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Revision of *Cran illia opaca* in New Caledonia

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Abstract. *Cranfillia opaca* is a fern species present in New Caledonia, for which a great variation in morphology is reported. Some other species such as *Blechnum deplanchei* have been proposed, but those were later synonymized with *C. opaca*. In this work, we have studied this taxon at both the morphological and the anatomical level, as well as its ecology and geographical distribution. We found differences between *C. opaca* s.s. and *B. deplanchei* in the morphology of the sterile and fertile fronds, in several morphoanatomical features such as trichome shape, length, and distribution, and length and/or shape of different structures of sporangia and spores. The distribution of both taxa was also different, but they are sympatric at some localities. The differences identified in this study support the recognition of both taxa, and the combination of *Cranfillia deplanchei* (Baker) Vázquez Ferreira & Gabriel y Galán, which we propose here. A new taxonomic description is provided for both species.
Keywords: *Cranfillia*, Blechnaceae, New Caledonia, new combination, taxonomy, anatomy.

[es] Revisión de *Cranfillia opaca* en Nueva Caledonia

Resumen. *Cranfillia opaca* es una especie de helecho presente en Nueva Caledonia, para la que se registra una gran variación morfológica. Otras especies, como *Blechnum deplanchei* han sido propuestas en el pasado, y se sinonimizaron más tarde con *C. opaca*. En este trabajo, hemos estudiado este taxón tanto a nivel morfológico como anatómico, así como su ecología y distribución geográfica. Encontramos diferencias entre *C. opaca* s.s. y *B. deplanchei* en la morfología tanto de frondas estériles como fértiles, y en rasgos morfo-anatómicos como son la forma, longitud y distribución de los tricomas y la longitud y/o forma de diferentes estructuras relativas a esporas y esporangios. La distribución de ambos taxones también fue distinta, aunque siendo simpátricos en algunas localidades. Todas estas evidencias apoyan el reconocimiento de ambos taxones, y la combinación de *Cranfillia deplanchei* (Baker) Vázquez Ferreira & Gabriel y Galán, la cual proponemos aquí. También proporcionamos descripciones taxonómicas para ambas especies.
Palabras clave: *Cranfillia*, Blechnaceae, Nueva Caledonia, combinación nueva, taxonomía, anatomía.

Introduction

The family Blechnaceae Newman is a group of leptosporangiate ferns, nested in the Aspleniinae clade (Eupolypods II), and sister to the Onocleaceae Pic. Serm., according to the latest classification derived from the global phylogeny of pteridophytes (PPG I 2016). Around 250 species are included in the family, making it a medium-sized richness family within the pteridophytes. This richness translates into many ecological life forms, with taxa of herbaceous, arborescent or subarborescent habit, also hemiepiphytes by means of fronds or by long-creeping rhizomes, and even submerged aquatic life forms (Veillon 1981; Rolleri & Prada 2006, Rolleri et al. 2012, 2013; Vicent et al. 2017; Cárdenas et al. 2019). Species of Blechnaceae are mainly distributed in tropical and subtropical regions of the Southern Hemisphere, with a minority of genera represented in temperate regions, some of which are restricted to the Northern Hemisphere (Li et al. 2014; Molino et al. 2019).

In the last few decades, the systematics of Blechnaceae has been subject of much controversy, as it was found that the genus *Blechnum* L., which included 80% of the diversity of the family, was paraphyletic (Cranfill 2001; Schuettpelz & Pryer 2007;

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Shepherd et al. 2007; Gabriel y Galán et al. 2013; Perrie et al. 2014; Gasper et al. 2017). As such, the family has undergone many nomenclatural changes, with new described genera, resurrected names, and new combinations (Gasper et al. 2016). This new classification has been adopted by different authors (Bauret 2017; Dittrich et al. 2017; Vicent et al. 2017, 2018; Moran et al. 2018; Smith & Kessler 2018; Molino et al. 2019; Silva et al. 2019; Bauret et al. 2020), and accepted by the global phylogeny of pteridophytes (PPG I 2016). However, there are detractors of this classification (Christenhusz & Chase 2018; Brownsey & Perrie 2019; Perrie et al. 2021), some of them following another less-segregated classification proposal (Perrie et al. 2014), or authors who have simply preferred to continue using the traditional nomenclature (Chambers & Wilson 2019), in which almost the entirety of the current subfamily Blechnoideae Gasper, V.A.O. Dittrich & Salino would correspond to *Blechnum*.

Because of the complex taxonomy of Blechnaceae, carrying out rigorous systematic reviews at all levels of classification is needed. Work is important below the genus level, as in recent decades some taxa have been resurrected, and some originally described varieties that had fallen into disuse, have now been elevated to the species category (Brown & Brown 1931; Lange & Parris 2019). Moreover, new species, new sections (Chambers & Farrant 1993; Rojas 2005, 2008; Rakotondrainibe et al. 2013), and new interspecific hybrids (Aguiar et al. 2007; Dittrich et al. 2015) have been described. In addition, some names have been synonymized, considering them conspecific with other related taxa (Brownlie 1969, Rakotondrainibe et al. 2013; Dittrich et al. 2017).

The genus *Cranfillia* Gasper & V.A.O. Dittrich currently includes 22 species, recognized by different authors (Gasper et al. 2016; Chambers & Wilson 2019; Lange & Parris 2019; Bauret et al. 2020), being the fourth largest genus in the family after *Parablechnum* C. Presl., *Austroblechnum* Gasper & V.A.O. Dittrich, and *Blechnum* s.s. *Cranfillia* is distributed throughout the Southern Hemisphere. Although species of *Cranfillia* are clearly supported as a clade by molecular data (Cranfill 2001; Gabriel y Galán et al. 2013; Perrie et al. 2014; Bauret 2017; Gasper et al. 2017; Bauret et al. 2020), in the studies carried out so far, there seems to be a large variation both at morphological and anatomical levels (Gabriel y Galán et al. 2008; Passarelli et al. 2010; Prada et al. 2016; Moran et al. 2018; Silva et al. 2019; Bauret et al. 2020).

Cranfillia opaca (Mett.) Gasper & V.A.O. Dittrich is a New Caledonian taxon, originally described by Mettenius (1861) as *Blechnum opacum* Mett., a species characterized for having atropurpureous to dark brown rhizome scales, dimorphic fronds, the sterile ones oblanceolate with a chartaceous texture and dark green shade, small and rigid black trichomes, and for sometimes having anastomosing nervures. Mettenius highlights as a diagnostic character of the species, the peculiar bifid-emarginate apices of both terminal and lateral pinnae present in the sterile fronds of all the individuals he observed. Later, *C. opaca* was cited in Vanuatu for the first time (Hooker & Baker 1867), pointing out that plants collected there by Milne do not present anastomosed veins as they do in specimens from New Caledonia (Grande Terre).

Mettenius related it to *Blechnum nigrum* Colenso (currently *Cranfillia nigra* (Colenso) Gasper & V.A.O. Dittrich), a New Zealand species, from which it differs by the sterile lamina contour. This relationship is evident in current phylogenies (Perrie et al. 2014; Gasper et al. 2017; Bauret et al. 2020), which show that both species are directly related to *C. fullagari* (F. Muel.) Gasper & V.A.O. Dittrich, from Lord Howe Island, as well as to *C. mucronata* (Fée) V.A.O. Dittrich & Gasper, and *C. bakeri* Vázquez Ferreira & S. Molino, from South America and Africa respectively.

In 1874 Baker described the species *Lomaria deplanchei* Baker, also from New Caledonia, which would be combined by Christensen (1905) as *Blechnum deplanchei* (Baker) C.Chr. The presence of this taxon in collections seems scarcer than *C. opaca*. Baker comments that this species presents an oblanceolate contour of sterile fronds, a coriaceous texture of the lamina, a dark green shade, and atropurpureous rhizome scales; he points out that this taxon does not present trichomes (Hooker & Baker 1867).

