcate, narrowly winged towards the apex, initially sparsely set with filiform scales and few-celled hairs bearing one or more glandular cells near the base, glabrous later; pinnae petiolate, the petiole up to 18 mm long, alternate, proximally widely spaced, somewhat overlapping, the basal pair longest, up to 3-pinnate, up to 440 × 215 mm, inconspicu-

ously basicopically developed or not, proximally inaequilaterally triangular, symmetrically lanceolate higher up, with up to 11 petiolated pinnule pairs; pinna-rachis castaneous, adaxially shallowly sulcate, narrowly winged towards the apex, initially sparsely set with hairs and glands similar to those on the rachis, glabrous later; pinnules petiolate, the petiole up to 6 mm long, distal pinnules becoming increasingly more broadly attached and basicopically decurrent, proximally widely spaced, more closely spaced distally, mostly slightly overlapping, up to 2-pinnate, acroscopic pinnule on basal pinnae up to

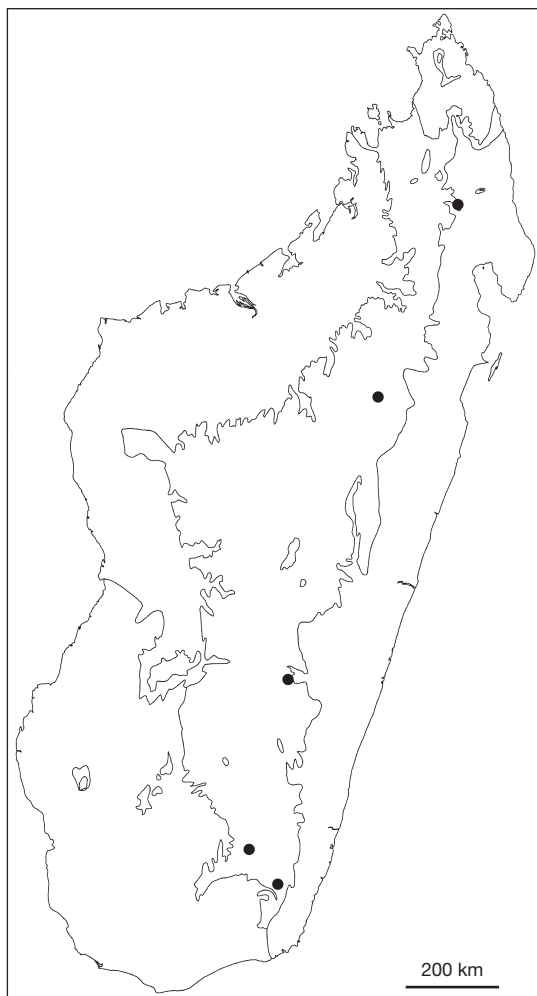


FIG. 27. — Distribution of *Dryopteris kilemensis* (Kuhn) Kuntze in Madagascar.

132 × 58 mm, basiscopic pinnule on basal pinnae ovate, lanceolate, or oblong-acuminate, up to 115 × 48 mm; pinnule-rachis shallowly sulcate adaxially, the sulcus confluent with that of the pinna-rachis, initially sparsely set with glands and hairs similar to those on the pinna-rachis, glabrous later; segments petiolate, the petiole up to 2 mm long, distal segments becoming increasingly more broadly attached and basiscopically decurrent along the costa, firmly herbaceous, mostly somewhat overlapping, up to 1-pinnate, acroscopic segment on basal pinnule

