

A synopsis of *Ptisana* Murdock ferns (Marattiaceae)
in New Caledonia based on sequence data
and morphology with the recognition of a new
vulnerable species, *P. soluta* (Compton)
Murdock & Perrie comb. nov., stat. nov.

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A synopsis of *Ptisana* Murdock ferns (Marattiaceae) in New Caledonia based on sequence data and morphology with the recognition of a new vulnerable species, *P. soluta* (Compton) Murdock & Perrie, comb. nov., stat. nov.

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ABSTRACT

While New Caledonia is known as a centre of plant endemism, its fern flora has been under-studied. Recent collections of *Ptisana* Murdock, a genus often poorly represented in herbaria due to their large size, enabled new molecular phylogenetic investigation and a reassessment of previously proposed taxonomies based on morphology. Sequence data from the endangered (EN) dwarf species *P. rolandi-principis* (Rosenst.) Christenh. are obtained for the first time and confirm that it is genetically distinct and warrants recognition at the species level. Previous studies suggested that the widespread South Pacific species *P. salicina* (Sm.) Murdock was present in New Caledonia. However, revised analyses indicate that the New Caledonian plants are an endemic species, recognised here for the first time at the species rank as *Ptisana soluta* (Compton) Murdock & Perrie, comb. nov., stat. nov., with a vulnerable (VU) conservation ranking. The most common species, the New Caledonian endemic *P. attenuata* (Labill.) Murdock, is shown to be genetically variable, and warrants further systematic and phylogeographic investigation.

KEY WORDS

Marattiaceae,
Ptisana,
New Caledonia,
conservation,
phylogeny,
lectotypification,
new combination,
new status.

RÉSUMÉ

Un synopsis des fougères du genre Ptisana Murdock (Marattiaceae) en Nouvelle-Calédonie fondé sur des données de séquence et sur la morphologie, avec reconnaissance d'une nouvelle espèce vulnérable P. soluta comb. nov., stat. nov.

Bien que la Nouvelle-Calédonie soit connue comme un centre d'endémisme botanique, sa flore des fougères a été sous-étudiée. De récentes collectes de *Ptisana* Murdock, un genre souvent faiblement représenté dans les herbiers en raison de sa grande taille, a permis une nouvelle étude de phylogénie moléculaire et une révision des taxonomies proposées précédemment, fondées sur la morphologie. Des données de séquence de l'espèce naine en danger (EN) *P. rolandi-principis* (Rosenst.) Christenh. sont obtenues pour la première fois et confirment qu'elle est génétiquement distincte, justifiant une reconnaissance au niveau spécifique. Des études précédentes suggéraient que l'espèce *P. salicina* (Sm.) Murdock, largement répandue dans le Pacifique Sud, était présente en Nouvelle-Calédonie. Cependant, de nouvelles analyses indiquent que les plantes de Nouvelle-Calédonie appartiennent à un taxon endémique, reconnu ici pour la première fois au rang d'espèce comme *Ptisana soluta* (Compton) Murdock & Perrie, comb. nov., stat. nov., avec un statut de conservation vulnérable (VU). L'espèce néocalédonienne la plus commune et endémique *P. attenuata* (Labill.) Murdock est génétiquement variable, ce qui justifie d'autres recherches systématiques et phylogéographiques.

MOTS CLÉS
Marattiaceae,
Ptisana,
Nouvelle Calédonie,
conservation,
phylogénie,
lectotypification,
combinaison nouvelle,
statut nouveau.

INTRODUCTION

Ptisana Murdock is a genus of ferns that is widely distributed in the Paleotropics. It was segregated from *Marattia* Sw. when the latter was found to be paraphyletic in a phylogenetic analysis of Marattiaceae (Murdock 2008a, b). *Ptisana* comprises 30–40 species, but determining the boundaries and relationships for some has proved challenging. The large size of most species means that herbarium collections are usually fragmentary, and poorly represent living plants. Furthermore, there can be discordance between morphological and genetic variation. For instance, a recent examination of *Ptisana* from the Solomon Islands revealed that some species with similar phenotypes were distantly related genetically and, conversely, some divergent phenotypes were genetically indistinguishable with the loci investigated (Murdock *et al.* 2020).