Later, Brownlie (1969) would synonymize *Blechnum deplanchei* with *B. opacum*, which would mean that some diagnostic characters for *B. opacum* would include greater variation in states. The author argues the synonymy he proposes describing *B. deplanchei* as "a larger and more developed form, with more regular contours and more erect fronds than *B. opacum*", and says that there are intermediate forms between the morphology associated with *B. opacum* and that described for *B. deplanchei*.

A recent study shows that *C. opaca* and *B. deplanchei* are phylogenetically closely related, being *B. deplanchei* a well-supported and distinctive lineage within the existing genetic variation of *C. opaca* s.l. sampled populations on the island of New Caledonia (Grande Terre, Perrie et al. 2021). This work proposed to reinstate the taxon *B. deplanchei* because of both its morphological and genetic divergence from *B. opacum* s.s. In addition, different distributions on the island were recorded for both species, but being sympatric at certain localities.

When Gasper et al. (2016), in the light of their phylogenetic hypothesis, combined *B. opacum* into the current genus *Cranfillia*, they did not make reference to *B. deplanchei*, so its combination in *Cranfillia* does not exist.

The aims of the present work are to carry out a more thorough review at the morpho-anatomical level of *C. opaca* s.l., studying its intraspecific variation and evaluating whether the proposal of *Blechnum deplanchei*, supported by molecular data and adopted

by Perrie et al. (2021), could correspond to a part of the intraspecific variation of *C. opaca*, and therefore the synonymy applied by Brownlie (1969) is correct, or if there is sufficient evidence to justify this taxon being considered a separate and independent taxonomic entity.

Material and methods

The protologues of the basionyms *Blechnum opacum* Mett. and *Lomaria deplanchei* Baker were studied. Designated type specimens were accessed through the virtual herbaria of Paris (P) and Kew (K) respectively. All the other available specimens belonging to the two species were analysed by means of visits to herbaria, observation through digital herbaria, or from loans. A detailed study of both morphology and anatomical traits of interest in fern systematics (rhizome scales, trichomes, epidermis, indusia, sporangia and spores, etc.) was conducted. The herbaria acronyms follow Thiers (2017).

The microscope sample assembly for the anatomical study was carried out by hand under a Leica Stereozoom S9i stereo microscope. Structures were also observed and measured with the Leica Application Suite software version 4.12.0. Samples were observed and measured in a Nikon optical microscope model Eclipse Ci-L, with the aid of the NIS-Elements F software version 4.00.00. When necessary, an acid phloroglucinol stain was applied. This stain reacts on the plant cell walls with lignin, producing a reddish pigment in an acidic medium (Pomar et al. 2002).

In order to better understand both the ecology and geographical distribution of the taxa involved, the specimen location, geographical coordinates, and altitude in New Caledonia and Southern Vanuatu were noted, as well as other ecological data, when available on herbarium labels.

Results and discussion

In general, the specimens consulted in this study were identified as one or another taxon with relative ease. The type of *Cranfillia opaca* collected by Vieillard in 1855, presents a very characteristic general morphology, which is different from that of the Deplanche type specimen designated as *Lomaria deplanchei*. However, these two taxa show coinciding characters, such as the atropurpureous uniseriate trichomes of relatively short length (Fig. 1 A-B), the atropurpureous rhizome scales, the finely papillose/denticulate leaf margin, the short, nigrescent and more or less entire indusium, and the first or first two (more rarely three) pairs of pinnae basiscopically free. This last character is also pointed out in the protologue of *B. opacum*, and has been illustrated in recent morphological reviews (Mettenius 1861; Bauret et al. 2020). These characters, together with the dark green shade of the lamina in most cases, easily differentiate both taxa from the rest of the Blechnaceae that occur in New Caledonia. Some minor cases of erroneously identified individuals corresponding to *Austroblechnum vieillardii* (Mett.) Gasper & V.A.O. Dittrich and *Lomaridium contiguum* (Mett.) Gasper & V.A.O. Dittrich were reported.

C. opaca has a wide distribution throughout the island, while *B. deplanchei* seems to be limited to the southern province of New Caledonia, being present not only in the locality of Mount Mou, but also in other localities in the south-east of the island (Fig. 2). This is consistent with the observations in Grande Terre by Perrie et al. (2021), although they considered that *B. deplanchei* had been recorded in Bourail. *Cranfillia opaca* was also observed by Baker in Vanuatu, to the North of New Caledonia (Hooker & Baker 1867).

These specimens from the island of Aneityum presented a somewhat peculiar morphology, with more linear, arched distal sterile pinnae, straighter and more regular margins, slightly emarginate pinnae apices, and absence of anastomosing veins.

At the altitudinal level, *C. opaca* seems to be recorded between 300 and 1200m, although individuals in the locality of Noumea are reported to grow close to sea level. On the other hand, *Blechnum deplanchei* does not reach such low areas, being recorded between 810 and 1320 m.

1) Morphology

Table 1 presents a comparison of the main distinguishing characters of *Cranfillia opaca* and *Blechnum deplanchei*. Importantly, *Cranfillia opaca* has a very characteristic contour, lamina texture and pigmentation of the sterile fronds, and irregularly lobed margins. *Blechnum deplanchei* has notably higher number of pinnae pairs and slightly sinuous or straight margins. Sterile pinnae apices that vary from bifid to emarginate (Fig. 1 C) in *C. opaca* (*vs.* entire, obtuse or subacute apices in *B. deplanchei*) is another feature that undoubtedly separate both taxa. Fertile fronds were also different between the two taxa.

The peculiarity of presenting anastomosed lateral veins that form areoles was observed in many specimens of *C. opaca* from New Caledonia, as described in the bibliography (Mettenius 1861; Hooker & Baker 1867); this, however, was not observed in *B. deplanchei*, which always presented free venation.

2) Anatomy

Cranfillia opaca s.s. and *B. deplanchei* share different anatomical features, such as dark brown to atropurpureous rhizome scales, presence of atropurpureous trichomes, or the spores with winged perispore (Fig.1 D), exhibiting straight and thick muri, clearly perceptible in optical microscope, and which have been described in previous works (Moran et al. 2018;

Bauret et al. 2020). This last character is also shared with the Brazilian endemic *C. mucronata* (sub *Blechnum sampaioanum* Brade; Passarelli et al. 2010; Silva et al. 2019) as well as with the African taxon *C. bakeri*, therefore relating *B. deplanchei* undoubtedly to *C. opaca* and close-related species in the genus *Cranfillia*.

The more detailed study of some characteristics, such as trichome shape, length, and location on leaf surfaces, together with other anatomical features, show many differences between the two taxa of this study (Table 1).

The epidermal model of sterile frond cells has been used in Blechnaceae from the systematic point of view as a discriminating character in close-related species (Rolleri & Prada 2006; Rolleri et al. 2012; Molino et al. 2019). While the cells of the adaxial epidermis are more or less polygonal in both species, the cells of the abaxial epidermis were different. *Cranfillia opaca* presented cells with U-shaped undulations (Fig. 1 E), while *B. deplanchei* showed cells with sinuous walls and shallower undulations.

Sporangia morphology is another discriminating character of related groups in Blechnaceae (Molino et al. 2020). The observation of these structures shows that *C. opaca* has shorter pedicels, different capsule shape, and different number of annulus cells (Table 1, Fig 3 D, Fig. 4 D). Mean values in measurements of 15-20 spores per fertile individual studied at the anatomical level, were also slightly larger in *C. opaca* than in *B. deplanchei*. Spore size contrasts with that obtained by Perrie et al. (2021) who mentioned that length differences were marginally larger in *B. deplanchei*. Our results suggest the opposite, that *C. opaca* spores are larger than *B. deplanchei* (Table 1). These conflicting results suggest that there is not a clear trend and that spore size of both taxa can be similar.

