

# An update of the revision of *Cyathea* subgen. *Alsophila* sect. *Gymnosphaera* (Cyatheaceae) in Madagascar and the Comoros including a discussion of putative hybridization events

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## ABSTRACT

A new revision of *Cyathea* sect. *Gymnosphaera* in Madagascar and the Comoros is proposed. Two new species, *Cyathea impolita* Rakotondr. & Janssen and *C. rouhaniana* Rakotondr. & Janssen, as well as a new variety, *C. impolita* var. *micheelii* Rakotondr. & Janssen are described. As opposed to all other members of the section in the region, *C. rouhaniana* does not possess bullate scales nor a dense indument on the adaxial face of the costae and costulae; the fertile basal pinnae of each leaf are more rapidly caducous than the sterile pinnae and sori include abundant paraphyses longer than the sporangia. *C. impolita* and its variety *micheelii* have dull, medium brown scales at their petiole base, isomorphic fertile and sterile pinnae and sori usually distributed over the entire abaxial surface in fertile leaves. The variety *micheelii* differs from the typical variety by the presence of aplebia. We provide original photos of the habit and trunk apex of each species that complement previously published descriptions. Putting more emphasis on soral paraphyses and lamina cutting for taxon delimitation allowed us to better circumscribe the three entities of the former *C. bullata* complex, now renamed to *C. boiviniiformis*, as well as to clarify the identity of *C. poolii*. A new key for determination and updated distribution maps are provided. Putative instances of hybridisation between closely related sympatric taxa are documented for the first time in Madagascan Cyatheaceae.

## KEY WORDS

Cyatheaceae,  
*Alsophila*,  
*Cyathea*,  
*Gymnosphaera*,  
Madagascar,  
Comoros,  
distribution maps,  
hybridization,  
new species,  
new variety.

## RÉSUMÉ

Mise à jour de la révision de *Cyathea* subgen. *Alsophila* sect. *Gymnosphaera* (*Cyatheaceae*) à Madagascar et aux Comores et discussion sur des cas d'hybridation présumée.

Une nouvelle révision de la section *Gymnosphaera* du genre *Cyathea* à Madagascar et aux Comores est proposée. Deux nouvelles espèces, *Cyathea impolita* Rakotondr. & Janssen et *C. rouhaniana* Rakotondr. & Janssen, ainsi qu'une variété nouvelle, *C. impolita* var. *micheelii* Rakotondr. & Janssen sont décrites. *C. rouhaniana*, à l'inverse de tous les autres représentants de la section dans la région, ne possède ni écailles bulleuses ni tomentum dense sur la face adaxiale des costae et costulae; les pennes basales fertiles de ses frondes sont plus rapidement caduques que les stériles et les sores renferment des paraphyses abondantes, plus longues que les sporanges. *Cyathea impolita* et sa variété *micheelii* possèdent à la base du pétiole des écailles ternes, de couleur brun moyen; les pinnules stériles et fertiles sont isomorphes et les sores sont répartis sur toute ou presque toute la longueur de la fronde fertile. La variété *micheelii* se différencie de la variété typique par la présence d'aphlébies. Des photos originales du port et du point végétatif de chaque espèce viennent compléter les descriptions précédemment publiées. Une meilleure prise en compte du critère des paraphyses et de la découpe du limbe dans la description des taxons nous permet d'apporter un éclairage nouveau sur la délimitation des trois entités de l'ancien complexe *C. bullata* renommé *C. boiviniformis* et sur l'identité de *C. poolii*. Une nouvelle clé de détermination et des cartes de distribution actualisées sont proposées. Des cas d'hybridation présumée entre taxons affins et sympatriques sont mis en évidence pour la première fois chez les *Cyatheaceae* de Madagascar.

## MOTS CLÉS

*Cyatheaceae*,  
*Alsophila*,  
*Cyathea*,  
*Gymnosphaera*,  
Madagascar,  
Comores,  
cartes de distribution,  
hybridation,  
espèces nouvelles,  
variété nouvelle.

## INTRODUCTION

*Cyathea* sect. *Gymnosphaera* (Blume) Holttum (Holttum & Edwards 1983; see Rakotondrainibe & Lobreau-Callen [1999] for a discussion of classifications) is well represented in Madagascar and the Comoros. The taxa of this section constitute a monophyletic lineage (Janssen *et al.* unpubl. data) and share the following morphological characters: exindusiate sori, frequent presence of usually well-developed aplebia near the bases of the petioles, and major axes (i.e. petiole, rachis and costae) dark brown to dark chestnut coloured. Bonaparte (1920) accepts seven Madagascan species of this section placing them in the genus *Alsophila* R.Br. In 1932, Christensen excludes two of Bonaparte's species from *Alsophila*, *A. baronii* Baker and *A. simulans* Baker, and only retains four species for Madagascar

and the Comoros: *A. boivinii* Mett. ex Ettingsh., *A. madagascariensis* Bonap. and *A. poolii* C. Chr. However, being aware of close affinities among these taxa and a very limited material available at that time, Christensen states that this can only be a preliminary treatment. Tardieu-Blot (1951) recognizes seven species in Madagascar and the Comoros which are placed in the genus *Gymnosphaera* Blume, but one of these, *C. melleri* (Baker) Tardieu, has been excluded from *Gymnosphaera* by Holttum (1981). After an extensive period of fieldwork in Madagascar, Rakotondrainibe & Lobreau-Callen (1999) publish a revision of *Cyathea* sect. *Gymnosphaera* including seven taxa, five species and two varieties. Further inventory campaigns conducted between 2000 and 2004 resulted in the present treatment. Two new species, *Cyathea impolita* Rakotondr. & Janssen and *C. rouhaniana* Rakotondr. & Janssen,

as well as one new variety, *C. impolita* var. *michellii* Rakotondr. & Janssen, are recognized and the habit of all species could be documented photographically complementing previously published descriptions (Rakotondrainibe & Lobreau-Callen 1999). The observation of an increased number of herbarium specimens and plants *in situ* has enabled us to appreciate the importance of characters pertaining to soral paraphyses and the degree of dissection of the lamina. This has helped in the clarification of the identity of *C. poolii* and the delimitation of the three varieties of the *C. bullata* complex for which the new name *C. boiviniiformis* is proposed here. Based on Rakotondrainibe & Lobreau-Callen (1999) a new determination key and updated distribution maps are proposed. We will furthermore discuss several putative hybridization events among the generally closely related and often sympatric taxa of this section.

MATERIAL AND METHODS

All relevant specimens, posterior and anterior to Rakotondrainibe & Lobreau-Callen (1999), deposited at P as well as selected specimens from B, BM, G, K, M, MO, TEF and W have been examined. Nomenclature, updated distribution and ecology, as well as new specimens are given for each taxon. If changes in determinations occurred due to a more precise delimitation of certain taxa and the creation of new species, the respective specimens are cited in an “excluded material” section under the name to which they were assigned in Rakotondrainibe & Lobreau-Callen (1999) together with a reference to the taxon of their current assignment where they are included in the “new material” section. We adopted the terminology proposed by Humbert (1955) for the phytogeographic divisions of Madagascar.

KEY TO THE SPECIES OF *CYATHEA* SECT. *GYMNOSPHAERA* IN MADAGASCAR AND THE COMOROS

1. Lamina bipinnate-pinnatifid in its sterile part, i.e. bipinnate with the sterile pinnules divided up to 2/3 down to the costula; sterile pinnules 1.4-4 cm long ..... 2  
 — Lamina bipinnate-pinnatisect to tripinnate in its sterile part, i.e. bipinnate with the sterile pinnules divided down to the costula, the proximal segments petiolulate to sessile, the distal segments broadly adnate to the costula; sterile pinnules 6-14 cm long ..... 3
2. Leaf 30-80 cm long; fertile and sterile pinnules isomorphic or subdimorphic ... *C. alticola*  
 — Leaf 1.5-2 m long; fertile and sterile pinnules strongly dimorphic ..... *C. andohabelensis*
3. Adaxial face of costae and costulae glabrous or only with sparse, rather soft hairs; bullate scales absent from the abaxial face of these axes; sterile pinnule segments more or less deltoid and with an acute apex ..... *C. rouhaniana*  
 — Adaxial face of costae and costulae with a dense indument of more or less stiff, antrorse, crispate hairs; bullate scales present on the abaxial face of these axes; sterile pinnule segments elliptic to oblong and with a rounded to obtuse apex ..... 4
4. Scales at the base of the petiole sparse, contiguous to slightly overlapping, strongly coriaceous, triangular to deltoid, with a more or less caudate apex, black, shiny, with a very narrow, erose, light brown margin ..... *C. poolii*  
 — Scales at the base of the petiole densely imbricate, subcoriaceous, narrowly triangular with a long caudate apex, bicolorous, centre dark brown to black, margin well developed, erose, light brown ..... 5
5. Scales at the petiole base narrowly triangular to linear, usually medium brown, dull; lamina fertile (almost) over its entire length; fertile and sterile pinnules isomorphic to subdimorphic; aplebia at the base of the petiole present or absent ..... *C. impolita*  
 — Scales at the petiole base narrowly triangular, usually dark brown to black, shiny; fertile pinnules restricted to the lower half of the lamina; fertile and sterile pinnules dimorphic; aplebia at the base of the petiole always present ..... *C. boiviniiformis*

SYSTEMATICS

1. *Cyathea alticola* (Tardieu) Tindale  
(Fig. 1F)

*Contributions from the New South Wales National Herbarium* 2: 331 (1956); Rakotondrainibe & Lobreau-Callen, *Adansonia*, sér. 3, 21 (1): 141 (1999). — *Alsophila alticola* (Tardieu) R.M. Tryon, *Contributions from the Gray Herbarium* 200: 29 (1970). — *Gymnosphaera alticola* Tardieu, *Le Naturaliste malgache* 3: 76, pl. 2 (1951); Tardieu in Humbert, *Flore de Madagascar et des Comores*, fam. 4: 34 (1951). — Type: Madagascar, sommet oriental du massif du Marojejy, XII.1948, *Humbert* 22670 (holo-, P!; iso-, P!, K!).