New Caledonia is an archipelago in the southwest Pacific. It has experienced a complex geological history, which has resulted in a variety of soil types including sedimentary and ultramafic substrates (Neall & Trewick 2008; Pillon *et al.* 2021). This variation in substrate, combined with the diverse terrain and climate has resulted in a high level of plant endemism, making it one of the world's biodiversity hotspots (Kier *et al.* 2009; Pillon *et al.* 2021). There are 267 species of ferns currently recognised from New Caledonia, 39% of which are endemic (Morat *et al.* 2012; Munzinger *et al.* 2021). Although regionally high for ferns (Perrie unpub.), this percentage of endemism is considerably lower than for New Caledonian angiosperms (78%) and gymnosperms (98%) (Munzinger *et al.* 2021). This reflects the generally higher dispersal abilities of ferns and the importance of long distance dispersal in the south-west Pacific, including New Caledonia (Ohlsen *et al.* 2014; Del Rio *et al.* 2017). However, ferns in New Caledonia are both under-collected and under-studied (Perrie *et al.* 2016; Del Rio *et al.* 2017), with

recent investigations revealing species that are new or needing reinstatement (Del Rio *et al.* 2017; Perrie *et al.* 2021a, b).

Three species of *Ptisana* are presently listed for New Caledonia (Munzinger *et al.* 2021; Endemia Red List Authority 2022): *Ptisana attenuata* (Labill.) Murdock, *P. rolandi-principis* (Rosenst.) Christenh., and *P. salicina* (Sm.) Murdock. A fourth species of the Marattiaceae is also indigenous to New Caledonia: *Angiopteris evecta* (G.Forst.) Hoffm. (Brownlie 1969; Munzinger *et al.* 2021), which has a widespread indigenous distribution through southern and eastern Asia, tropical Australia, and many Pacific Islands. In *Angiopteris* Hoffm. the sporangia in each sorus are free, at least distally, whereas they are fused into a synangium in *Ptisana*.

New Caledonia's *Ptisana rolandi-principis* is unique in the genus for its very small size. Lavalley & Stampella (2004) said that mature plants could attain a height of 50–60 cm, but the longest frond that we have seen on a herbarium specimen is only 38 cm (P00522609), and fronds of only 14 cm long can be fertile (K000229609) (Herbarium codes follow Thiers 2022). Other species are never fertile so small, and have fronds a few metres in length. Murdock (2008a) knew this species from only two historic collections, and did not list it as distinct, stating that it appeared “to be a juvenile but precociously fertile form of the typical *M. attenuata*”. Christenhusz *et al.* (2011) reinstated it, without justification, although it had been accepted as a distinct species by Brownlie (1969, under *Marattia*) and Sahashi (2008, also under *Marattia*). The only collection cited by Brownlie (1969) additional to the type – *Guillaumin & Baumann-Bodenheim* 8662, P00522611 – is not *P. rolandi-principis* but juvenile *P. attenuata*. Additional collections of *P. rolandi-principis* have been made in the last 15 years, but it remains known from only a single location, Plateau de Dogny, where it grows on riverbanks at 900 to 930 m above sea level within an area of approximately 8 km² (Endemia Red List Authority 2022). *Ptisana rolandi-principis*



FIG. 1. — *Ptisana attenuata* (Labill.) Murdock, field photos: **A**, 3-pinnate frond; **B**, stipes are dark at a distance; **C**, abaxial surface of costae and lamina, with synangia; **D**, stipe dark and wrinkled; **E**, divided stipules around stipe bases. Photos: Leon Perrie, from near Nouméa.

is considered *Critically Endangered* (CR) but remains unprotected by legislation, and it is not within a protected area (Endemia Red List Authority 2022).

Ptisana attenuata is the most abundant species of the genus in New Caledonia. It is endemic to New Caledonia, where it has a widespread distribution on Grande Terre, and is occasionally found in cultivation. However, it is considered

Near Threatened (NT) (Endemia Red List Authority 2022), because of browsing by rusa deer and feral pigs. Earlier authors have suggested that *P. attenuata* might encompass several taxa based on morphological studies of collections (de Vriese & Harting 1853; Fournier 1873) and due to an unusually high level of sequence variability among the collections sampled (Murdock 2008a; Murdock *et al.* 2020).

Only the preceding two species were listed (as *Marattia*) for New Caledonia by Brownlie (1969) and Sahashi (2008), but a third form, found in various states of transition between 2- and 3-pinnate in herbarium collections, has been a source of confusion for earlier authors. Fournier (1873) referred this form to *Marattia pellucida* C.Presl and a 2-pinnate fragment to *Marattia smithii* Kuhn. Compton (1922) similarly referred 2-pinnate collections to *M. smithii*, and gave the bi-tri-pinnate form the name *Marattia smithii* forma *soluta* Compton. Copeland (1929) identified this form as *Marattia mertensiana* C.Presl described from the Caroline Islands while stating that it is “most unlike *M. mertensiana* in appearance.” Murdock (2008a) identified this form as being closest to *Ptisana salicina* (Sm.) Murdock based on DNA sequence data from a plant collected at Koghis.