The morphological and anatomical evidence we provide here, supports the proposal to combine *B. deplanchei* in the current genus *Cranfillia*, contrary to the proposal made by Brownlie (1969) who synonymized this taxon with *B. opacum*.

Taxonomic treatment

1. *Cranfillia deplanchei* (Baker) Vázquez Ferreira & Gabriel y Galán **comb. nov.** – *Lomaria deplanchei* Baker, Syn. Fil. (Hooker & Baker), ed. 2: 481 (1874).

Blechnum deplanchei (Baker) C.Chr., Index Filicum, 153 (1905).

Type: New Caledonia, Mont Mou, 22º 04’ S, 166º 21’ E (VII-1863) *Deplanche s.n.* (here designated as lectotype**:** K 000722686).

= *Blechnum subopacum* Rosenst. nom. nud. New Caledonia, Mont Mou (XI-1908) *Franc I. 2049* [(S), S-P-2170].

Plants terrestrial or saxicolous, herbaceous, rhizome short, around 1,6 cm thick, erect to suberect, covered with the base of old petioles behind the apex, this one with tufted fronds; rhizome scales 1,8 x 0,13 cm, linear-lanceolate, subulate, entire, concolorous, very dark atropurpureous, sometimes nigrescent. Fronds dimorphic, the fertile ones completely erect, growing in the middle of the crown, surrounded by semi-erect trophophylls. Sterile fronds 40,5–56,88 x 6,1–9,2 cm, with stipes adaxially sulcated and abaxially smooth, very dark at the base almost atropurpureous, becoming stramineous distally, having trichomes and scales. Trichomes 0,81-1,4 mm, pluricellular (5-8 cells), uniseriate, shiny atropurpureous and opaque, slightly tuberculate, habitually contorted helically, glabrescent and very scattered abaxially on the rachis, costae and lateral veins, denser at the base of stipes; scales and trichomes when detached, leaving dark spots on the surface of the organs where they grow. Rachis adaxially sulcate, light-stramineous; costae adaxially smooth, light-stramineous; lateral veins free, 1-furcate, sometimes 2-furcate, rarely simple, reaching up to submarginal adaxial hydathodes, these constituting bulging little groups of hyaline epidermic cells. Sterile lamina lanceolate, coriaceous and smooth, with margins straight to slightly wavy, subrevolute and finely denticulate, from glabrescent to completely glabrous, dark to light green. Lamina 1-divided, pinnae (26-) 35–40 (-45) pairs, contiguous, ovate-lanceolate, habitually falcate, with obtuse to subacute apices, and truncate bases, completely adnate to the rachis throughout their width; basal pinnae gradually reduced to vestigial auricles often strongly surcurrent with rounded apices downwardly displaced; the 2-3 first pairs of basal auricles basiscopically free and acroscopically adnate. Distal end of the fronds gradually reduced to a pinnatifid apex with 4-5 pairs of decreasing subterminal pinnae, topped with an ovate terminal segment. Fertile fronds 65,2–78,1 x 5,3–6,4 cm, lanceolate, 1-divided, pinnae 21-33 pairs, stipes and rachis similar to sterile ones, but with trichomes only located on the basal end of the stipe. Fertile pinnae linear and very narrow, gradually shortening in both ends of the fronds, with rounded apices and truncate or narrowed bases; terminal segment elongated; costae stramineous, adaxially smooth, abaxially rarely having very scarce and inconspicuous glandular trichomes (100µm long), pediculated, with a terminal swollen cell with mucilaginous content. Margins of fertile pinnae elongated and arched, forming a short and nigrescent indusium, with rectangular cells with thickened walls; margins entire and more or less straight. Sori linear, extending to both sides of costae, sporangia with brown pedicels, ending in a clear rosette funnel-shaped, higher than wide; sporangium capsule ovate, with 2-3 cells forming the stomium; annulus having (13-) 14–16 (-18) cells. Spores 43 x 27 µm, with winged perispore and straight thick muri delimiting areoles. (Fig. 3.)

Distribution and habitat: Southern province of New Caledonia (localities of Thio, Yaté, Le Mont-Dore, Dumbéa, and Païta), altitudinal range of 810-1320m. It grows in shady areas of rainforests and cloud forests, often colonizing slopes. In localities such as Mount Mou, where it reaches its altitudinal limit, this species is cited as rare, while in its lower altitude localities, *C. deplanchei* appears to be locally abundant. The localities where it is cited in New Caledonia correspond to territories with a predominantly ultramafic rock nature, different from that found in more central areas on the island and much of the Northern province (Swenson et al. 2018).

Studied specimens

Mt. Dzumac: forest patches in scrub, 22º 02' S, 166º 28' E, terrestrial, on dark, steep slope, 900m, 14/XI/1999, *Van der Werff H. & McPherson G. 16107* (NY 04187141); Forest patches in scrub, 900m, 14/XI/1999, *H. van der Werff & G. Pherson 16107* (UC 1750393); ibidem, terrestrial, pinnae gradually reduced to base (NOU 055649 [photo]); ibidem (NOU 055648 [photo]). **Humboldt source**: forêt rivulaire, substrat ultramafique, long: 166º 24' 47'' E, lat: 21º 52' 49'', fougère terrestre, fertile, 1320m, 31/VII/2009, *Grignon C. 356* (NOU 051512 [photo]). **Kouakoué:** forêt humide à *Nothofagus*; substrat ultramafique, fougère terrestre, fertile, long: 166º 30' 34'' E, lat: 21º 57' 54'', 1050m, *Grignon C. 479* (NOU 052660 [photo]); Mt. Kouakoué, 21º 57' 31'' S, 166º 32' 11'' E, terrestre à la base de rochers, 26/XI/2002, *Munzinger 1683* (NOU 002901 [photo]). **Mount Mou:** 01/XI/08, *L. Franc 2049* (US 1205019) ibidem (UC 394309); XI/1908, *Bonati 2049* (US 2427225); sommet du Mont Mou, rare, 1200m, I/1907, *Franc I. 604* (P 01557374 [photo]); 1861, *Vieillard E. 1533* (P 01618505 [photo]); ibidem (P 01411550 [photo]) ibidem (P 01411565 [photo]); 1150m, III/1870, *Balansa B. 2715* (P 01411555 [photo]); Montagne Mu, haute vallée au pied du pic, lieux humides, 23/VII/1863, *Deplanche E. 135* (P 01411567 [photo]); Montagnes de Mi, VII/1881, *Pompéry M. s.n.* (P 01411590 [photo]); sommet du Mont Mou, Rare, 1200m, I/1907, *Franc I. 604* (P 01411592 [photo]); ibidem (P 01557374 [photo]); 1908, *Franc I. 2049* (P 01411593 [photo]); 22º 04' S, 166º 21' E, 23/VII/1863, *Deplanche s.n.* (lectotype of *Lomaria deplanchei* Baker K 000722686 [photo]); bord de ruisseau, en forêt, 1100m, 29/IX/1965, *Schmid M. 510* (NOU 055646 [photo]). **La Rivière Bleue:** Sentier de la Haute Pourina, 29/VII/2017, *Perrie L. s.n.* (P 028706/A [photo]). **Montagne des Sources:** 29/VII/2017, *Perrie L. s.n.* (P 028710 [photo]). **Haute Tamoa:** forêt humide, terrain rocheux serpentineux, terrestre, humicole à l'ombre, 1020m, 09/VI/1993, *Mckee H.S. 46247* (NOU 055643 [photo]). **Thio**: Mé Ouébo, upper catchment of Nèmirî River, lat. 21 39.53' S, long. 166 17.02' E, damp depression high on range, under shaded forest, locally abundant, 810m, 25/X/2019, *Perrie L. LRP8374* (WELT P030356/B [photo]); ibidem, *Perrie L. LRP8374* (WELT P030356/A [photo]); ibidem, *Perrie L. LRP 8376* (WELT P030358 [photo]); ibidem, *Perrie L. LRP 8373* (WELT P030355 [photo]); ibidem, *Perrie L. LRP 8372* (WELT P030354 [photo]); ibidem, *Perrie L. LRP 8375* (WELT P030357 [photo]); ibidem, *Perrie L. LRP 8372* (WELT P030354/A [photo]); foret des Sailles, wet forest and cloud forest above Xwe Re Me River, upper crests and ridges, Terrestrial, rhizome short-creeping to erect, 1100m, 08/VI/1996, *Hodel D.R. 1512* (UC 1613868). **Tontouta:** Pied du Pic des Mousses (creek vers la rivière de Tontouta), forêt à *Nothofagus*, 27/VIII/1963, *Blanchon J.P. 352* (NOU 055653 [photo]). **no loc. (New Caledonia):** 1907, *2049* (UC 393022); *Baudouin A. 954* (P 01411557 [photo] mixed collection with *Austroblechnum vieillardii* fronds).