up to 33 × 16 mm, basiscopic segment on basal pinnule up to 29 × 18 mm, ovate to narrowly lanceolate, oblong and falcate towards the apex; costa narrowly winged for most of the length, sparsely set with glands and hairs bearing one or more glandular cells near the base; ultimate segments sessile, becoming increasingly more broadly attached towards the segment apex, the basal ultimate segments inaequilaterally elliptic to oblong, up to 11 × 6 mm, trapeziform to falcate higher up, obtusely dentate, glabrous adaxially, abaxially sparsely set with glands (56-)68(-90) mm long and hairs bearing one or more glandular cells near the base. Venation anadromous, evident, pinnately branched in ultimate segments, ending in teeth near the margin. Stomata mostly of the polocytic type, (38-)48(-58) mm long. Sori 2-seriate on larger ultimate segments, medial on anadromous vein branches; indusium castaneous, chartaceous, up to 1.2 mm in diameter, reniform, entire or with scattered glands, glandular and haired adaxially, the hairs often bearing a gland near the base. Sporangium stalk simple or haired, apical cell of hair pyriform and gland-like, capsule with (13-)14(-17) indurated annulus cells, epistomium (3-)4(-5)-celled, hypostomium (3-)4(-5)-celled. Spores 64 per sporangium, brown, with narrow to broad reticulate ridges, exospore (22-)47(-52) × (24-)26(-30) mm.

REMARKS

Baker (1874: 500) cited three collections, *Ward s.n.*, *Neville s.n.* and *Horne 177*, when he described *Nephrodium wardii*. Tardieu-Blot (1960: 180) cites the *Ward s.n.* and *Neville s.n.* collections from the BM and the *Horne 177* collection from K. The *Ward s.n.* collection (BM000801014) was made at Mahé, Seychelles. The sheet contains three immature fronds and a label in the hand of Baker reading “*Lastrea* 27-from Mahé-Seychelles-elev 1800 ft Swinburn Ward Esq Febr/69”, “*Lastrea*” and the date appear to have been added later as it is in a darker ink. This sheet conforms to the protologue and it may serve as one of the syntypes.

Two further sheets at BM under this name have labels in the hand of Baker. The first, BM000801015, formed part of the Sir H. & Lady Barkly Herbarium. The label reads “*Lastrea* Seychelles W. Nevill. I be-

lieve this to be new. It is certainly nothing in the Synopsis and would come in near *N. amplum* page 285(.) Baker 29/1/68(.) We have not received any Seychelles ferns from W. Nevill." This specimen is viewed as one of the syntypes.

The second sheet, BM000801016, also formed part of the Sir H. & Lady Barkly Herbarium. This sheet contains two different elements, the frond on the left has a typed label reading "Seychelles-John Horne". A further label on brown paper in the hand of Baker gives "*Lastrea Wardii* Baker MSS". This material belongs to a *Lastreopsis* species. At the right bottom corner of this sheet are two labels, the upper one on white paper and the lower one on brown paper. The upper label reads "*Lastrea* 27 Seychelles(.) I cannot make this out from the specimen sent. It is certainly a *Lastrea*(.) Baker 29/1/68". The label on brown paper reads "7-Reduit(.) *Acrophorus* sp: unnamed Baker-Mahé, Seychelles(.) This is appearing to be the *Microlepia?* 27 Seychelles which Captain Beddome states to be a *Lastrea*. Letter of 15/3/67(.) May this not be the same as W Nevill's *Lastrea*-A-while M Baker says is new and nearest *N. amplum?* It has a close resemblance." The frond fragment above these labels is that of *D. wardii*. Since there is no clear indication as to who the collector of the material is, it cannot be considered as one of the syntypes.

As a result of the distinct features of this species, Tardieu-Blot (1956b: 176) transferred it to *Poly-stichopsis* (J.Sm.) Holttum, a name now considered synonymous with *Arachniodes* Blume (Kramer *et al.* 1990: 112).

DIAGNOSTIC FEATURES AND RELATIONSHIPS

Dryopteris wardii is characterised by the near glabrous 4-pinnate fronds. Scales occur on the upper part of the stipe and lamina, and are mostly subulate and terminate in a short series of oblong cells. Hairs occurring on the lamina axes and veins are often branched and generally bear one or more glands near the base. The sporangium stalk is also haired, but the terminal cell is pyriform and glandular. In *Dryopteris* species where the sporangium stalk is haired, the apical cell is eglandular. The indusium, which bears hairs and glands on the laminae are also characteristic (Fig. 26C).