DISTRIBUTION AND ECOLOGY

Madagascar, Province d'Antsiranana, endemic to the Marojejy massif. From 1900 to 2100 m (Fig. 2).

2. *Cyathea andohabelensis* (Tardieu) Tindale  
(Fig. 1A, A')

*Contributions from the New South Wales national herbarium* 2: 331 (1956). — *Cyathea andohabelensis* (Tardieu) Rakotondr. in Rakotondrainibe & Lobreau-Callen, *Adansonia*, sér. 3, 21 (1): 141 (1999), *comb. superfl.* — *Alsophila*

*andohabelensis* Tardieu, *Bulletin de la Société botanique de France* 88: 683 (1941). — *Gymnosphaera andohabelensis* (Tardieu) Tardieu in Humbert, *Flore de Madagascar et des Comores*, fam. 4: 34, fig. 4 (1-3) (1951). — Type: Madagascar, massif de l'Andohahela, X.1928, *Humbert* 6094 (holo-, P!; iso-, P!).

NEW MATERIAL EXAMINED. — **Madagascar.** Province de Fianarantsoa, Réserve spéciale du Pic d'Ivohibe, 1250-1580 m, 24.IV.2005, *Janssen et al.* 2812 (MO, P), *Janssen et al.* 2813 (P, TEF), *Janssen et al.* 2814 (MO, P, TEF). — Parc national de Ranomafana, forêt de Talataky, 1010 m, 26.IV.2005, *Janssen et al.* 2833 (P). — Parc national de Ranomafana, 900 m, 10.XII.2000, *Rabarimanarivo & Rakotoarimanana* 203 (P). — Province de Fianarantsoa, forêt d'Andrambovato, 1100 m, 13.X.2000, *Rakotondrainibe et al.* 5974 (K, P, TEF).

DISTRIBUTION AND ECOLOGY

Madagascar, endemic to the meridional part of the Central Domain, i.e. between the latitudes of Tolanaro and Fianarantsoa. Dense, evergreen rain-forest, from (900) 1100 to 1700 m (Fig. 2).

3. *Cyathea boiviniiformis*  
Rakotondr. & Janssen, nom. nov.  
(Fig. 1B, B')

KEY TO THE VARIETIES OF *CYATHEA BOIVINIIFORMIS*

1. Segments of the sterile pinnules (ultimate segments of the leaf) pinnatifid, i.e. divided up to 2/3 down to their midrib, rarely with a crenate margin only; 8-14 pairs of proximal pinnule segments free, most of these petiolulate ..... *C. boiviniiformis* var. *lobata*
- Segments of the sterile pinnules (ultimate segments of the leaf) with a sinuate to crenulate margin; 1-6 pairs of proximal pinnule segments free, petiolulate to sessile, all others confluent ..... 2
2. Lamina herbaceous to subcoriaceous; veins not salient on the abaxial face, usually coloured like the rest of the lamina; 3-6 pairs of proximal pinnule segments free, shortly petiolulate or sessile ..... *C. boiviniiformis* var. *boiviniiformis*
- Lamina subcoriaceous to coriaceous; veins salient on the abaxial face, of a paler colour than the rest of the lamina; 1 or 2 (3) pairs of proximal pinnule segments free, sessile to adnate ..... *C. boiviniiformis* var. *madagascarica*

3a. *Cyathea boiviniiformis*  
Rakotondr. & Janssen var. *boiviniiformis*

*Alsophila boivini* Mett. ex Ettingsh., *Die Farnkräuter der Jetztwelt*: 220 (1865); Christensen, *Dansk Botanisk Arkiv* 7: 38, pl. 8, figs 5-11 (1932). — *Gymnosphaera*

*boivini* (Mett. ex Ettingsh.) Tardieu in Humbert, *Flore de Madagascar et des Comores*, fam. 4: 41 (1951). — Type: Ins. Comores, *Boivin s.n.* (holo-, W!); Comores, Grande Comore, versant ouest du massif du Karthala, piste menant de Boboni à Convalescence, alt. 1000 m, 19.XI.2002, *Rakotondrainibe et al.* 6732 (epi-, P! [4 sheets], here designated).

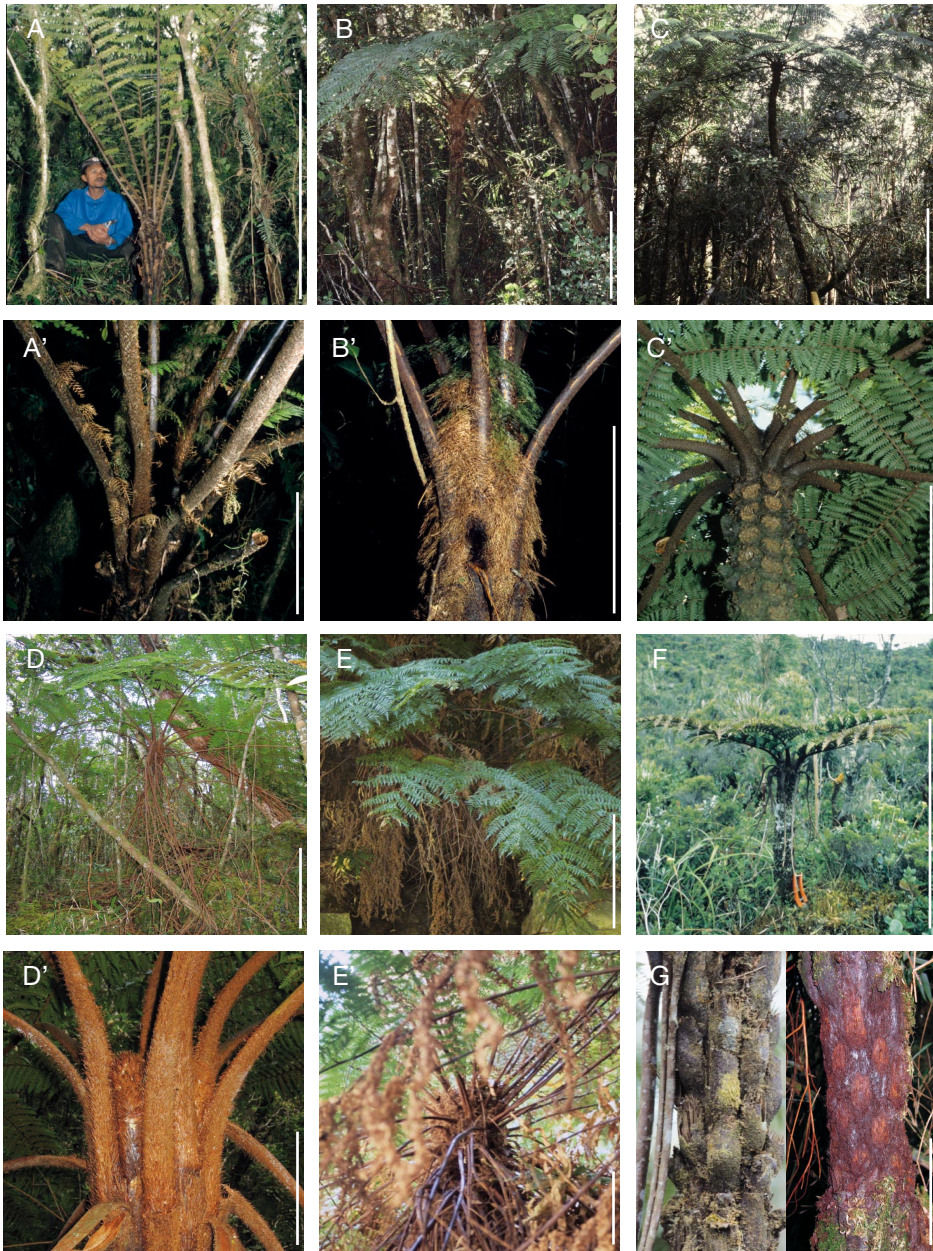


FIG. 1. — Photographic documentation of field characters: habit (A-E), and shoot apex (A'-E') are shown for each species; A, A', *Cyathea andohahelensis* (Tardieu) Rakotondr.; B, B', *C. boiviniiformis* Rakotondr. & Janssen s.l.; C, C', *C. poolii* (C.Chr.) Domin; D, D', *C. impolita* Rakotondr. & Janssen; E, E', *C. rouhaniiana* Rakotondr. & Janssen; F, *C. alticola* (Tardieu) Rakotondr., habit; G, trunk surfaces in sect. *Gymnosphaera* are more or less uniform and typically covered by persistent petiole bases like in *C. boiviniiformis* (left) and *C. impolita* with the petiole bases partly removed (right). A, A', Rakotondrainibe et al. 4185; B, Janssen et al. 2844; B', Rakotondrainibe et al. 2061; C, Janssen et al. 2846; C', uncollected; D, D', Janssen et al. 2592; E, E', uncollected; F, Rakotondrainibe et al. 3686; G, left, uncollected; right, Janssen et al. 2596. Vouchers at P. Scale bars: A-F, 1 m; A'-E', G, 10 cm. Photos D, D', E, G (right) by G. Rouhan, MNHN.

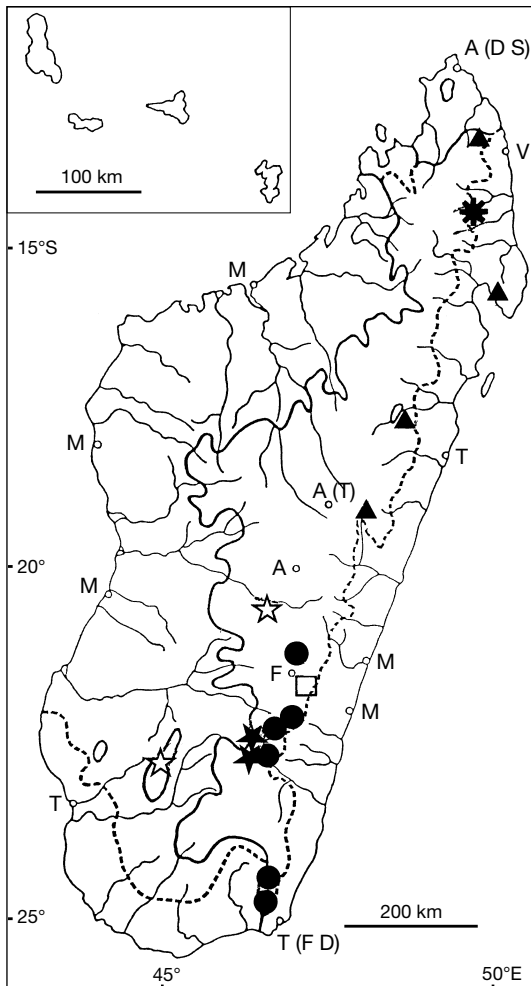


FIG. 2. — Distribution of *Cyathea* sect. *Gymnosphaera* in Madagascar and the Comoros: \*, *C. alticola*; ●, *C. andohahelensis*; ☆, *C. rouhaniana*; ▲, *C. impolita* var. *impolita*; □, *C. impolita* var. *michellii*, ▲, *C. boiviniformis* var. *madagascariaca*.