Comments

The only type specimen that we found in the Kew herbarium (*Deplanche s.n.* K 000722686) corresponding to the original Deplanche collection, is designated here as the lectotype, since we did not find any originally designated holotype. The name *Blechnum subopacum* provided in 1908 by Rosenstock was not published and its protologue is present on the plate of the type specimen he designated. This specimen, collected at Mount Mou, undoubtedly corresponds to *Cranfillia deplanchei*, and in the protologue, the author refers to diagnostic characters that segregate this species from *Blechnum opacum*, such as the non-emarginate apices, the almost absence of trichomes in the lamina, or the absence of anastomosing lateral veins. This name is also used by some authors who have collected *C. deplanchei*.

On some specimens of *C. deplanchei* the locality "Montagnes le Mi" is reported. This has been interpreted in this work as belonging to Mount Mou, the type locality of *C. deplanchei*, but Perrie et al. (2021) comment that it could be another locality in Bourail. If this were true, *C. deplanchei* would extend into the more western territories of the South Province of Grande Terre, closer to the North Province. It is possible that this species prefers volcanic rock soils of an ultramafic composition (Perrie et al. 2021), as the territories in which is found (Fig. 2), correspond to soils of this nature (Swenson et al. 2018). However, *C. opaca* does not seem to be selective in this aspect, as it grows all over the island in areas with different soils. This soil preference could have relegated *C. deplanchei* to these territories in the past, causing an allopatric speciation with the rest of its relatives; *C. opaca* could have reached some of these regions on the island later, where both species are sympatric today.

In general, many species in the genus *Cranfillia* exhibit both glabrescent trichomes and scales, which often leave small spots-scars when detached. This oc-

curs in *C. opaca* and *C. deplanchei*, the latter retaining much less trichomes on sterile and fertile fronds on adult forms. Perrie et al. (2021) say that the presence of abundant trichomes does not seem to be more associated with *C. opaca* or *C. deplanchei*, and that they have reported individuals of *C. deplanchei* with abundant trichomes. In this study we have not observed any adult individual of this species with such a density of trichomes on the abaxial surface of sterile fronds, along the leaf margins, and on immature or even mature fertile fronds, as we have frequently observed in *C. opaca*. Instead, we observed for most adult individuals of *C. deplanchei*, trichomes often confined to the base of the petiole or along the petiole, and abaxially on rachis, costae and lateral veins. The spores of *C. deplanchei* seem to be slightly smaller than those of *C. opaca* (Table 1), although both appear to be similarly winged. Moran et al. (2018) published scanning electronic microscope images of the spores of *C. opaca*; however, the review of the specimen reveals that they correspond to what is proposed here as *C. deplanchei*.

2. *Cranfillia opaca* (Mett.) Gasper & V.A.O. Phytotaxa 275(3): 208 (2016) —*Blechnum opacum* Mett., Ann. Sci. Nat. Bot., sér. 4, 15: 69 (1861).

Lomaria opaca (Mett.) Baker, Syn. Fil.: 176 (1867).

Struthiopteris opaca (Mett.) Ching, Sunyatsenia 5: 243 (1940).

Type: New Caledonia, Bord des ruisseau dans les montagnes, à Kanala (1855) *Vieillard E. 1533* (here designated as lectotype: New Caledonia, Kanala, *Vieillard E. 1533* P 00627676 [photo], and isolectotypes: P 01411552 [photo], P 01411582 [photo], P 01571509 [photo], P 01618507 [photo], P 01618506 [photo]).

= *Lomaria emarginata* Carruth., Fl. Vit.[Seemann]: 350 (1873).

Plants terrestrial and herbaceous, rhizome short, 1,4 cm thick, vertical to erect, covered with bases of old petioles behind the apex, this last tufted and forming a crown of fronds. Rhizome scales 1,3 x 0,27 cm, ovate to lanceolate, subulate, entire, concolorous and very dark, atropurpureous to nigrescent. Fronds dimorphic, with fertile fronds erect, growing in the middle and surrounded by decumbent sterile ones. Sterile fronds 24,2–43,5 x 3,6–9,6 cm, with stipes adaxially sulcate and abaxially smooth, dark, nigrescent, having trichomes and scales similar to those of the rhizome but sometimes falcate. Trichomes 0,32–0,66 mm, pluricellular (3-6 cells), uniseriate, shiny atropurpureous, opaque, slightly tuberculate, rigid, glabrescent and densely distributed covering rachis, costae and veins abaxially, growing at least in a row, sometimes even growing on the lamina tissue abaxially between the veins, as well as along the frond margins. Rachis adaxially sulcate, nigrescent to stramineous; costae adaxially smooth; lateral veins partially free with simple, 1 or 2-furcate veins, but also anastomosing veins forming subtriangular areoles (Fig. 4 E); hydathodes submarginal and adaxially located, conspicuous, consisting of bulging hyaline epidermal cell groups. Sterile lamina oblanceolate to slightly spathulate, dark green shaded, subcoriaceous to chartaceous and notably irregularly corrugated, with irregularly lobed, sinuous margins, finely denticulate and pilose. Lamina 1-divided, pinnae (10-) 17–20 (-28) pairs, contiguous, ovate to triangular-ovate, with bifid to emarginate apices and truncate bases, completely adnate to rachis; basal pinnae gradually reduced to vestigial auricles, the 2-3 lower pairs of auricles basiscopically free and acroscopically adnate. Distal end of the sterile fronds becoming a big ovate pinnatifid segment with 2-3 lateral decreasing lobes, with a bifid apex. Fertile fronds 25,6–44,3 x 4,4–15,4 cm, elliptic, 1-divided, pinnae 13-25 pairs, with petioles and rachis similar to those of sterile fronds, having the same glabrescent trichomes and scales, but with lighter tone; trichomes also located on both surfaces of fertile costae, as well as adaxially along indusia in one or two rows in juvenile immature fronds. Fertile pinnae linear and narrowed, the apical segment notably elongated; apices mucronate, bases narrowed to slightly or shortly subpetiolulate, the first lower pair of pinnae petiolulate, often deflexed and sterile. Costae stramineous, adaxially smooth; pinnae margin elongated and arched, forming a short and nigrescent indusium, with rectangular cells with thickened walls; margins entire and more or less straight. Sori linear, extending to both sides of costae, sporangia with brown pedicels, ending in a clear rosette funnel-shaped, wider than high; sporangium capsule elliptic, with 2-3 cells forming the stomium; annulus having (11-) 12–14 (-15) cells. Spores 49 x 31 µm, with winged perispore and straight thick muri delimiting areoles. (Fig. 4).