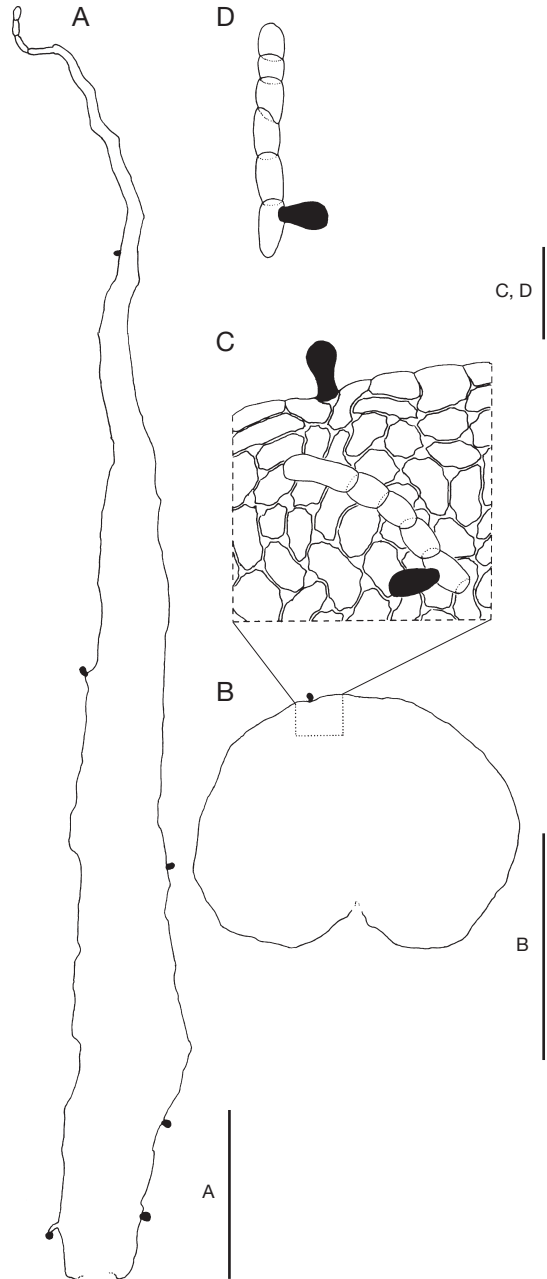


Fig. 28. — Indumentum and indusium of *Dryopteris wardii* (Baker) Kuntze: A, stipe scale; B, indusium; C, section of indusium showing gland and hair of lamina; D, hair from abaxial lamina surface. Gardiner s.n. (BM000801018). Scale bars: A, B, 1 mm; C, D, 0.1 mm.

DISTRIBUTION AND HABITAT

Dryopteris wardii is known from the Seychelles only, where it is restricted to Silhouette (4°30'S, 55°15'E) and Mahé (4°45'S, 55°30'E) islands (Fig. 29). Little is known about the ecology of the species, except that one of the collections was made at *c.* 550 m on Mahé. No recent collections of the species appear to have been made.

PUTATIVE HYBRID

Dryopteris hybrid

“La Réunion” (*D. pentheri* × *D. aquilinoïdes*), Roux, *Flore de Mascareignes, Ptéridophytes*: 272, 273 (2008).

MATERIAL EXAMINED. — Réunion. Plateau des Fleurs Jaunes au-dessous du col de Taïbit, cirque de Cilaos, 1700 m, 22.III.1974, *Cadet 4558* (P00349602, P00349603).