*Alsophila castanea* Baker, *Journal of Botany (Hooker)* 29: 3 (1891). — Type: Madagascar, Mont Bekilus, nord-ouest de Madagascar, XII.1892, *Last s.n.* (holo-, K!).

NEW MATERIAL EXAMINED. — **Madagascar.** Province d'Antsiranana. Presqu'île Masoala, Ambanizana, 1100 m, 23.X.2004, *Janssen et al.* 2497 (MO, P, TEF). — Province de Toamasina, réserve de Betampona, Rendriendry, 500 m, 7.XI.2004, *Janssen et al.* 2540 (MO, P, TEF). — Mont Taolana, vers 1600 m, 9.IV.1941, *Jardin Botanique* 4547 (P). — Mont Tsitondroina, vers 1800 m, 16.IV.1941, *Jardin Botanique* 4787 (P). — Province de Fianarantsoa, forêt de Vinanitelo, 1000-1200 m, 29.X.2000, *Rako-*

*tondrainibe et al.* 6163 (P). — Province de Toamasina, Parc national de Zahamena, 910-1020 m, 2.X.2002, *Rasolobery* 637 (P).

EXCLUDED MATERIAL. — *Decary* 16419 (P); *Humbert & Cours* 17822 (type of *Alsophila melanotricha* Tardieu); *Rakotondrainibe* 3055; *Rakotondrainibe & Raharimalala* 2654 and 2674; *Rakotondrainibe & Randriambololona* 4334; *Randriambololona* 273bis; *van der Werff & McPherson* 1349; see *C. boiviniformis* var. *lobata*. — *d'Alleizette* 59 and 106; *Rakotondrainibe* 438 and 3565; see *C. boiviniformis* var. *madagascariaca*. — *Humbert* 28214; *Labat et al.* 2393; see *C. rouhaniana*.

#### DISTRIBUTION AND ECOLOGY

Madagascar (Central Domain, from northern to southern sector) and Comoros (Anjouan and Grande Comore), endemic. Dense evergreen rainforest, from (500) 800 to 1900 m (Fig. 3).

#### TIPIFICATION AND SYNONYMY

The holotype specimen, *Boivin s.n.* (W!), of *Alsophila boivinii* Mett. ex Ettingsh. contains a single pinna, not attached to a rachis fragment. This pinna is fertile in its proximal half only. The lamina is herbaceous, costae and costulae have a dense indument of antrorse hairs on their adaxial face and sparse bicolorous lanceolate as well as more abundant bullate scales on their abaxial face. Fertile and sterile pinnules are dimorphic with fertile segments 0.4-0.5 cm broad having dentate margins and sterile segments 0.5 cm broad having subentire margins. Up to six proximal pairs of pinnule segments are free. Sori are exindusiate and the receptacle carries hairy paraphyses that are shorter than the sporangia.

Due to the fragmentary nature of the material, scale characters and the distribution of fertile pinnules on the lamina cannot be assessed and the holotype specimen thus cannot be unambiguously distinguished from *C. impolita* s.l. and *C. poolii*. We therefore consider it necessary to designate an epitype and choose *Rakotondrainibe et al.* 6732 which has been collected on the Comoros, comprises petiole, fertile and sterile middle pinnae as well as a leaf apex and which is morphologically identical to the holotype of *A. boivinii* in all observable characters.

*Cyathea bullata* has been removed from synonymy after re-examination of the type specimen for reasons detailed at the end of this treatment under

the heading "doubtful species". The epithet *bullata* is hence no longer available to designate this taxon and *A. boivini* had to be combined under *Cyathea* choosing a replacement name because the name *Cyathea boivini* Mett. ex Kuhn (*Filices Africanae*: 161 [1868]), a Madagascan taxon, already exists. The epithet *castanea* is unavailable in *Cyathea* as well because of the description of the South American *C. castanea* Baker (*Synopsis Filicum*: 451 [1874]).

3b. *Cyathea boiviniiformis*

Rakotondr. & Janssen

var. *lobata* (Rakotondr.)

Rakotondr. & Janssen, comb. nov.

*Cyathea bullata* (Baker) Domin. var. *lobata* Rakotondr. in Rakotondrainibe & Lobreau-Callen, *Adansonia*, sér. 3, 21 (1): 147, fig. 4 (1999). — Type: Madagascar, massif d'Anjanaharibe-Nord, XII.1950, *Humbert, Capuron & Cours 24683* (holo-, P!; iso-, P!).

*Alsophila melanotricha* Tardieu, *Bulletin de la Société botanique de France* 88: 684, pl. 2, figs 2, 3 (1941). — *Gymnosphaera melanotricha* (Tardieu) Tardieu in *Humbert, Flore de Madagascar et des Comores*, fam. 4: 36 (1951). — *Cyathea melanotricha* (Tardieu) Tindale, *Contributions from the New South Wales National Herbarium* 2: 331 (1956). — Type: Madagascar, massif de l'Andrangovallo, réserve de Zahamena, 1400-1500 m, X.1937, *Humbert & Cours 17822* (lecto-, P!, here designated; isolecto-, P! [4 sheets]).

NEW MATERIAL EXAMINED. — Madagascar. Province de Toamasina, Andasibe, forêt d'Ambatovy, 1131 m, 3.II.2005, *Antilabimena et al. 3286* (P). — Province d'Antsiranana, massif du Manongarivo, 1610 m, 26.VIII.2004, *Janssen et al. 2394* (MO, P, TEF). — Massif du Manongarivo, 1625 m, 27.X.2004, *Janssen et al. 2405* (MO, P, TEF). — Presqu'île de Masoala, Ambanizana, 620-1109 m, 23.X.2004, *Janssen et al. 2498* (MO, P, TEF); *Janssen et al. 2499* (P, TEF). — Province de Toamasina, Parc national de Mantadia, 930-1000 m, 12.XII.2004, *Janssen et al. 2574* (MO, P, TEF). — Province de Fianarantsoa, Mandriandry, 750 m, 26.X.2000, *Rabarinarivo & Rakotoharimanana 73* (P). — Province de Fianarantsoa, massif de l'Andringitra, 800 m, 19.V.1995, *Rakotondrainibe & Raharimalala 2654* (P, TEF). — *Idem*, 20.V.1995, *Rakotondrainibe & Raharimalala 2674* (P, TEF). — Province de Toliara, Tolanaro, massif d'Andohahela, 1100 m, 8.XI.1995, *Rakotondrainibe 3055*. — Province de Fianarantsoa, corridor forestier entre les massifs d'Andringitra et d'Ivohibe, 1150-1300 m, 9.XI.1997, *Rakotondrainibe & Randriambololona 4344* (P). — Province de Fianarantsoa, forêt d'Andrambovato,

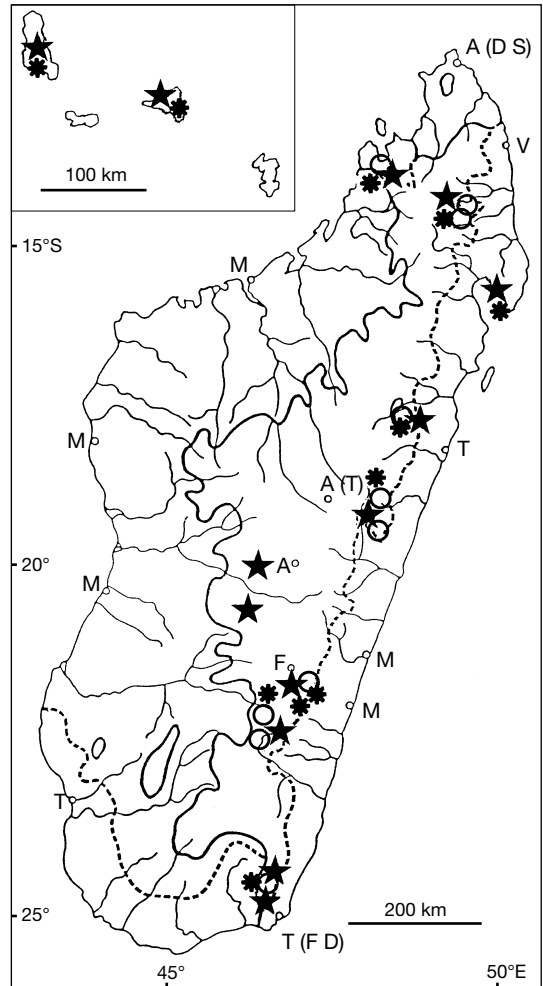


FIG. 3. — Distribution of *Cyathea* sect. *Gymnosphaera* in Madagascar and the Comoros: ○, *C. poolii*; ★, *C. boiviniiformis* var. *boiviniiformis*; ★, *C. boiviniiformis* var. *lobata*.