Distribution and habitat: Disjunct distribution, along the whole island of New Caledonia (Grande Terre), and 500km NE, on the island of Aneityum (S of Vanuatu). It occurs from sea level in locations such as Noumea, up to 1200m in altitude. It grows in shaded areas of dense and humid rainforests.

Studied specimens

New Caledonia (Grande Terre) – Vallée Creek Tao (Oua Pandième): 20° 34’ 15.996’’ S, 164° 48’ 9’’ E, Fougère terrestre en endroits rocheux très ombragés. Feuilles vert foncé brillant en dessus, vert clair en dessous, Forêt humide sur terrain schisteux, 300-400m, 09/XI/1965, *MacKee H.S. 13797* (P 01617243 [photo]); ibidem (P 01411544 [photo]); ibidem (P 01411545 [photo]). **Forêts situées au NE de la Conception**: 600m, 09/VI/1870, *Balansa B. 1569* (P 01411556 [photo]). **Sommet Aragoi** (Houaïlou), 600m, IV/1901, *Cribs I. 1034* (P 01411561 [photo]). **Dogny:** Prov. Nord: trail to plateau du Dogny, 02/IV/2000, *Lemieux T. 2032a* (UC 2082843); near Sarraméa, Plateau de Dogny track, 26/IX/2016, *Perrie L. s.n.* (P 028717 [photo]); Plateau de Dogny, 1072m,

IX/1909, *Le Rat A. 808* (P 01411594 [photo]). **Kanala:** Bord des ruisseau dans les montagnes, à Kanala, 1855, *Vieillard E. 1533* (lectotype of *Lomaria opaca* (Mett.) Baker: P 00627676 [photo], isolectotypes: P 01571509 [photo], P 01618506 [photo], P 01618507 [photo], P 01411552 [photo], P 01411582 [photo]; de Kanala à Uarail, *Mazagot M.* (P 01411587 [photo]). **La Foa:** Doguy, La Foa, *Franc 45* (US 1096842). **Mandjélia:** above Pouébo, Terrestrial, 600-700m, 15/IV/1984, *McPherson G. 6477* (P 01573171 [photo]); ibidem (P 01573171 [photo]); ibidem, forested slopes, terrestrial, 600-700m, 15/IV/1984, *McPherson G. 6477* (NOU 055651 [photo]); Mont Ignambi, 1100m, 19/VIII/1965, *Veillon J.M. 397* (NOU 055652 [photo]). **Mount Chapeau:** Mt./Chapeau de Gendarme/Crête Koghi, 22° 11' 17.988'' S, 166° 30' 46.008'' E, 600-700m, 22/IX/1956, *MacKee H.S. 5305* (P 01411589 [photo]). **Mount Mou:** XI/1908, *Rosenstock E. 45* (UC 352546); Montagne Mu, haute vallée au pied du pic, lieux humides, 23/VII/1863, *Deplanche E. 135* (P 01618509 [photo]). **Mount Panié:** dense very wet forest, 500m, 15/XII/1995, *Hodel D.R. 1436* (UC 1606655); above Haut Coulna, on SW forested slopes, 20º 37' 22'' S, 164º 44' 40'' E, 970-1060m, 29/X/1999, *Van der Werff H. & McPherson G. 16005* (UC 1750400); ibidem, dimorphic fern, terrestrial, on steep clay bank, 970-1060m, 29/X/1999, *Vander Werff H. 16005* (NOU 055654 [photo]); north of Hienghène, north-eastern flank of Mont Panié, inland from Wara (Tao), 06/X/2012, *Perrie L. s.n.* (P 026070/A [photo]); ibidem (P 026069 [photo]); vers 500m, sur les parois subverticales et humides en forêt, 18/IX/1966, *Schmid M. 1428* (NOU 055647 [photo]). **Noumea:** Forêt Demazure, 28/IX/2016, *Perrie L. s.n.* (P 028719/A [photo]); Monts Koghis, 29/VII/2017, *Perrie L. s.n.* (P 028703/A [photo]); ibidem, sentier vers le "Chapeau de Gendarme", 650m, 20/V/1965, *Veillon J.M. 157* (NOU 055642 [photo]); *s.n.* (LYJB 000785 [photo]); forêt humide, argile, terrestre, très ombragé, 27/VI/2005, *Allard M, 14* (NOU 014512 [photo]); pente S.W., vers 650m, Relevé KO20, forêt dense, moyenne altitude, schistes, terrestre, 13/X/1994, *Veillon J.M. 7793* (NOU 055641 [photo]); Thy, forêt sur crête; substrat volcano-sédimentaire, fougère terrestre, fertile, long: 166º 31' 6''E, lat: 22º 11' 5'' N, 587m, 23/VII/2009, *Grignon C. 369* (NOU 051529 [photo]). **La Rivière Bleue:** forêt des Electriques, forêt dense humide de moyenne altitude; roches ultramafiques, fougère terrestre, fertile, 12/XII/2006, *Dagostini G. 1217* (NOU 018977 [photo]); Rivière Bleue vers 200-300m, forêt sur péridotites (abundant), 28/IX/1967, *Schmid M. 2.385* (NOU 055644 [photo]); Haute Rivière Blanche, 400m, 14/X/1981, *Veillon J.M. 4559* (NOU 055645 [photo]); Bon Secours, Sur les pentes d'un petit talus, fougére terrestre, fertile, 13/III/2007, *Munzinger J. 4226* (NOU 01745 [photo]). **Wagap**: 1864, *Vieillard E. 1533* (P 01571510 [photo]); ibidem (P 01571511 [photo]; P 01573237 [photo]; P 01618510 [photo]; P 01411551 [photo]; P 01411553 [photo]; P 01411554 [photo]; P 01411566 [photo]; P 01411568 [photo]; P 01571510 [photo]); ibidem (P 01571511 [photo] mixed collection with *C. deplanchei* frond); ibidem (P 01573237 [photo]); Bagup, 1847, *Vieillard E. 1533* (BR 0000013305864 [photo]); ibidem (BR 0000013305871 [photo]). **No loc. (Grande Terre):** 21º 35' S, 165º 56' E, 1855, *Vieillard E. 1933* (K 000722681 [photo]); *Baudouin A. 954* (P 01411559 [photo]); *Le Jolis A. s.n.* (P 01411585 [photo]); VIII/1958, *McGillivray M. 30* (P 01411586 [photo]); ibidem (P 01411591 [photo]); forêts humides, 600m, *Pancher J. 47* (P 01411558 [photo]); 1870, *unknown collector* (US 483253); creeks des forêts profondes, II/1910, *Le Rat A. s.n.* (P 01411595 [photo]); hautes montagnes boisées, 1200m, 1860, *Pancher J. 217* (P 01411546 [photo]); ibidem (P 01411547 [photo]); ibidem (P 01411548 [photo]); ibidem (P 01411549 [photo]); ibidem (P 01411564 [photo]).

Vanuatu – Aneityum island: 20º 12' S, 169º 49' E, *MacGillivray J. s.n.* (K 000722685 [photo]); Aneityum, Mountain Woods, *MacGillivray 47* (P 01532194 [photo]); ibidem , *MacGillivray 47* (P 01532195 [photo]); ibidem, 1859, *MacGillivray 47* (P 01532196 [photo]); ibidem (P 01532197 [photo]); ibidem, 1860, *MacGillivray 47* (P 01532198 [photo]); ibidem, XII/1858, *MacGillivray 47* (P 01532199 [photo]); ibidem, II/1860, *Gillivray M. 47* (P 01411563 [photo]); ibidem, *Paris E.G. 47* (P 01573236 [photo]); ibidem, II/1859, *Gillivray M. 47* (P 01573236 [photo]); New Hebrides-Aneiteum, / II/1859, *47* (US 1431859); New Hebrides-Aneiteum, mountain woods, II/1859, *M. Gillivray 47* (US 1431860); Aneityum Island, Anelgauhat Bay, 2000ft, 05/III/1929, *S.F. Kajewski 879* (US 1550771); II/1859, *M. Gillivray 47a* (US 2987104); Anelgauhat Bay, Rain forest, Common, 610m, 05/III/1929, *Kajewski S.F. 879* (UC 398593).