The type locality of *Ptisana salicina* is Australia’s Norfolk Island, but it also occurs in New Zealand, the Cook Islands, and French Polynesia (Marquesas Islands, Society Islands and Austral Islands) (Murdock 2008a). Both the identity and the status of this third taxon in New Caledonia have been unclear. It was listed as *P. salicina* in 2017 as *Data Deficient* (DD) by the local Red List Authority (Endemia Red List Authority 2022), on the basis of a single collection known to them, which was from Mont Panié in the north-east of Grande Terre. Two of the present authors (LRP, RA) were involved in this assessment. They, along with LDS, during a workshop on fern identification for local botanists, chanced upon a population of this bi-tri-pinnate *Ptisana* at Koghis previously unknown to them. This site overlooks Nouméa, New Caledonia’s principal population centre, and has been visited multiple times by the aforementioned authors, as well as by many local and visiting botanists. That this large species, with fronds several metres long, remained unrecognised by most recent botanists at this popular site attests to the limited understanding of *P. salicina* in New Caledonia. Along with the recent description of the tree *Alectryon hirsutus* Munzinger *et al.* from the same area (Munzinger *et al.* 2020), it is also an indication of the considerable work still required to adequately document the rich New Caledonian flora.

More broadly, the taxonomy of *Ptisana salicina* is also unclear. Phylogenetic analyses of chloroplast DNA sequences indicate samples of *P. salicina* from the Cook Islands, the Marquesas Islands, New Caledonia, and New Zealand form a well-supported clade that also includes samples of *P. smithii* (Kuhn) Murdock from Fiji and the Santa Cruz Islands (Murdock 2008b; Murdock *et al.* 2020). *Ptisana smithii* also occurs in Samoa, Tonga, and its type collection is from Aneityum, the southernmost island in Vanuatu (Murdock 2008a). *Ptisana salicina* and *P. smithii* have been morphologically separated by the synangia being longer and marginal in the former versus shorter and more distant in the latter (Copeland 1932; Christensen 1943). Moreover, *P. smithii* has rust-coloured scales (versus tan in *P. salicina*), a strong bend in the vein at the attachment point of the synangium (less apparent in *P. salicina* because the synangium sits at the margin), and strongly repand lamina margins in living plants (subtly so in *P. salicina*) (AGM pers. obs.). However, these two species are not clearly separated in phylogenetic analyses. Additionally, the morphology of plants identified as *P. salicina* varies from island group to island group, suggesting further

study is required within this clade (Murdock *et al.* 2020). The form found in New Caledonia is unique in the *P. salicina* clade for its bi-tri-pinnate fronds.

Here we provide an overview of *Ptisana* in New Caledonia. New results include the first published DNA sequences for *P. rolandi-principis*, the recognition of *P. soluta* (Compton) Murdock & Perrie, comb. nov., stat. nov. at species rank (for the New Caledonian plants previously referred to *P. salicina*), as well as additional sequenced samples for *P. attenuata* from new localities.

METHODS

MORPHOLOGY

The species of *Ptisana* in New Caledonia were characterised using collections in BM, NOU, P, UC, and WELT, as well as our local field experience. With regard to *P. salicina* outside New Caledonia, we consulted Green (1994, for Norfolk Island), Brownsey & Perrie (2014, for New Zealand), Copeland (1932, for the Society Islands), Brown & Brown (1931, for south-eastern Polynesia) and Sykes (2016, for the Cook Islands), as well as Brownlie (1977), Sahashi (2008), and Murdock *et al.* (2020) for *P. smithii*.

Distributions were mapped using QGIS 3.10.2 (QGIS 2020) with layers from GeoRép (<https://georep.nc>, accessed 24 March 2020). The conservation status of *Ptisana soluta* comb. nov., stat. nov. was assessed against the IUCN Red list criteria (IUCN 2012), with Extent of Occurrence and Area of Occupancy (with a cell width of the default 2 km) calculated using GeoCAT (<http://geocat.kew.org>, accessed 1 March 2022; Bachman *et al.* 2011). Four unvouchered field observations of *P. soluta* comb. nov., stat. nov. by RA (Thy Valley, Dzumac, Colnett, Diahoue; the first three have accompanying photos on www.endemia.nc) were included in the map and the area calculations.

DNA ANALYSES

Sequences were newly-generated from four specimens of *Ptisana attenuata*, including a specimen that was collected from Plateau de Dogny where it is sympatric with *P. rolandi-principis*. Sequences were also newly-generated from one sample each of *P. rolandi-principis* and *P. soluta* comb. nov., stat. nov. (Appendix 1).