1100 m, 13.X.2000, *Rakotondrainibe et al. 5971* (P), *Rakotondrainibe et al. 5977* (P, TEF), *Rakotondrainibe et al. 5978* (P, TEF), *Rakotondrainibe et al. 6002* (P). — *Idem*, 16.X.2000, *Rakotondrainibe et al. 6035* (K, P). — Province de Fianarantsoa, forêt de Vinanitelo, 1100 m, 23.X.2000, *Rakotondrainibe et al. 6090* (P). — *Idem*, 24.X.2000, *Rakotondrainibe et al. 6091* (K, P). — Province de Fianarantsoa, Ranomafana, forêt de Vatoharanana, 980 m, 16.XI.1994, *Randriambololona 273bis* (P). — Province d'Antsiranana, Masoala, 430 m, 18.II.2001, *Rasolobery 314* (P). — Province d'Antsiranana, massif du Manongarivo, env. 1100 m, 17.X.1994, *van der Werff & McPherson 13496* (P). — Province de Toamasina, Andasibe, forêt de Mantadia, 900 m,

3.XI.1994, *van der Werff & McPherson 13614* (P). — *Idem*, 7.XI.1994, *van der Werff & McPherson 13725* (P).  
**Comoros.** Grande Comore, massif du Karthala, 900-1400 m, 4.XII.1967, *Bernardi 11712* (P). — Nioubadjou, 28.XI.1975, *Coulon 263* (P). — Massif du Karthala, 1000 m, 19.XI.2002, *Rakotondrainibe et al. 6731* (P).  
 Anjouan, VII.1940, *Decary 16419* (P).

#### DISTRIBUTION

Madagascar (within the boundaries of a triangle formed by the cities of Tolanaro in the SE, Maroantsetra in the NE and Ambanja in the NW) and Comoros (Grande Comore and Anjouan), endemic. Dense evergreen rainforest, from 800 to 1800 m (Fig. 3).

#### REMARKS

Reconsidering the delimitation of the varieties of *C. boiviniiformis* (new name for *C. bullata*) after analysis of a considerable amount of new specimens, more emphasis was put on lamina cutting. As a result, the variety *lobata* differs from the typical variety and var. *madagascariensis* not only by its crenate to pinnatifid pinnule segments, but also by an increased number (8 to 14) of free, petiolulate to sessile, proximal pinnule segments. Taking into account the latter character, *Alsophila melanotricha* Tardieu has been transferred from *C. boiviniiformis* var. *boiviniiformis* to var. *lobata*. As this transfer was necessary for several specimens, the area of distribution of *C. boiviniiformis* var. *lobata* is considerably expanded with respect to Rakotondrainibe & Lobreau-Callen (1999).

#### TYPEIFICATION

Type material of *Alsophila melanotricha* Tardieu could not be traced at B, BM, G, K, M, MO, TEF, W and we hence suppose that all sheets of *Humbert & Cours 17822* are currently at P. Five sheets have been found (P00134646, P00134647, P00134648, P00134649 and P00547066), all carrying the determination “(*Alsophila*) *Gymnosphaera melanotricha* Tardieu” in Tardieu’s hand. Tardieu usually designated holotype specimens with the annotation “type”, which is lacking from all sheets. Diameters of petioles and rachises suggest that the material of this collection pertains to several different leaves, or even to different individuals. Humbert wrote on one label “voir autres parts complétant ce spécimen”. Despite this remark and considering the slight heterogeneity of

the material, we choose the sheet P00134647 as lectotype of *Alsophila melanotricha* Tardieu. This sheet contains the petiole, a middle pinna and an apex, presumably from the same leaf.

#### 3c. *Cyathea boiviniiformis*

Rakotondr. & Janssen

var. *madagascariensis* (Bonap.)

Rakotondr. & Janssen, comb. nov.

*Alsophila madagascariensis* Bonap., *Notes ptéridologiques* 5: 53 (1917); Christensen, *Dansk Botanisk Arkiv* 7: 39, pl. 8, fig. 12-19 (1932). — *Cyathea malegassica* (Bonap.) Domin, *Acta Botanica Bohemica* 9: 133 (1930), nom. nov. — *Gymnosphaera madagascariensis* (Bonap.) Tardieu in Humbert, *Flore de Madagascar et des Comores*, fam. 4: 35 (1951). — *Cyathea bullata* (Baker) Rakotondr. var. *madagascariensis* (Bonap.) Rakotondr. in Rakotondrainibe & Lobreau-Callen, *Adansonia*, sér. 3, 21 (1): 146 (1999). — Type: Madagascar, forêt d’Analamaitso, VIII.1907, *Perrier de la Bâthie 7640* (lecto-, P!, designated by Rakotondrainibe & Lobreau-Callen 1999; isolecto-, P!).

NEW MATERIAL EXAMINED. — **Madagascar.** Ambatolaona, VIII.1906, *d’Alleizette 59* (P). — La Mandraka, VIII.1906, *d’Alleizette 106* (P). — Province de Toamasina, Monokambo, Varaina, vers 1200 m, 17.I.1947, *Cours 2384* (P). — Province de Toamasina, Sahalampy, colline du sud-ouest, 18.I.1945, *Cours 2410* (P). — Province de Toamasina, Ambatoharanana près d’Antsevabe, 1000 m, 6.III.1951, *Cours 4125* (P). — Province d’Antsiranana, presqu’île Masoala, Ambanizana, 620-1109 m, 23.X.2004, *Janssen et al. 2501* (MO, P, TEF), *Janssen et al. 2502* (P, TEF). — Province d’Antananarivo, forêt d’Ambohitantely, 1200-1650 m, 24.II.1984, *Rakotondrainibe 438* (P, TEF). — Province d’Antsiranana, forêt de Betaolana, 1200 m, 16.X.1999, *Rakotondrainibe & Florens 4935* (P, TEF). — Province d’Antsiranana, massif du Marojejy, 1150 m, 23.X.2001, *Rakotondrainibe & Rasolohery 6357* (K, P, TEF). — Province d’Antsiranana, forêt de Binara, 1000 m, 9.XI.2001, *Rakotondrainibe & Rasolohery 6550* (P). — Province de Toamasina, Zahamena, 650 m, 11.VI.2001, *Rasolohery 468* (P). — *Idem*, 13.VI.2001, *Rasolohery 527* (P). — *Idem*, 1350-1450 m, 15.VII.2002, *Rasolohery et al. 677* (P). — Province de Toamasina, massif d’Ankiridro, 671 m, 1.II.1999, *Schatz et al. 3923* (P).

#### DISTRIBUTION

Madagascar (Central Domain, northern and middle sectors; north of the latitude of Antananarivo), endemic. Dense evergreen rainforests, 600-1650 m. (Fig. 2).



REMARKS

This taxon must not be confounded with the bipinnate Madagascan endemic *Cyathea madagascanica* Bonap.

4. *Cyathea impolita*

Rakotondr. & Janssen, sp. nov.  
(Figs 1D, D'; 4)

KEY TO THE VARIETIES OF *CYATHEA IMPOLITA*

- Aphlebia absent from the bases of the petioles of all leaves of the same plant ..... *C. impolita* var. *impolita*
- 1 or 2 pairs of aphlebia present at the bases of the petioles of a majority of leaves of the same plant ..... *C. impolita* var. *ichelii*

4a. *Cyathea impolita* Rakotondr. & Janssen  
var. *impolita*

*A Cyathea boiviniiformis* (Baker) Domin *sensu lato*, *squamarum colore ad petioli basin, brunei medio impolitisque vs. brunei nigro politoque pinnis aphlebioidis nullis ad petioli basin, bene dimorpho inter fertilibus sterilibusque pinnularum nullo, et fertilibus pinnarum positione vel quasi ubique frondis amplitudine, differt.*

TYPUS. — Madagascar. Province de Fianarantsoa, massif de l'Andringitra, 1800 m, 20.XI.2004, *Janssen et al.* 2602 (holo-, P [3 sheets]!; iso-, P!, TEF!).

PARATYPES. — Madagascar. Province de Fianarantsoa, Parc national d'Andringitra, forêt d'Imaitso, 1580-1650 m, 18.XI.2004, *Janssen et al.* 2592 (MO, P, TEF). — Province de Fianarantsoa, Parc national d'Andringitra, forêt d'Anjavidilava et descente vers le camp Imaitso, 1800-2000 m, 19.XI.2004, *Janssen et al.* 2596 (MO, P, TEF). — Province de Fianarantsoa, Ambalavao, massif de l'Andringitra, versant est, 1650 m, 30.V.1995, *Rakotondrainibe & Rabarimalala* 2738 (P, TEF). — Province de Fianarantsoa, corridor forestier entre le massif de l'Andringitra et le pic d'Ivohibe, à 8 km au nord-est du village d'Ivohibe, 1150-1300 m, *Rakotondrainibe & Randriambololona* 4316 (P, TEF).

DESCRIPTION

Trunk up to 4.5 m tall, diameter 8 cm, covered at least in its upper half by persistent dead petiole bases; dead leaves persistent for some time and hanging from the trunk apex; leaf scars ovate to elliptic, 2.5-5 × 3-4.5 cm.

Petiole dark brown to ochre, 25-60 cm long, bearing at its base a coating of densely imbricate scales, individual scales 0.8-1.3 cm long, narrowly triangular to linear, their apex long caudate; scale centre coriaceous to subcoriaceous, brown to black, narrow; scale margin light brown, erose, ochre to

medium brown, dull, more or less well developed. Aphlebia absent from the basal part of the petioles of all leaves.

Lamina herbaceous to subcoriaceous, 120-210 cm long, bipinnate-pinnatisect to tripinnate, bearing 10-13 pairs of lateral pinnae, middle pinnae 45-75 cm long, their apex crenate to lobate and more or less caudate. Pinnules 8-10 cm long, their apex caudate in the upper 1.5-2 cm. Pinnule segments elliptic, margin crenate, 4-10 proximal segments free, petiolulate or sessile, segments progressively adnate and then confluent towards the pinnule apex. Fertile and sterile pinnules isomorphic or subdimorphic; sori usually distributed over all or almost all pinnae of a leaf, sometimes with the exception of the apical or basal 1 or 2 pinna pairs. Rachis, costae and costulae ochre. On the adaxial face of the costae, costulae and veins an indument of ochre to reddish brown, thick and dense multicellular hairs; on the abaxial face with two types of scales, narrowly triangular, bicolorous scales with a light brown erose margin and whitish, bullate scales.

Sori in median position between segment margin and middle vein, exindusiate. Numerous filiform, pluricellular, uniseriate paraphyses present on the receptacle, shorter than the sporangia. Spores trilete.