Comments

The type of *Lomaria opaca* (Mett.) Baker is designated at P herbarium on the plate of the specimen as the holotype (*Vieillard E. 1533* P 00627676), but it seems that Baker originally did not designate this specimen. Even if it had been designated, this specimen would not be a holotype, as Mettenius did not designate it. For this reason, here we consider it as lectotype and isolectotypes the other specimens from the same collection.

Cranfillia opaca has a general distribution throughout New Caledonia, and occurs in lower areas than *C. deplanchei* such as Noumea, but it can also be sympatric with this species in other locations such as Mount Mou. It can be found in many different soil types, so we believe that soil is not a limiting factor for the establishment of the species. This greater ecological plasticity also translates into a wider morphological variation throughout its populations, including some peculiar morphologies, such as *Pancher J.*

217 (P 01411546 and P 01411547) specimens, with more defined and regularly undulating lamina contour. Also, *Paris s.n.* (US 483253) presented much longer and helically curly trichomes, as observed in *C. deplanchei*. This individual was collected in New Caledonia although the specific location is unknown, and it undoubtedly corresponds to *C. opaca* because of the corrugated lamina, irregular contour and bifid apices. The specimen presented well-developed spores, with perispore exhibiting normal ornamentation, which could discard the assumption of a hybrid entity.

Even considering *C. deplanchei* as a separate taxon from *C. opaca*, the latter species still shows a large morphological variation itself. Perrie et al. (2021) considered that there are forms in *C. opaca* of intermediate morphology with *C. deplanchei*, with fronds somewhat more divided than usual, less corrugated lamina and more regular leaf margins than the type of *C. opaca*. In this study we do not consider these individuals intermediate in morphology between the two species, but as intraspecific variation of *Cranfillia opaca*. Among other few morphological characters, Perrie et al. (2021) focused on frond division, being lobate, pinnatifid or pinnatisect in *C. opaca* and only pinnatisect in *C. deplanchei*. Although we think this description is appropriate for both taxa, we do not agree that a deeper division of the sterile lamina in a specimen of *C. opaca* makes it closer to the morphology of *C. deplanchei*. However, other morphological characters such as the bifid-emarginate apices are virtually always present in all individuals of *C. opaca* in this study. Those individuals with "intermediate morphology" clearly exhibit this character. Another character that distinguishes *C. opaca* is the presence of partially areolate venation. This, however, is not a character that can be observed in all individuals, and as Hooker & Baker (1867) say, it is not present in the specimens of the Vanuatu population of *C. opaca*. However, this disjunct population located in Aneityum island, shows some evidence of possibly corresponding to a population with early divergence from those on Grande Terre. All the specimens observed in this study from this location have weaklier emarginate apices, straighter leaf margins, more arched pinnae, and distal end of sterile fronds more divided. While Perrie et al. (2021) considered specimens of this population as "morphological intermediate forms" from Grande Terre, and argued that they could be a third separate species from *C. opaca* and *C. deplanchei*, our results support the hypothesis that this population corresponds to *C. opaca*, as they present emarginated apices, irregularly lobed leaf margins, and short, rigid, and atropurpureous trichomes. Even so, this population on the island of Aneityum could have recently diverged from that of New Caledonia, and therefore it could correspond to an emerging species.

At the phylogenetic level, as shown in the work of Perrie et al. (2021), if we consider all the individuals designated in this study as belonging to *C. opaca* different from those here designated as *C. deplanchei*, *C. opaca* would be a paraphyletic species, with great intraspecific genetic distances and variation among its representatives. However, this is a usual type of phylogenetic relationship between closely related species (Crisp & Chandler 1996; Funk & Omland 2003).

Conclusions

Cranfillia opaca and *C. deplanchei* are considered here as two distinct but closely related species, which fall within the *Cranfillia* group of species that includes *C. nigra*, *C. mucronata*, *C. bakeri*, and *C. fullagari*. In the light of the phylogenetic results obtained by Perrie et al. (2021), the relationship between *C. opaca* and *C. deplanchei* is closer than expected, as based on morphology they are easily recognisable species. In fact, *C. deplanchei* is a monophyletic taxon nested within *C. opaca*, which makes *C. opaca* a paraphyletic taxon.

The individuals considered "of intermediate morphology" between *C. opaca* and *C. deplanchei* by Brownlie (1969) and Perrie et al. (2021) have not been detected in this study. Instead, we found that *C. opaca* is a relatively variable taxon in terms of morphology and size of the sterile fronds, but whose diagnostic characters such as the emarginate apices of pinnae, the abaxially hairy axes, and the irregularly wavy-lobed contour of the sterile fronds, prevail in all individuals. All these features are contrasted with those individuals with obtuse or subacute apices, glabrescent or glabrous axes, and a regular and more divided contour of the sterile fronds, here considered as *C. deplanchei*. Along with these characters, there are also anatomical traits of taxonomic value that separate both species, such as the length and shape of the trichomes, the shape of the abaxial epidermis cells, and the shape, number, and size of different sporangial structures. These morpho-anatomical observations are not the result of more developed individuals considered as *C. deplanchei*, since in the South province small young plants with some of these characteristics have been registered.

The distribution of both species overlaps, both geographically and altitudinally. *Cranfillia opaca* is distributed throughout the main island of New Caledonia, with a disjunct population in Vanuatu. *Cranfillia deplanchei* only occurs in some locations in the Southern Province of New Caledonia, some of which are sympatric with *C. opaca* on Mount Mou, the type locality of *C. deplanchei*, among other areas.

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CHARACTERS	Cranfillia opaca (Mett.) Gasper & V.A.O. Dittrich	Blechnum deplanchei Lenorm.
Sterile frond shape	Oblanceolate, sometimes obovate to spathulate.	Lanceolate.
Rhachis, costae and lateral veins indument	Pilose to glabrescent.	Glabrescent to glabrous.
Sterile lamina margins and contour	Irregular to sublobate, densely pilose.	Slightly winding to straight, glabrescent to glabrous.
Sterile pinnae apex	Bifid to emarginate.	Obtuse to subacute.
Lateral veins	Free, 1 or 2-furcate, as well as areolate.	Free, with simple or 1 to 2-furcate veins.
Pinnae pair numbers	(10-)17-20 (-28)	(26-) 35-40 (-45)
Trichomes	Smooth, 0,32 – 0,66 mm; 3-6 cells.	Taped, helically curly, ≥ 1mm; 5-8 cells.
Abaxial epidermis cells shape.	Undulated, with "U" shaped defined undulations.	Sinuous, with shallow undulations.
Stomata measures	58 x 39 µm	65 x 45 µm
Subterminal fertile pinnae	Scarce (1-3 pairs).	Abundant (4-6 pairs).
Fertile rhachis, costae and indusia indument	Pilose to glabrescent.	Glabrous.
Glandular trichomes	Not observed.	Present on the abaxial surface of fertile costae.
Sporangia capsule	308 x 232 µm	336 x 240 µm
Capsule shape	Elliptic.	Ovate.
Number of annulus cells	(11-) 12-14 (-15)	(13-) 14-16 (-18)
Rosette	31,62 x 66,7 µm	83,66 x 64,62 µm
Pedicel lenght	377,6 µm	462,4 µm
Spores	49 x 31 µm	43 x 27 µm

Table 1. Morpho-anatomical features and measurements in *Cranfillia opaca* and *Blechnum deplanchei*.