DESCRIPTION

Plants terrestrial. Rhizome unknown, but probably short-decumbent. Fronds caespitose, erect, up to 1.4 m long; stipe brown to stramineous, up to 550 mm long and 10 mm in diameter, cicatricate, proximally densely scaled, the scales higher up fugacious, ferruginous, narrowly lanceolate to oblong-acuminate, up to 55 × 7 mm, with filiform marginal outgrowths; lamina firmly herbaceous, ovate, up to 840 × 460 mm, 3-pinnate-pinnatifid, with up to 17 petiolated pinna pairs; rachis stramineous, initially moderately scaled, the scales stramineous, narrowly lanceolate to oblong-acuminate, with filiform marginal outgrowths, up to 16 × 3 mm; pinnae petiolate, the petiole up to 13 mm long, basal pinnae basiscopically developed, inaequilaterally narrowly ovate, up to 350 × 140 mm, oblong-acuminate towards the apex, to 2-pinnate-pinnatifid, basal pinna pair longest, opposite to alternate, with up to 11 petiolated pinnule pairs; pinna-rachis narrowly winged distally, sparsely to moderately scaled, the scales stramineous, narrowly lanceolate-caudate to oblong-caudate, up to 7 × 3 mm, with filiform outgrowths along the margin; pinnules petiolate, the petiole up to 2 mm long, the basal pinnules somewhat basiscopically developed, lanceolate to oblong-acuminate, up

to 180 × 30 mm, to 1-pinnate-pinnatifid; costa moderately scaled abaxially, the scales stramineous, narrowly lanceolate to filiform, up to 3 × 1 m, with filiform marginal outgrowths; segments petiolate, the petiole up to 1 mm long, sessile to adnate and basiscopically decurrent towards the pinnule apex, lanceolate, ovate, or oblong-obtuse, up to 18 × 9 mm, obtusely lobed, denticulate, abaxially sparsely set with stramineous to ferruginous filiform scales and hairs, also with unicellular oblong hairs up to 134 µm long along the costules and veins, glabrous adaxially. Sori circular, medial on predominantly anadromous vein branches, discrete or touching at maturity, essentially uniseriate; sporangium stalk haired; indusium persistent, brown, firmly herbaceous, reniform, repand, up to 8 mm in diameter. Spores black, aborted.

DISTRIBUTION AND HABITAT

In pioneer vegetation among rocks at about 1700 m.

Genus *Nothoperanema* (Tagawa) Ching

Acta Phytotaxonomica Sinica 11: 25 (1966). — *Dryopteris* Adans. subgen. *Nothoperanema* Tagawa, *Acta Phytotaxonomica et Geobotanica* 7: 199 (1938). — Type: *Nothoperanema squamisetum* (Hook.) Ching; *Nephrodium squamisetum* Hook.

DESCRIPTION

Plants terrestrial or epilithic. Rhizome dictyostelic, suberect to erect. Fronds monomorphic, caespitose; stipe and rachis adaxially sulcate, sulcus open to that of the pinna-rachis; lamina pinnately compound, the basal pinna pair basiscopically developed; hypostomatic, stomata of the anomo- and polocytic types; venation of the pectopterid-type, anadromous or catadromous, forked or pinnately branched, ultimate vein branches free, ending near the margin, the endings enlarged and often “hydathode”-like adaxially. Indumentum composed of patent, broadly attached, basally multistratose scales occurring on the rhizome, frond axes, and adaxially on the veins, the larger scale margins regularly set with short multicellular, uniseriate hairs and capitate glands, glands may also occur on the scale lamina, also with