DISTRIBUTION AND ECOLOGY

Madagascar, Central domain, middle sector; endemic to the region of the nature reserves of Andringitra and Pic d'Ivohibe. Dense evergreen rainforests, from 1100 to 1900 m (Fig. 2).

AFFINITIES

*Cyathea impolita* differs from *C. boiviniiformis* and its varieties by the colour of its scales at the base of the

petiole that are medium brown and dull, not shiny blackish brown to black. Furthermore, it is distinct by the absence of a marked dimorphism between fertile and sterile pinnules as well as the distribution of fertile pinnae over the entire or almost the entire length of the lamina. The densely imbricate arrangement of the scales at the base of the petiole, their narrowly triangular form, and their dull brown colour distinguish *C. impolita* from *C. poolii*, which has contiguous to sparse deltoid, shiny black scales.

#### ETYMOLOGY

The epithet *impolita* alludes to the characteristic colour of the scales at the base of the petiole that have a dull brown appearance to the unaided eye.

4b. *Cyathea impolita* Rakotondr. & Janssen  
var. *michelii* Rakotondr. & Janssen, var. nov.

*A Cyathea impolita* var. *impolita* differt pinnis aplebioidis 1-2 paribus prope basin petioli instructis.

**TYPUS.** — **Madagascar.** Province de Fianarantsoa, forêt d'Andrambovato, à 2 km à l'ouest du village d'Andrambovato, au bord de la rivière Tatamaly, 1000 m, 18.X.2000, *Rakotondrainibe et al.* 6060 (holo-, P!; iso-, TEF!).

**PARATYPES.** — **Madagascar.** Province de Fianarantsoa, forêt d'Andrambovato, au bord de la rivière Tatamaly, 1000 m, 13.X.2000, *Rakotondrainibe et al.* 5966 (K, MO, P). — *Idem*, 1100 m; 17.X.2000, *Rakotondrainibe et al.* 6036 (P).

#### DESCRIPTION

Certain specimens from Madagascar, collected in the Adrambovato forest at about 80-100 km to the northeast of the Andringitra and Ivohibe nature reserves, show the same morphological characters as the typical variety, especially the dull brown petiole scales. However, a majority of the leaves of a given individual have one to two pairs of aplebia inserted near the base of their petioles. This latter character appears to be sufficient to distinguish a new variety.

#### DISTRIBUTION AND ECOLOGY

Madagascar, Central Domain; endemic to the forest of Andrambovato, east of Fianarantsoa. Dense evergreen rainforest, from 1000 to 1100 m (Fig. 2).

#### ETYMOLOGY

This variety is dedicated to Michel Randriambololona, botanist and ecologist, who was strongly involved with biodiversity inventories of the natural forests in the Fianarantsoa Province of Madagascar.

#### 5. *Cyathea poolii* (C.Chr.) Domin (Fig. 1C, C')

*Preridophyta*: 263 (1929). — *Alsophila vestita* Baker, *Journal of the Linnean Society, Botany*, London 15: 412 (1876), *nom. illeg., non* C.Presl, *Epimeliae botanicae*: 27 (1849). — *Alsophila poolii* C.Chr., *Index Filicum*: 46 (1905); *Dansk Botanisk Arkiv* 7: 38, pl. 8, figs 20-23 (1932). — *Cyathea poolii* (C.Chr.) Rakotondr., *Adansoniana*, sér. 3, 21 (1): 141 (1999), *comb. superfl.* — Type: Madagascar, Antananarivo, IV.1876, *Pool s.n.*, (holo-, K!); Madagascar, Province de Toamasina, Parc national de Zahamena, 17°41'08"S, 48°59'43"E, 650 m, 16.VI.2001, *Rasolohery 547* (epi-, P! [2 sheets], here designated; isoepi-, MO, TEF).

*Alsophila coursii* Tardieu, *Bulletin de la Société botanique de France* 88: 684 (1941). — *Gymnosphaera coursii* (Tardieu) Tardieu in Humbert, *Flore de Madagascar et des Comores*, fam. 4: 40 (1951). — *Cyathea coursii* (Tardieu) Tindale, *Contributions from the New South Wales National Herbarium* 2: 331 (1956). — *Cyathea coursii* (Tardieu) Rakotondr., *Fieldiana, Zoology*, new series 90: 37 (1998), *comb. superfl.* — Type: Madagascar, massif de l'Andrangovallo, réserve naturelle de Zahamena, vers 1200 m, X.1937, *Humbert & Cours 17861* (holo-, P!; iso-, P!).

**NEW MATERIAL EXAMINED.** — **Madagascar.** Province d'Antsiranana, Andranomalaza, 1600 m, 22.III.1999, *Gautier 3646* (G, P). — Massif du Beampingaratra, vallée de la Maloto, 600-800 m, X-XI.1928, *Humbert 6292 p.p.* (BM, P). — Province d'Antananarivo, Ambositra, forêt d'Ambatofitorahana, 1600-1700 m, 26.VII.1928, *Humbert & Swingle 4870* (P). — Province de Toamasina, Andasibe, forêt de Mantadia, 930-1000 m, 12.XI.2004, *Janssen et al.* 2577 (MO, P, TEF). — Province de Fianarantsoa, Parc national de Ranomafana, forêt de Talatakely, 1020 m, 26.IV.2005, *Janssen et al.* 2827 (P, TEF). — Province de Fianarantsoa, Parc national de Ranomafana, forêt de Vohiparara, 1190 m, 27.IV.2005, *Janssen et al.* 2846 (MO, P, TEF). — Parc national de Ranomafana, 930 m, 9.XII.2000, *Rabanarivo & Rakotoarimanana 198* (P). — Province d'Antsiranana, Andapa, forêt de Betaolana, 1200 m, 16.X.1999, *Rakotondrainibe & Florens 4924* (MO, P, TEF), *Rakotondrainibe & Florens 4931* (P, TEF), *Rakotondrainibe & Florens 4937* (P). — Province d'Antsiranana, massif d'Anjanaharibe-

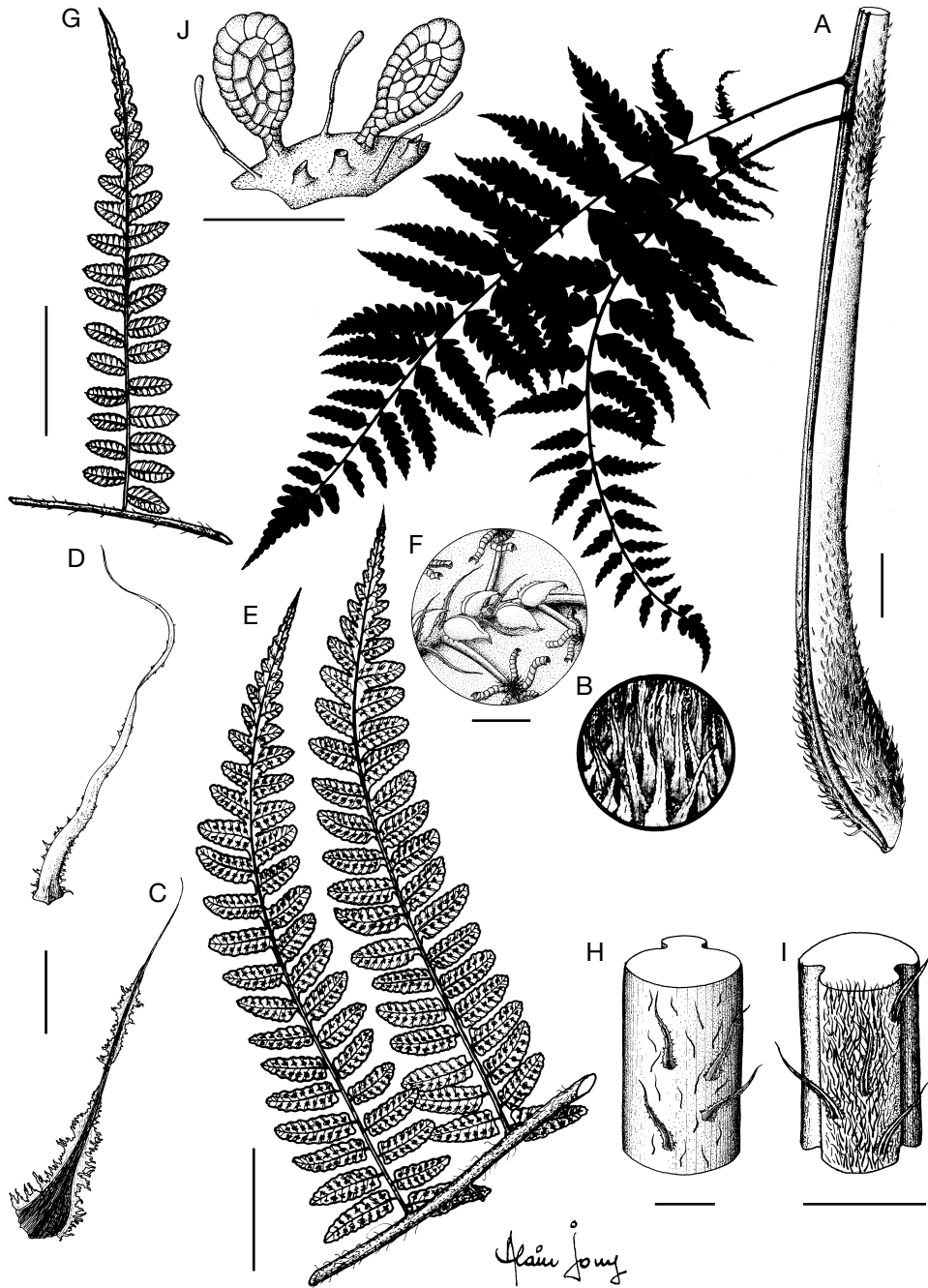


FIG. 4. — *Cyathea impolita* Rakotondr. & Janssen: **A**, petiole; **B**, imbricate arrangement of scales at the base of the petiole; **C**, **D**, morphology of scales at the base of the petiole; **E**, two fertile pinnules with a fragment of the costa; **F**, bullate scales on the abaxial face of the middle vein of a pinnule segment; **G**, pinnule of a sterile pinna at the base of the lamina with a fragment of the costa; **H**, abaxial face of a costa fragment; **I**, adaxial face of a costa fragment; **J**, sporangia and paraphyses. A-F, Janssen *et al.* 2602; G, Janssen *et al.* 2592; H-J, Janssen *et al.* 2602. Scale bars: A, E, 20 mm; C, D, G, I, 2 mm; F, 0.5 mm; H, 1 mm; J, 0.3 mm.