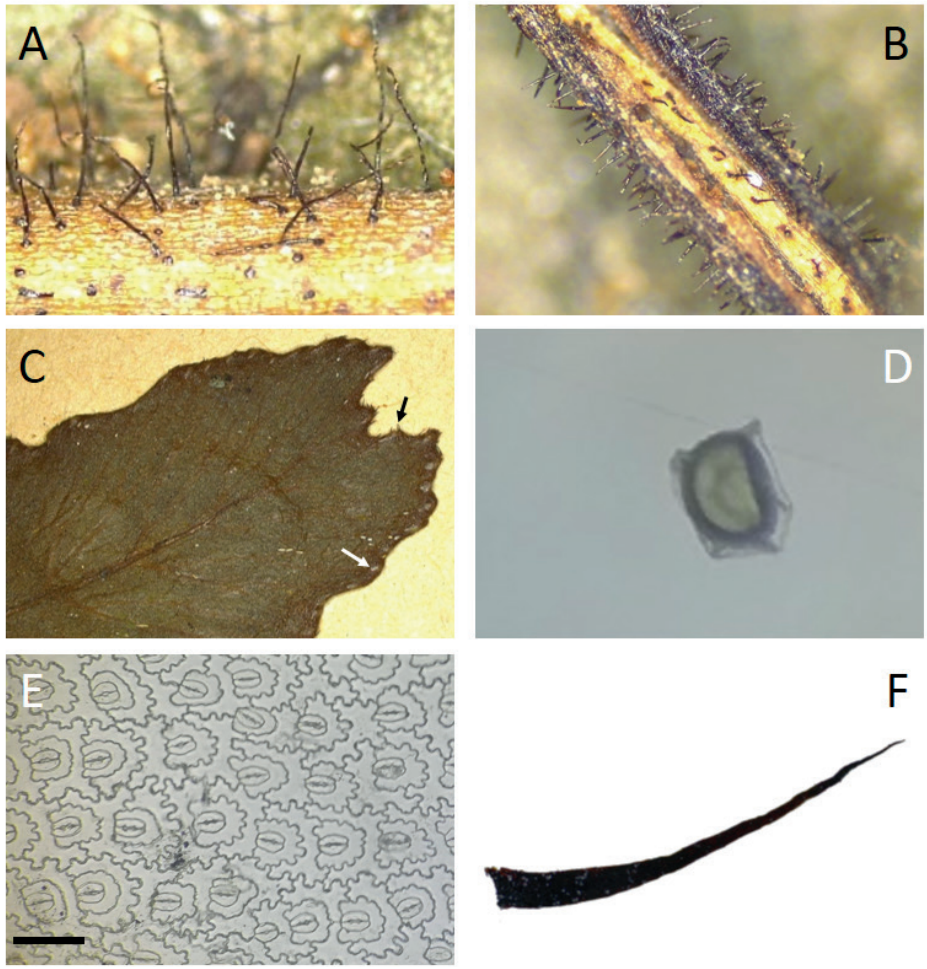

Figure 1. Morpho-anatomical features in *Cranfillia opaca* and *Blechnum deplanchei*. **A**: Trichomes in *B. deplanchei* (*Van der Werff H. & McPherson G. 16107* NY 04187141). **B**: Trichomes on fertile pinnae in *C. opaca* (*Franc 45* US 1096842). **C**: Bifid apex of sterile pinnae in *C. opaca* (*no name 47* US 1431859). **D**: Spores in *C. opaca* (*Lemieux T. 2032a* UC 2082843). **E**: Abaxial epidermis in sterile fronds in *C. opaca* (*Franc 45* US 1096842). **F**: Rhizome scale in *B. deplanchei* (*Van der Werff H. & McPherson G. 16107* NY 04187141). Bar – **A**: 340 µm. **B**: 300 µm. **C**: 2 mm. **D**: 29 µm. **E**: 130 µm. **F**: 3 mm. **Black arrow**: short rigid trichomes. **White arrow**: hydathode.

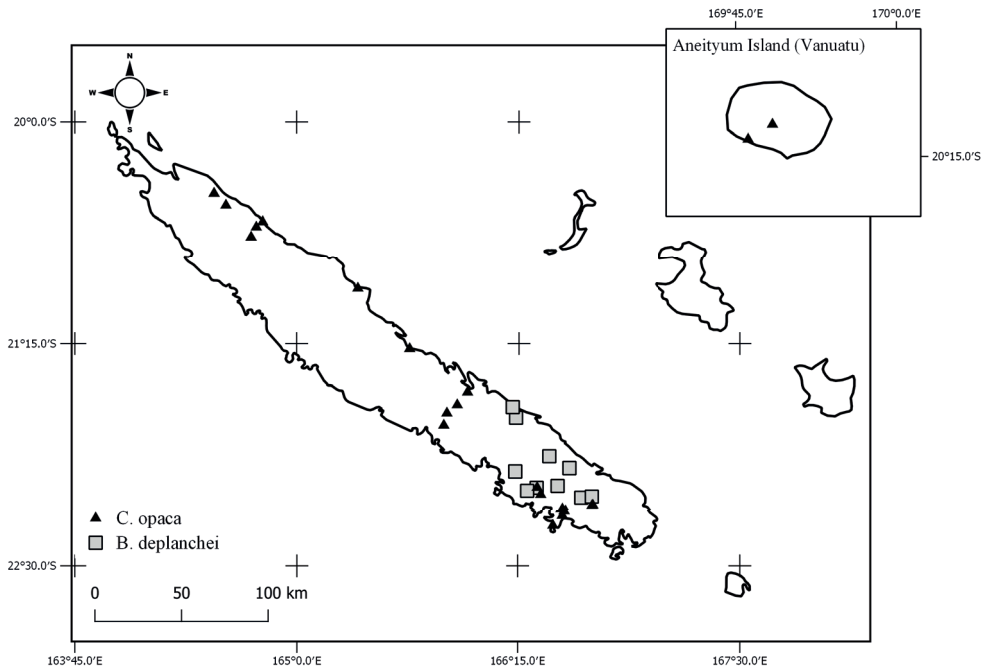

Figure 2. Global distribution of *Cranfillia opaca* and *Blechnum deplanchei* in New Caledonia (Grande Terre) and Vanuatu (Aneityum Island).