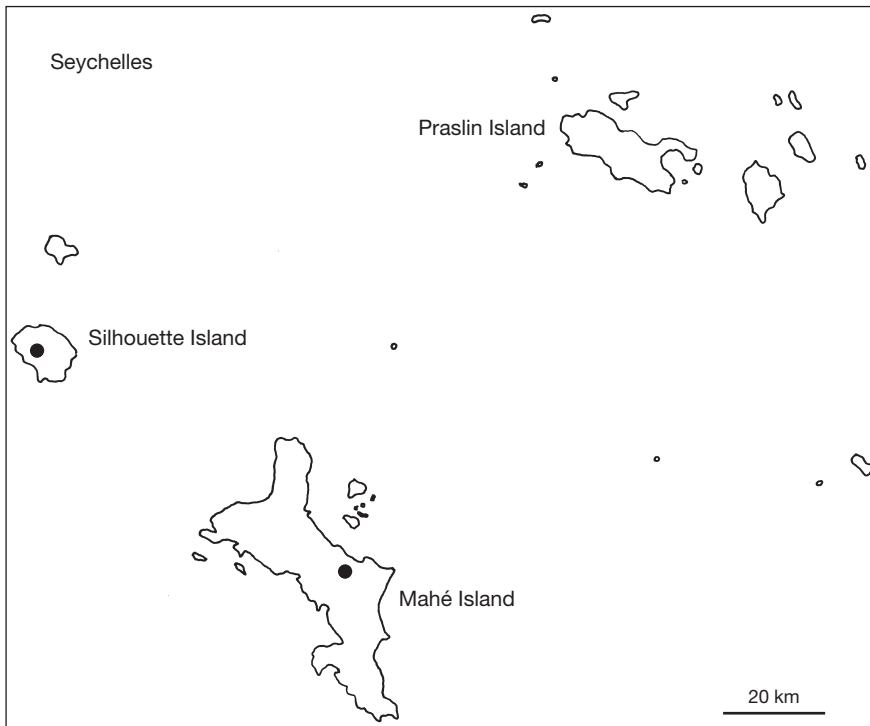


FIG. 29. — Distribution of *Dryopteris wardii* (Baker) Kuntze in the Seychelles islands group.

clavate, unicellular glands and simple uniseriate trichomes abaxially along the veins. Sori circular, inframedial on unmodified vein branches, or terminal on abbreviated vein branches; sporangium long-stalked, 3-seriate below the capsule, simple, or with a long isocytic hair; capsule globose, with (13-)15(-17) indurated annulus cells and a well defined stomium, epistomium 4(-5)-celled, hypostomium 4(-5)-celled; indusium reniform, entire, adaxially with numerous unicellular, clavate glands. Spores 64 per sporangium, ellipsoidal, monolete, with prominent folds, tuberculate, 27-40 μm long. Chromosome number based on $2n = 82$.

Nothoperanema squamiseta (Hook.) Ching
(Figs 30; 31)

Acta Phytotaxonomica Sinica 11 (1): 25, 26 (Jan. 1966). — *Nephrodium squamiseta* Hook., *Species filicum* 4 (14): 140 (Aug. 1862); 4 (15/16): pl. 268 (1863). —

Aspidium squamiseta (Hook.) Kuhn, *Filices africanae*: 24, 142 (Oct. 1867). — *Dryopteris squamiseta* (Hook.) Kuntze, *Revisio generum plantarum* 2: 813 (5 Nov. 1891). — Type: Fernando Po, Clarence Peak, alt. 4000 ft., *G. Mann* 380 (holo-, K000351166!, K000351167!).

Nephrodium buchananii Baker, *Synopsis filicum*, ed. 2: 498, 499 (Oct. 1874), as "*buchanani*". — *Lastrea buchananii* (Baker) Bedd., *Handbook to the Ferns of British India*: 255 (1883). — *Dryopteris buchananii* (Baker) Kuntze, *Revisio generum plantarum* 2: 812 (5 Nov. 1892). — Type: Natal, *Buchanan* 108 (lecto-, K000351168!, K000351169!, here designated); Bourbon, *Boivin s.n.* (syn-, K?).