Sud, forêt d'Analabe, 1150-1240 m, 26.X.1999, *Rakotondrainibe* & *Florens 5058* (P, K). — *Idem*, 1150 m, 26.X.1999, *Rakotondrainibe* & *Florens 5059* (P). — *Idem*, 1140 m, 29.X.1999, *Rakotondrainibe* & *Florens 5084* (MO, P). — *Idem*, 1650 m, 6.XI.1999, *Rakotondrainibe* & *Florens 5173* (K, P). — Province de Fianarantsoa, Ranomafana-Ifanadiana, forêt de Vatoharanana, 980 m, 5.X.2000, *Rakotondrainibe* et al. 5912 (P, TEF). — *Idem*, 100-1100 m, 8.X.2000, *Rakotondrainibe* et al. 5948 (P). — Province de Fianarantsoa, forêt d'Andrambovato, 1000 m, 13.X.2000, *Rakotondrainibe* et al. 5970 (K, P), *Rakotondrainibe* et al. 5976 (P). — Province de Fianarantsoa, forêt de Vinanitelona, 1000 m, 24.X.2000, *Rakotondrainibe* et al. 6110 (P, TEF). — *Idem*, 29.X.2000, *Rakotondrainibe* et al. 6150 (K, MO, P). — Province de Fianarantsoa, Ranomafana-Ifanadiana, 1270 m, 24.XI.1994, *Randriambololona* et al. 310 (P). — Province de Toamasina, Parc national de Zahamena, 1100-1330 m, 28.I.2001, *Rasolohery 235* (P). — *Idem*, 650 m, 16.VI.2001, *Rasolohery 547* (P). — Province de Toamasina, Andasibe, forêt de Mantadia, 900 m, 3.XI.1994, *van der Werff 13615* (P).

EXCLUDED MATERIAL. — *Rakotondrainibe* & *Raharimalala 2738*; *Rakotondrainibe* & *Randriambololona 4316*: see *Cyathea impolita*.

#### DISTRIBUTION

Madagascar, Central Domain, from northern to southern sector, endemic. Dense evergreen rainforest, from (600) 800 to 1800 m (Fig. 3).

#### AFFINITIES

*Cyathea poolii* is closely related to *C. boiviniiformis* and *C. impolita* but by its basal petiole scales contiguous to slightly overlapping, strongly coriaceous, triangular to deltoid, with a very narrow light brown margin it can be easily distinguished from these two species (see the included key).

#### REMARKS

*Cyathea poolii* (= *C. coursii*) is a polymorphic species. Intraspecific variation has been discussed by Rakotondrainibe & Lobreau-Callen (1999: 149) and includes morphology and abundance of receptacular paraphyses, the degree of dimorphism between fertile and sterile pinnules as well as the distribution of sori, i.e. either all pinnae of a leaf are fertile or fertile pinnae are restricted to the lower half of the leaf. Detailed study of 24 new collections confirms the continuous nature of these

morphological variations and has not permitted to distinguish varieties within this polymorphic taxon. Morphology and arrangement of scales at the base of the petiole (see above) are stable characters usually permitting to easily determine this species despite the above-mentioned variability.

A small number of specimens, six in total, are morphologically intermediate between *C. poolii* (40 specimens seen) and *C. boiviniiformis* s.l. (60 specimens seen). These cases are supposed to be of hybrid origin and will be discussed below.

#### TYPEIFICATION AND SYNONYMY

The holotype of *Alsophila poolii* (*A. vestita*, nom. illeg.), *Pool s.n.* (K!), comprises three sheets. One contains a fertile apical part of a leaf; the other two carry each two fertile middle pinnae lacking an associated rachis fragment. Sterile pinnules and a petiole with scales are unavailable in the original material. The fertile lamina is bipinnate-pinnatisect to tripinnate in its middle part. Fertile pinnules are 4-6 cm long and 1-1.5 cm wide with the proximal pinnule segments shortly petiolulate, then progressively adnate and eventually confluent towards the pinnule apex. The adaxial face of the costae is covered by a tomentum formed of short erect hairs. Bullate scales are present on the abaxial face of the costae. Sori have numerous filiform to scaly receptacular paraphyses, that are whitish to brownish and longer than the sporangia.

The fragmentary holotype specimen led to putting into question the status of *A. poolii* in previous treatments. Christensen (1932: 38) recognized the species and observed a close affinity to *Alsophila boivinii* Mett. ex Ettingsh.: "Closely related to *A. Boivinii* and perhaps not specifically different". Tardieu-Blot (1951) disregards the species in her treatment, but describes *Alsophila coursii*. Rakotondrainibe & Lobreau-Callen (1999: 143, 144, 148) accept three species *Cyathea poolii* (= *A. poolii*), *C. bullata* (= *A. boivinii*) and *C. coursii* (= *A. coursii*). After examining an important number of new collections, some of the specimens attributed to *C. poolii* sensu Rakotondrainibe & Lobreau-Callen (1999), have been transferred to the newly described *C. impolita* and intraspecific variation of *C. coursii* and *C. boiviniiformis* (formerly *C. bullata* = *A. boivinii*) as well

as the morphological characters of the holotype of *C. poolii* have been reconsidered. The comparison of the holotype specimen of *C. poolii* with the specimens previously determined as *C. coursii* is made difficult by a pronounced polymorphism in that material. Among the studied specimens, only those in provenance of northeastern Madagascar (district d'Andapa) and of the Lac Alaotra region (district d'Ambatondrazaka, East-Central Domain), are strictly identical to the holotype of *C. poolii*. Sori are present over the entire length of the lamina, fertile and sterile pinnules are isomorphic to subdimorphic, and abundant paraphyses longer than the sporangia are present on the receptacle. An imprecise locality is indicated on the holotype specimen *Pool s.n.* ("near Antananarivo") and in spite of the lacking petiole, paraphysis characters in combination with the distribution of sori on the leaf are sufficient to justify synonymy between *C. poolii* and *C. coursii*. A complete specimen, *Rasolohery 547* (P, MO, TEF), collected in the Lac Alaotra region, has been chosen as an epitype to unambiguously establish the identity of the holotype *Pool s.n.* (K!).

### 6. *Cyathea rouhaniana*

Rakotondr. & Janssen, sp. nov.

(Figs 1E, E'; 5)

*A Cyathea boiviniiformi sensu lato, axibus (costae, costulae nervique) sine squamis bullatis, pagina supera costarum costularumque sine tomento dense, segmentis ultimis saepe triangularibus, plus raro ellipticis, pinnis fertilibus in positione basali vel subbasali in fronde, desiccatis demissisque saepe ante pinnas superiorum steriles, paraphysibus numerosissimis longioribus sporangiis, differt.*

**TYPUS.** — **Madagascar.** Province de Fianarantsoa, massif de l'Isalo, à l'entrée du Canyon des Makis, falaise rocheuse gréseuse dominant la rivière, 22.XI.2004, *Rakotondrainibe et al. 6958* (holo-, P! [6 sheets]; iso-, MO!, P!, TEF!).

**PARATYPES.** — **Madagascar.** Province de Fianarantsoa, Ambatofinandrahana, massif de l'Itremo, 1524 m, 26.XI.2004, *Birkinshaw 1393* (P). — Province de Fianarantsoa, Ouest Betsileo, montagnes à l'ouest d'Itremo, 1500-1700 m, I ou IV.1958, *Humbert 28214* (P). — Province de Fianarantsoa, Parc national de l'Isalo, canyon des Makis, 750-800 m, 22.XI.2004, *Janssen et al. 2605*

(MO, P, TEF), 2606 (MO, P, TEF). — Province de Fianarantsoa, Ambatofinandrahana, massif de l'Itremo, 1320 m, 22.XI.1993, *Labat et al. 2393*. — Province de Fianarantsoa, Ranohira, massif de l'Isalo, canyon des Makis, 750-800 m, 22.XI.2004, *Rakotondrainibe et al. 6958bis* (MO, P, TEF).

### DESCRIPTION

Trunk up to 3 m tall, 12 cm diameter, covered almost over its entire length by persistent dead petiole bases; dead leaves persistent for some time and hanging from the trunk apex; leaf scars not visible.

Petiole dark chestnut coloured to dark violaceous brown, sometimes greenish on its adaxial face, 20-60 cm long; bearing at its base numerous imbricate scales, individual scales 0.7-1.1 cm long, narrowly triangular, bicolorous, shiny brown in the centre, margin lighter, erose. One to two pairs of aplebia present near the petiole base.

Lamina herbaceous to subcoriaceous, 140-200 cm long, bipinnate-pinnatisect to tripinnate, bearing 10-15 pairs of lateral pinnae, middle pinnae 35-40 cm long, their apex pinnatifid; pinnules alternate, 8-10 × 2-3 cm, their apex long attenuate and crenulate; sterile pinnule segments alternate, their margin sinuate to crenulate, their apex acute to obtuse, proximal 1 or 2 pairs free and shortly petiolulate, elliptic to lanceolate, the following sessile to adnate and deltoid, distal segments confluent; 2-4 pairs of fertile pinnae per leaf in a basal or subbasal position, drying up rapidly after maturation of sporangia and often earlier than the sterile pinnae, caducous before these; fertile pinnule segments narrower and more deeply incised than the sterile segments. Abaxial face of rachis, costae and costulae dark violaceous brown, subglabrous, without hairs, bearing small, sparse, caducous, bicolorous, linear, lanceolate or deltoid, but never bullate scales; adaxial face of the same axes more or less greenish, glabrous or with some appressed, more or less crispate hairs, never with a dense hairy indument, also with sparse scales of the same type as on the abaxial face.

Sori exindusiate, at maturity covering the entire surface of the fertile segments. Numerous filiform to scaly paraphyses present on the receptacle, whitish to brownish, longer than the sporangia. Spores trilete.