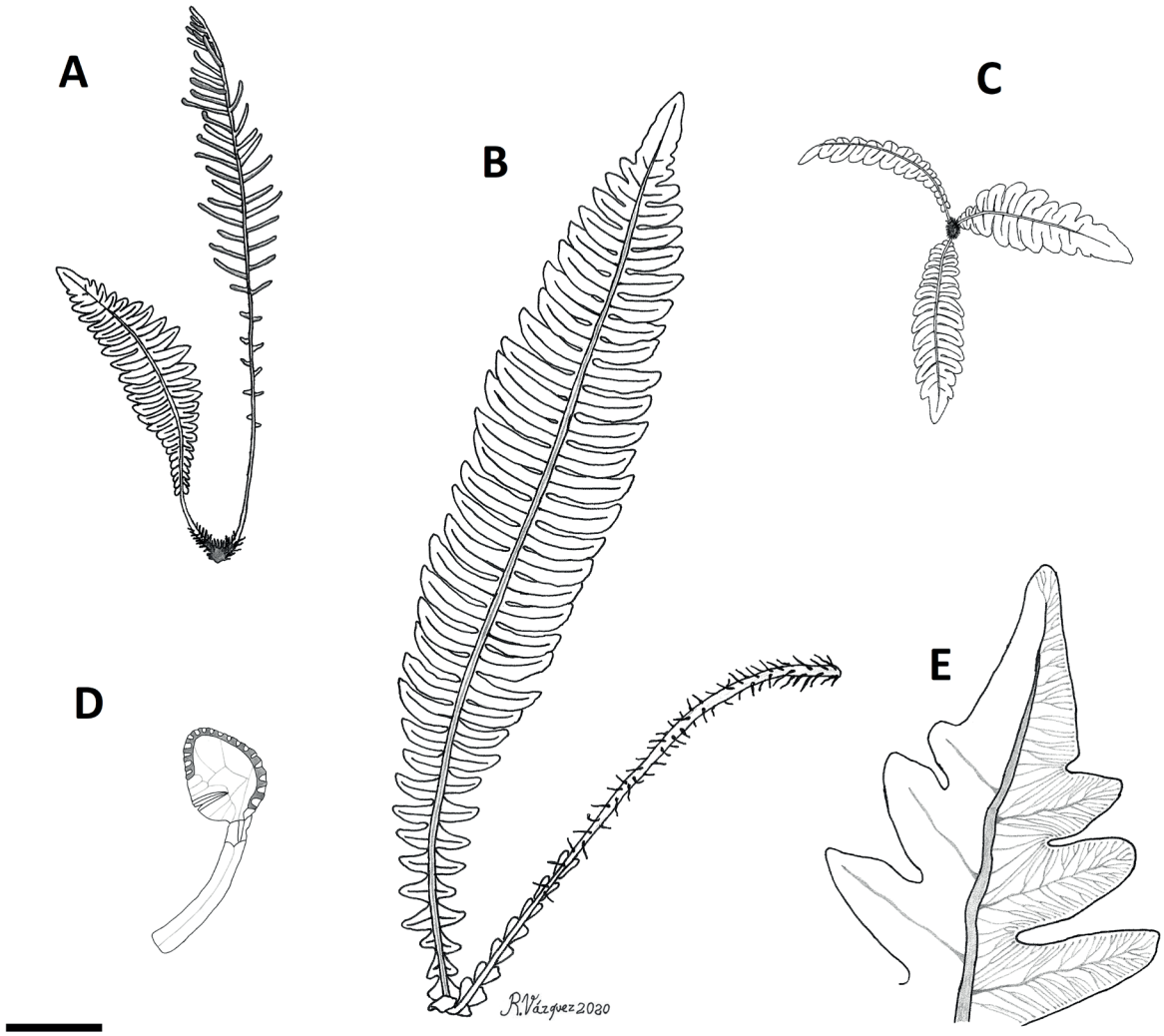

Figure 3. *Cranfillia deplanchei* (Baker) Vázquez Ferreira & Gabriel y Galán comb. nov. **A**: General habit (*Perrie L. 2017-07-29* P028706/A); **B:** Morphology of sterile frond (*Van der Werff H. & McPherson G. 16107* NY 04187141); **C:** Juvenile specimen habit (*Perrie L. 2019-10-25* P030357); **D:** Mature sporangium (*Franc L. 2049* UC 394309); **E:** Sterile frond apex showing lateral vein pattern (*Vieillard E. 1533* P 01411565). Bar – A: 12 cm. B: 4 cm. C: 6,5 cm. D: 300 µm. E: 1 cm.

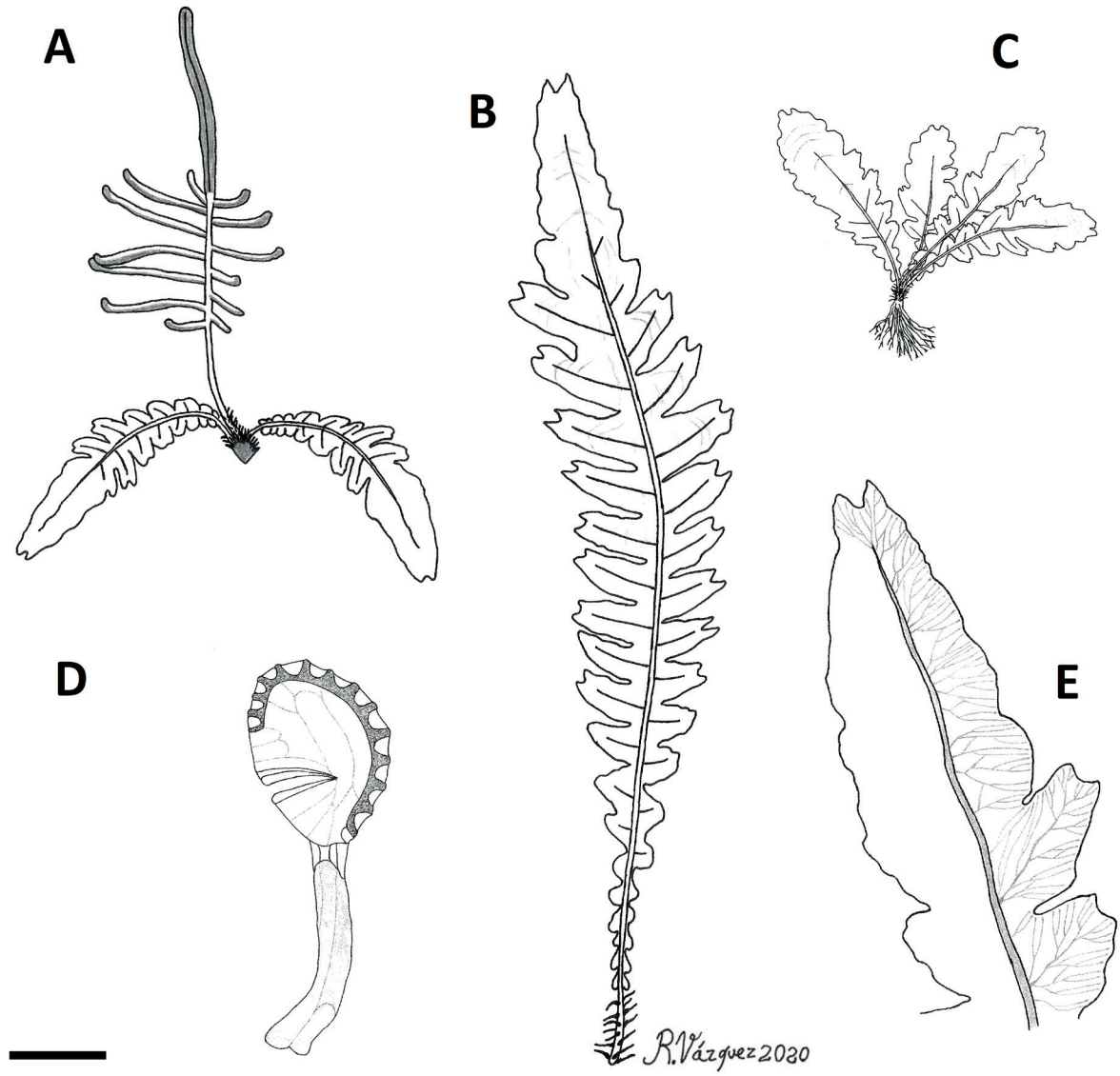

Figure 4. *Cranfillia opaca* (Mett.) Gasper & V.A.O Dittrich. **A:** General habit (*Perrie L. 2016-09-26* P028717); **B:** morphology of sterile frond (*Mazagot M.* P 01411587); **C:** morphology of juvenile specimen (*Pancher J. 217* P 01411548); **D:** mature sporangium (*Lemieux T. 2032a* UC 2082843); **E:** sterile frond apex showing lateral vein pattern (*Mazagot M.* P 01411587). Bar – A: 7 cm. B: 3 cm. C: 5 cm. D: 170 µm. E: 2 cm