OTHER MATERIAL EXAMINED. — **Madagascar.** Tsaratanana, *Perrier de la Bathie* 16448 (P). — Montagnes au nord du Mangindrano, partage des eaux Mahavary-Androranga, *Humbert* 25043 (P). — Près de Tananarivo, *Gilpin s.n.* (K). — Ambanja Antsiranana, massif de Tsaratanana, montagne au nord de Mangindrano, Marotolana, Ampanopia, Ampitsinjovana, *Rasolohery* 424 (P00338498). — Ambalavao Fianarantsoa, Réserve Spéciale d'Ivohibe à 6,5 km à l'est-sud-est du village d'Ivohibe, près de la source de la rivière Andranomainty,

Rakotondrainibe 4213 bis (P00134242), *Rakotondrainibe 4263* (P00134295). — Région de Tsinjoarivo, forêt de Mahatsinjo, à 10 km au SE de Tsinjoarivo, *Rakotondrainibe 4588* (P00134734).

Réunion. Le Maïdo, forêt de Maïdo, route forestière des Tamarins, au croisement avec le ravin “Bras la Pompe”, *Janssen 2714* (P00590820). — Île de la Réunion, *De l’Isle 391* (P00411951). — Cirque de Salazie, sentier vers La Nouvelle, *Badré 1061* (P00411950).

DESCRIPTION

Plants terrestrial. Rhizome erect to suberect, usually unbranched, up to 60 mm long and 8 mm in diameter, closely set with roots, stipe bases, and scales, the scales chartaceous, castaneous, adnate, narrowly triangular to subulate, up to 11 × 2 mm, the margins regularly set with short multicellular, uniseriate hairs and capitate glands, the glands also occur on the scale laminae, the scale apex terminates in a short uniseriate series of cells. Fronds up to 8 per plant, suberect to arching, up to 925 mm long; stipe firm, proximally castaneous, brown to stramineous higher up, adaxially sulcate, up to 460 mm long and 5 mm in diameter, closely set with patent scales, hairs, and glands, the scales chartaceous to thinly crustaceous, castaneous, adnate, narrowly triangular to subulate, up to 11 × 2 mm, entire, or those near the base often with short multicellular, uniseriate hairs and capitate glands, the glands often also occur on the scale laminae, the scale apex terminates in a short uniseriate series of cells, the hairs are of 2 kinds: 1) inconspicuous, pale, multicellular uniseriate appressed hairs and, 2) castaneous, multicellular uniseriate patent hairs, the cells collapsing in the ctenitoid fashion upon drying, the glands calcate; lamina proximally anadromous, catadromous towards the apex, to 3-pinnate, ovate, up to 460 × 390 mm, with up to 10 petiolated pinna pairs; rachis stramineous, adaxially sulcate, the sulcus open to that of the pinna-rachis, closely set with scales similar to, but smaller than those on the stipe; pinnae petiolate, the petiole up to 13 mm long, opposite to alternate, overlapping, the basal pinna pair strongly basiscopically developed, inaequilaterally narrowly ovate, lanceolate to oblong-acute towards the apex, up to 220 × 125 mm, 1-pinnate-pinnatifid to 2-pinnate, with up to 5 pairs of free pinnules; pinna-rachis stramineous, adaxially shallowly sulcate, moderately

scaled, the scales patent, chartaceous, castaneous, adnate, subulate, up to 3 mm long; pinnules petiolate, the petiole up to 2 mm long, catadromous, alternate, spaced or overlapping, oblong-acute to oblong-attenuate, acroscopic pinnule on basal pinnae up to 44 × 17 mm, basiscopically pinnule on basal pinnae up to 82 × 24 mm, pinnatifid to 1-pinnate; segments herbaceous, trapeziform to inaequilaterally oblong-obtuse, often acroscopically auricled, basiscopically decurrent along the costa towards the pinnule apex, lobed to crenulate, up to 14 × 6 mm, adaxially with simple, proximally multistratose subulate hairs along the veins, up to 1.2 mm long, abaxially with proximally multistratose subulate hairs and clavate, pluricellular, uniseriate hairs, up to 0.85 mm long, and capitate glands up to 30 mm long along the veins. Venation anadromous, evident, pinnately branched, free vein branches end near the margin, fertile vein branches undifferentiated or variously shortened beyond the sorus. Sori circular, usually restricted to the pinnule and segment apices, medially to inframedially on unmodified vein branches, up to 1.5 mm in diameter; indusium firmly herbaceous, brown, persistent, reniform to subcircular, entire, up to 1.2 mm in diameter, adaxially with numerous capitate glands and rarely also with a few short hairs near the point of attachment; sporangium long-stalked, the stalk simple or with a long uniseriate trichome, 3-seriate below the capsule, the capsule globose, with 13(-15) indurated annulus cells, epistomium 4(-5)-celled, hypostomium 4(-5)-celled. Spores 64 per sporangium, brown, ellipsoidal, monolet, with prominent folds, tuberculate, (32-)35(-36) × (18-)20(-22) mm (Tryon & Lugardon 1990: 422, figs 158.4; 158.5).