## DISTRIBUTION AND ECOLOGY

Madagascar, Central Domain, forests of the occidental slopes, endemic. On sandstone (Isalo massif) or gneiss and quartzite (Itremo massif), from 700 to 1700 m (Fig. 2).

## AFFINITIES

Like *C. boiviniiformis* and its varieties, *C. rouhaniana* displays numerous imbricate, narrowly triangular, bicolorous scales and sterile pinnae are strongly dimorphic and the fertile pinnae restricted to the basal part of the lamina. However, it is clearly distinguished by the absence of a dense hairy indument on the adaxial face of the costae and costulae and the absence of bullate scales on the abaxial face of these axes. Its deltoid pinnule segments, the tendency of the fertile pinnae to wither and fall before the sterile pinnae, and the abundant receptacular paraphyses, that are longer than the sporangia represent further discriminative characters.

## REMARKS

Two specimens collected in the Itremo massif, *Humbert 28214* and *Labat et al. 239*, have been ascribed to *C. boiviniiformis* var. *boiviniiformis* (formerly *C. bullata* var. *bullata*) with hesitation in an earlier treatment (Rakotondrainibe & Lobreau-Callen 1999: 146) notwithstanding size and abundance of their receptacular paraphyses. The presence of such paraphyses together with the absence of bullate scales and lack of a dense hairy indument on the adaxial face of major axes let us now ascribe these specimens to the new species, *C. rouhaniana*. It should be pointed out, however, that these specimens, coming from the Itremo massif, seem to have fertile pinnae that are less precociously caducous, more coriaceous aplebia with rather stiff segments and usually narrower paraphyses as compared to the specimens collected in the Isalo massif. Considering the available specimens, we judge this variation to be minor and not justifying the recognition of separate varieties despite the fact that the two localities where *C. rouhaniana* has been found, the Isalo and Itremo massifs, are separated by an approximately 200 km wide savanna.

## ETYMOLOGY

This species is dedicated to Germinal Rouhan in acknowledgement of his contributions to the collection of numerous specimens of *Cyathea*, amongst others this new species.

## DOUBTFUL SPECIES

*Alsophila bullata* Baker

*Journal of the Linnean Society, Botany*, London 15: 412 (1876). — *Cyathea bullata* (Baker) Domin, *Pteridophyta*: 262 (1929). — *C. bullata* (Baker) Rakotondr., *Bulletin du Muséum d'Histoire naturelle*, Paris, 4<sup>e</sup> série, sect. B, *Adansonia*, 10 (4): 376 (1988), *comb. superfl.*; Rakotondrainibe & Lobreau-Callen, *Adansonia*, sér. 3, 21 (1): 141 (1999). — Type: Madagascar. "Intérieur de Madagascar", IV.1876, *Pool s.n.* (holo-, K!).

## REMARKS

The holotype of *Alsophila bullata* Baker, *Pool s.n.* (K!), comprises two identical sheets carrying fragmentary specimens. Each sheet contains a single entirely fertile pinna lacking an associated rachis fragment. In the pinnules, five to six proximal segments are free and sessile, 1 × 0.3 cm and have a crenulate margin. Segments are progressively adnate and the distal segments are confluent. The sori are exindusiate and display small receptacular paraphyses, shorter than the sporangia. The costa has a dense hairy indument on its adaxial face and bullate as well as bicolorous lanceolate scales on its abaxial face. Taking into account our current knowledge of sect. *Gymnosphaera*, these two sheets may correspond to at least five taxa: *C. boiviniiformis* and its two varieties (var. *lobata*, var. *madagascarica*), *C. impolita*, or *C. poolii*. In the absence of sterile pinnules (dimorphism?), the leaf apex (distribution of fertile pinnae?), and the petiole base (scale morphology?), the material is ambiguous and the choice of an epitype to allow for a precise application of the name *A. bullata* Baker would be much more arbitrary than in the case of *A. boivinii* Mett. ex Ettingsh. The holotype of *A. boivinii*, *Boivin s.n.*, collected in the Comoros, can be confounded with two taxa only, that are, according to the presently known material, not occurring in the Comoros.

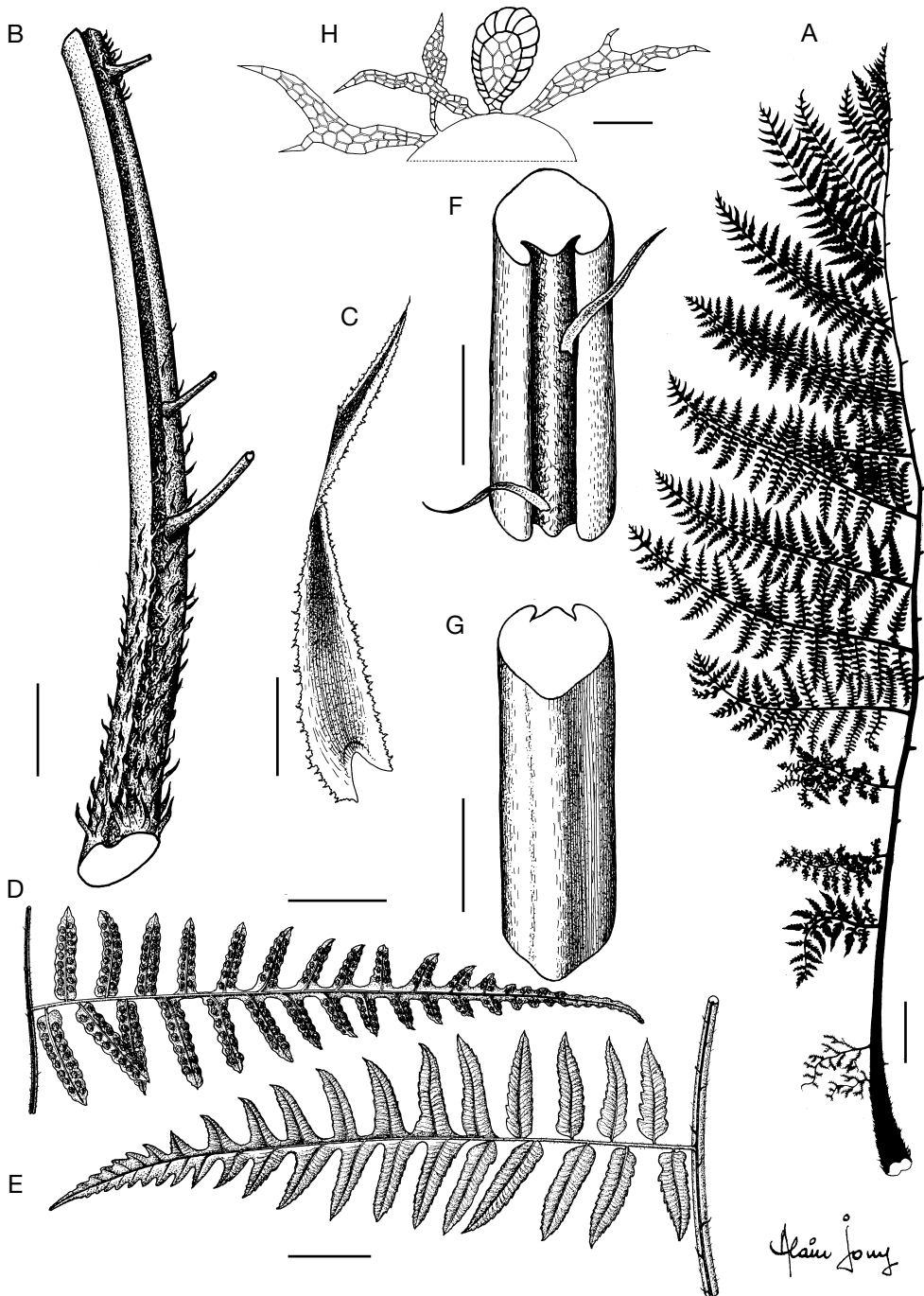


FIG. 5. — *Cyathea rouhaniana* Rakotondr. & Janssen: **A**, silhouette of a leaf; **B**, base of the petiole; **C**, scale from the base of the petiole; **D**, fertile pinnule with a fragment of the costa; **E**, sterile pinnule with a fragment of the costa; **F**, adaxial face of a costa fragment; **G**, abaxial face of a costa fragment; **H**, sporangia and paraphyses. A, *Rakotondrainibe et al.* 6958 (leaf A); B-H, *Rakotondrainibe et al.* 6958 (leaf B). Scale bars: A, 10 cm; B, 20 mm; C, 2 mm; D, E, 10 mm; F, G, 1.5 mm; H, 0.2 mm

TABLE 1. — Putative hybrids in Madagascan Cyatheaceae. Morphological characters of some specimens corresponding to intermediate forms between *Cyathea boiviniiformis* s.l. and *C. poolii*. Types: **B**, *C. boiviniiformis* s.l.; **BB**, *C. boiviniiformis* var. *boiviniiformis*; **BL**, *C. boiviniiformis* var. *lobata*; **P**, *C. poolii*.

Specimens	Petiole scales	Distribution of sori	Cutting of lamina	Receptacular paraphyses	Sporangia and spores	Status
<i>Rakotondrainibe</i> 4281bis; <i>Janssen</i> 2797, 2798	<b>Type B</b> narrowly triangular, subcoriaceous, densely imbricate	<b>Type B or P</b> lower half of the lamina	<b>Type BL</b> 8-11 proximal pairs of pinnule segments free and with crenulate margin	<b>Type P</b> scaly, longer than sporangia	sporangia malformed, empty or with aborted spores	<i>C. boiviniiformis</i> var. <i>lobata</i> × <i>C. poolii</i>
<i>van der Werff</i> 12815	<b>Type B × P</b> narrowly triangular, coriaceous, sparse and distant	<b>Type B or P</b> lower half of the lamina	<b>Type BB</b> 3-4 proximal pairs of pinnule segments free and with entire margin	<b>Type P</b> scaly, longer than sporangia	sporangia normal, spores aborted	<i>C. boiviniiformis</i> var. <i>boiviniiformis</i> × <i>C. poolii</i>
<i>Janssen</i> 2844	<b>Type B × P</b> narrowly triangular, coriaceous, very narrow erose margin, densely imbricate	<b>Type P</b> lower ¾ of the lamina	<b>Type BB</b> 2-4 proximal pairs of pinnule segments free and with entire margin (only small fragments at P)	<b>Type B × P</b> scaly or filiform, as long as sporangia	sporangia normal, spores hyaline, small, agglutinating	<i>C. boiviniiformis</i> var. <i>boiviniiformis</i> × <i>C. poolii</i>
<i>Rakotondrainibe</i> 3699	<b>Type B × P</b> narrowly triangular, coriaceous, very narrow erose margin, densely imbricate	<b>Type P</b> over entire length of lamina	<b>?</b> (sterile material not available)	<b>Type B or P</b> filiform, shorter than sporangia	mixture of normal spore- bearing and malformed empty sporangia	<i>C. boiviniiformis</i> s.l. × <i>C. poolii</i>

The holotype of *A. bullata*, *Pool s.n.*, has been collected in Madagascar and can be confounded with five distinct Madagascan taxa. This difference led to the decision to epitypify *A. boivinii*, but to refrain from epitypification of *A. bullata*.

## DISCUSSION AND CONCLUSION

Six species and three varieties are recognized in this treatment. With the exception of *C. boiviniiformis* var. *boiviniiformis* and *C. boiviniiformis* var. *lobata* also occurring in the Comoros, all taxa are endemic to Madagascar (Figs 2; 3).

Among these nine taxa, four species and two varieties have restricted distribution areas in Madagascar, limited to a single locality or one to two sectors of the Central phytogeographic Domain (Fig. 2). Thus, *C. alticola* is known only from the Marojejy massif, *C. andohahelensis* occurs only in the southern half

of Madagascar, *C. rouhaniana* grows in the Isalo and Ireimo massifs of the western Central Domain, *C. impolita* and its var. *michelii* are known from the Fianarantsoa region and *C. boiviniiformis* var. *madagascarica* has been found in the northern half of Madagascar only. The discriminative morphological characters for these taxa appear to be distinct and quite stable suggesting these taxa to represent well-established and presumably isolated evolutionary entities.

The remaining species and varieties, *C. poolii*, *C. boiviniiformis* var. *boiviniiformis* and *C. boiviniiformis* var. *lobata* have a wider distributional range covering the entire Central Domain from northern to southern Madagascar and hence frequently occur sympatrically along the eastern cliff of the Madagascan high plateau (Fig. 3). As witnessed by the presence of some intermediate forms, these taxa do not seem to be reproductively isolated (Table 1). Thus, the specimens *Rakotondrainibe* 4281bis (Fig. 6A, C-F)



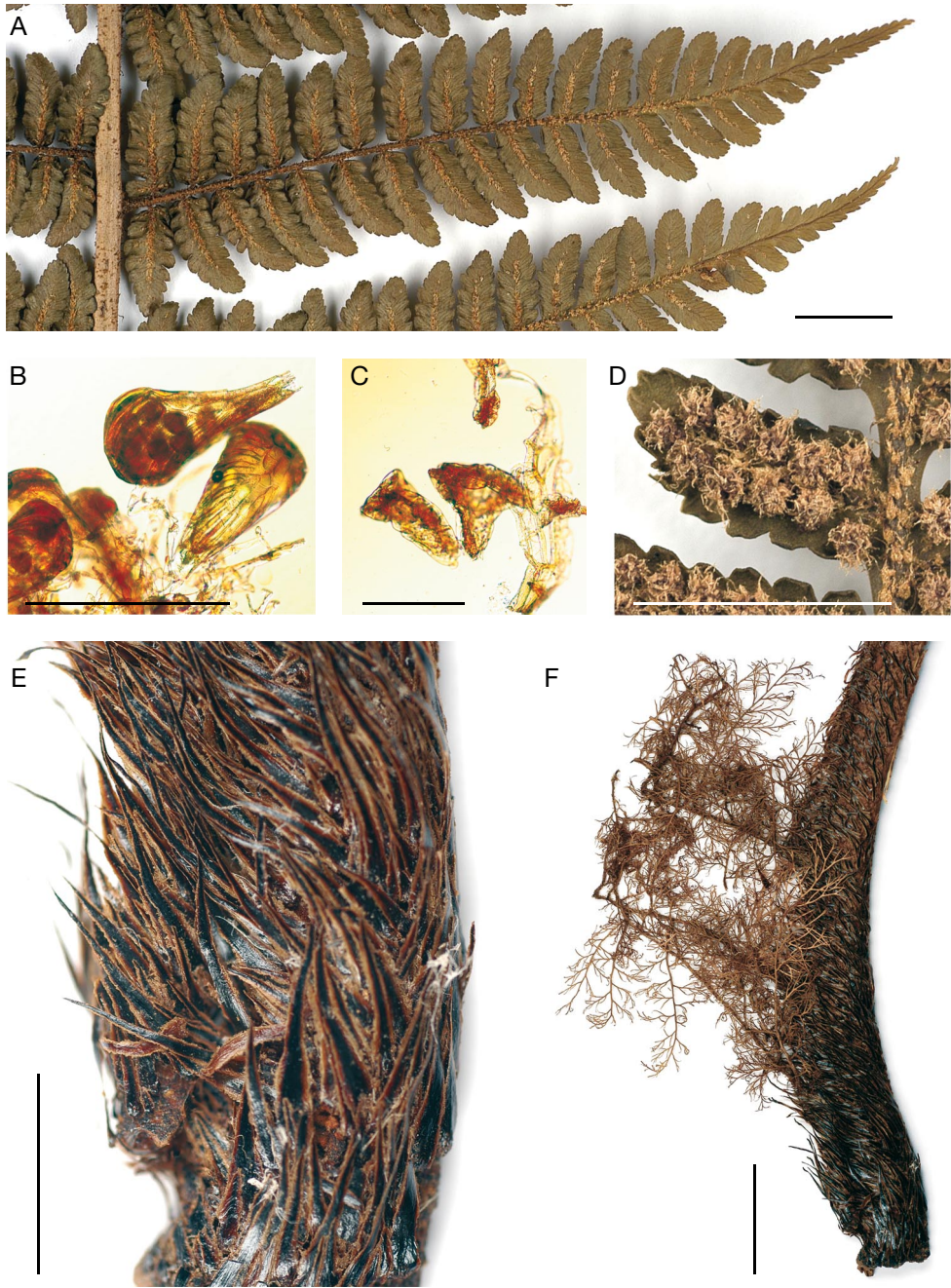


FIG. 6. — **A, C-F**, *Cyathea boiviniiformis* Rakotondr. & Janssen var. *lobata* (Rakotondr. & Janssen) × *Cyathea poolii* (C. Chr.) Domin; **A**, sterile pinnule; **C**, empty and malformed sporangia with a scaly paraphysis; **D**, fertile pinnule segment; **E**, detail of the scales at the base of the petiole; **F**, base of the petiole; **B**, *Cyathea boiviniiformis* var. *lobata*, normally developed sporangia and spores. **A, C-F**, *Rakotondrainibe* & *Randriambololona 4281bis*; **B**, *Janssen et al. 2394*. Vouchers at P. Scale bars: **A, E**, 1 cm; **B**, 0.4 mm; **C**, 0.2 mm; **D**, 0.5 cm; **F**, 2 cm.

and *Janssen 2797* and *2798* represent morphological intermediates between *C. boiviniiformis* var. *lobata* and *C. poolii*. Actually, their petiole scales are identical to the scales of *C. boiviniiformis* s.l. (Fig. 6E, F), but just like in *C. poolii* their scaly receptacular paraphyses are longer than the sporangia (Fig. 6C, D). In addition, eight to nine proximal pairs of pinnule segments are free and crenate to pinnatifid (Fig. 6A), a character of *C. boiviniiformis* var. *lobata*. The study of microscopical preparations revealed several malformed sporangia, containing aborted spores or being empty, in all three specimens (Fig. 6C; compare to regularly developed sporangia in Fig. 6B). This is evidence suggesting a hybrid origin of these specimens. Yet, the available material is insufficient to calculate a percentage of aborted or sterile sporangia. Fertile hybrids with at least partially well-formed spores are known to occur in *Cyathea* subgen. *Alsophila* (Table 1, *Rakotondrainibe 3699*). Such plants may produce a variable F2 generation explaining morphological differences in specimens supposed to have the same progenitors (Table 1, *Janssen 2844* vs. *van der Werff 12815*).

In analogy to the preceding case, the characters detailed in Table 1 show that the specimens *van der Werff 12815* and *Janssen 2844* represent morphological intermediates between *C. boiviniiformis* var. *boiviniiformis* and *C. poolii*. The specimen *Rakotondrainibe 3699* is intermediate between *C. poolii* and one variety of *C. boiviniiformis* that cannot be unambiguously determined in the lack of sterile pinnae.

Natural interspecific or even intergeneric hybridization events are presumably frequent in Cyatheaceae and have been suggested or proven in numerous instances for the Greater Antilles (Conant 1975, 1990; Tryon 1976; Conant & Cooper-Driver 1980; Conant *et al.* 1996; Caluff 2002a, b; Caluff & Serrano 2002), for Mexico and Costa Rica (Tryon 1976), for Brazil (Holttum 1981), for Venezuela and Colombia (Conant *et al.* 1996), for Malaysia, Sumatra, and Borneo (Holttum & Sen 1961) as well as for Australia, Tasmania, New Zealand and the Philippines (Large & Braggins 2004). To our knowledge, a single case has been reported for Africa (Edwards 2005) and we here present first evidence for naturally occurring hybridization events in Madagascan Cyatheaceae.

Building a hypothesis on the origin, mechanism and magnitude of hybridization in Madagascan Cyatheaceae is out of the scope of this paper. Cytological, chemical and population level studies as demonstrated by Conant & Cooper-Driver (1980) or investigation into the germination potential of spores and the structure of prothallia and reproductive structures (Conant 1990) would be necessary for this purpose. The putative hybrids cited in this paper are too few to provide material for a sound analysis. However, the examined plants appear to be sterile and hence instable entities. If the existence of such hybrids is going to be confirmed, we suppose that they should be of much more recent origin than the numerous and well established cases that have been observed in the Greater Antilles.

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