DISTRIBUTION AND HABITAT

The species is widespread in sub-Saharan Africa, with the exception of west tropical Africa, extending to Réunion and Madagascar. It is generally confined to moist evergreen forests (Fig. 32).

EXCLUDED NAME

Dryopteris perrieriana C.Chr. = *Lastreopsis perrieriana* (C.Chr.) J.P.Roux



FIG. 30. — Specimen of *Nothoperanema squamiseta* (Tagawa) Ching, Roux 3251 (NBG0221782-0).

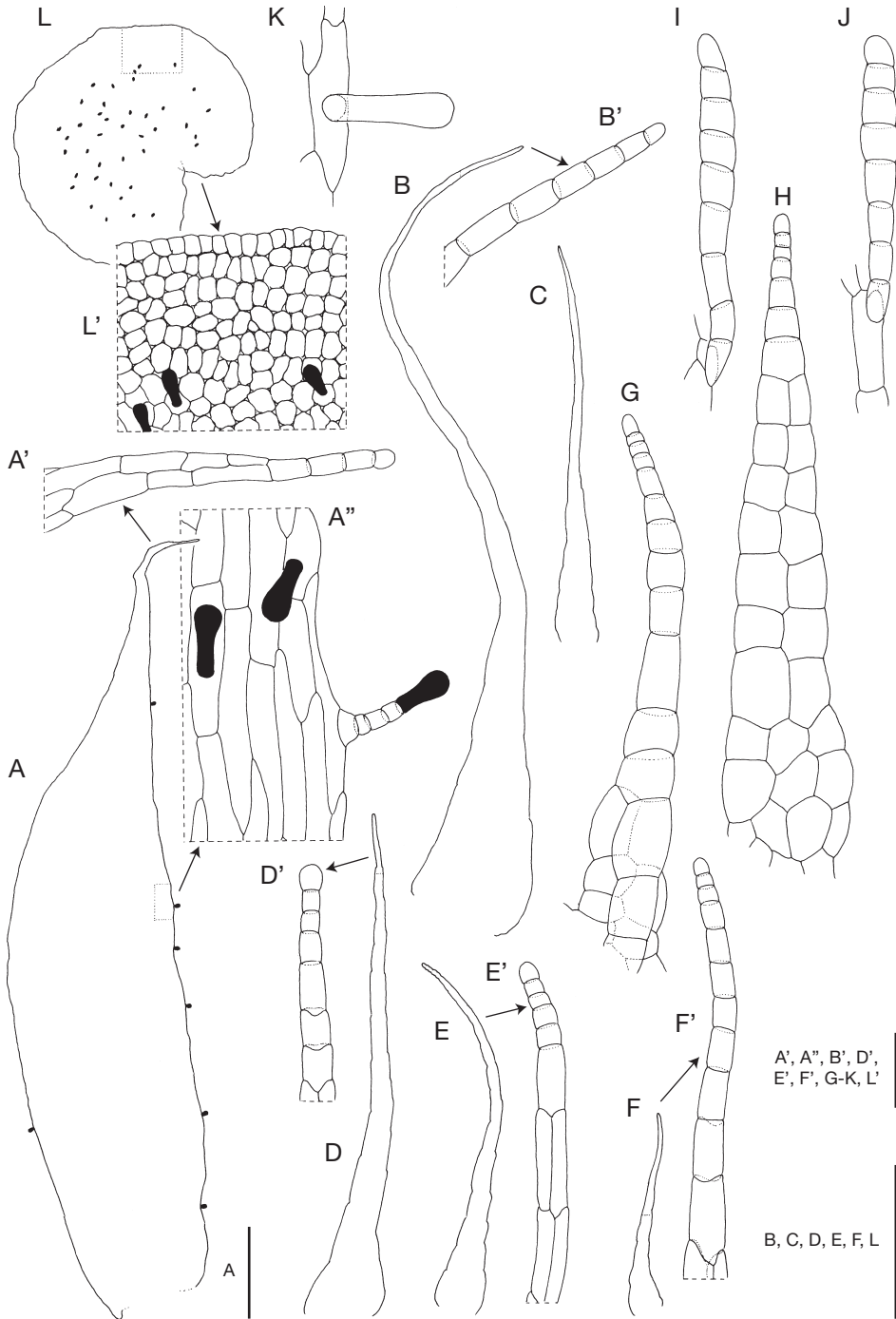


FIG. 31. — Indumentum and indusium of *Nothoperanema squamiseta* (Tagawa) Ching: **A-B'**, stipe scales; **C-D'**, rachis scales; **E-F'**, pinna-rachis scales; **G, H**, multistratose hairs from abaxial lamina surface; **I, J**, nothoperanemoid hairs; **K**, gland from adaxial lamina surface; **L, L'**, indusium. *Kluge 2457* (NBG). Scale bars: A, 0.5 mm; A-F, L, 0.5 mm; A', A'', B', D', E', F', G-K, L', 0.1 mm.

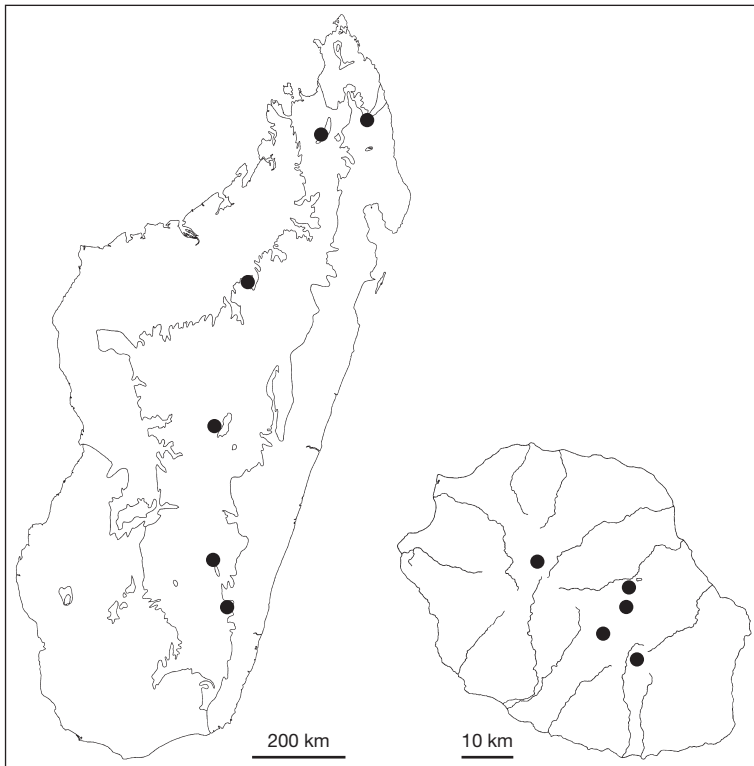


FIG. 32. — Distribution of *Nothoperanema squamiseta* (Tagawa) Ching in Madagascar and la Réunion.

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