DNA was extracted from silica gel-dried frond tissue using a modified-CTAB extraction method (steps 1, 3-7 from Table 1 in Shepherd & McLay 2011). Two chloroplast regions were sequenced following Murdock *et al.* (2020): *trnSGG* (the region from *trnS* GCU to *trnG* UUC, including the *trnG* intron), and *rps4-trnS* (*rps4* gene plus the *rps4-trnSGGA* intergenic spacer). PCR amplifications were performed using the primers in Murdock (2008b). Each locus was amplified in 12 µL PCR reactions that contained 1 µL of diluted template DNA, 1 × MyTaq mix (Bioline), 0.5 µM each primer and 0.1 M betaine. All loci were PCR amplified using the ‘slow and cold’ thermocycling protocol of Shaw *et al.* (2005). PCR products were purified by digestion with 0.5 U shrimp alkaline phos-



FIG. 2. — *Ptisana rolandi-principis* (Rosenst.) Christenh. field photos: **A**, adaxial surface of individual with several fronds, with finger for scale. **B**, abaxial surface of frond with immature synangia. Photos: Leon Perrie, from Plateau de Dogny.

TABLE 1. — Morphological characters distinguishing the three species of *Ptisana* Murdock in New Caledonia. All characters need further investigation, particularly those marked * which are difficult to assess in herbarium material or images thereof.

	<i>P. attenuata</i> (Labill.) Murdock	<i>P. rolandi-principis</i> (Rosenst.) Christenh.	<i>P. soluta</i> comb. nov., stat. nov.
Stipe length	> 100 cm except in juveniles	≤ 25 cm	> 100 cm except in juveniles
Stipe colour	purplish-black	brown, speckled blackish-purple	patchy dark-brown to green
Stipe texture	transversely and irregularly wrinkled	smooth	smooth
Lamina dimensions	> 100 cm for both length and width, except in juveniles	fertile plants 5.9-15.6 cm long, 5.1-13.3 cm wide	> 100 cm for both length and width, except in juveniles
Lamina division	uniformly 3-pinnate when fertile, but 2-pinnate in juveniles up to c. 40 cm long.	1- to 2-pinnate	fertile plants 3-pinnate proximally but 2-pinnate distally; juveniles unknown but presumably may be 2-pinnate
Number of secondary pinnae	many	absent, or up to 2 pairs on a primary pinna	many
Pinnule margins	serrulate to serrate, more prominently towards the pinnule apex where it is sometimes doubly-serrate (with 2-3 veins per tooth). Juveniles can approach <i>P. rolandi-principis</i> , though rarely so irregular.	prominently and irregularly serrate; larger teeth comprising multiple veins	sub-entire to serrulate, more clearly serrated towards the pinnule apex
Colour of costae*	green-brown or brown (perhaps darker in juveniles)	purplish-black on both surfaces (at least when fresh)	green-brown or brown
Vein colour on abaxial surface*	pinnule mid-veins green or brown (at least with magnification); lateral veins usually green but can be c. black	pinnule mid-veins purplish-black; lateral veins black	pinnule mid-veins green or brown (at least with magnification); lateral veins usually green but can be c. black
Scales on abaxial lamina*	dark brown, flexuous, narrowly triangular with multiple marginal cilia on costae and pinnule mid-veins, to brown, curly c. stellate on lateral veins	black, narrowly triangular with multiple marginal cilia on costae and pinnule mid-veins, to c. stellate on lateral veins	black, flexuous, narrowly triangular sometimes with marginal cilia on costae and pinnule mid-veins, to brown, c. stellate on lateral veins
Stipule morphology*	Deeply divided to claw-like	Divided, chartaceous	Shallowly divided to nearly entire with ragged margins

phatase (rSAP; New England Biolabs, Massachusetts, United States) and 2.5 U exonuclease I (ExoI; New England Biolabs, Massachusetts, United States at 37°C for 15 min, followed by inactivation of the enzymes by 15 min at 80°C. DNA sequencing was performed in both directions by capillary separation at Macrogen (Seoul, South Korea). Sequences were edited in Sequencher 5.4.6 (Gene Codes Corporation).

For phylogenetic analysis, our newly-generated DNA sequences were aligned to all of the sequences of *Ptisana attenuata*, *P. smithii* and *P. salicina* that were available from GenBank, as well as sequences representing the other *Ptisana* clades identified by Murdock *et al.* (2020). *Ptisana fraxinea* (Sm.) Murdock was used to root the phylogenies, based on its position in the phylogenies of Murdock (2008b) and Murdock *et al.* (2020). Sequences were aligned with MAFFT 6.849 (Katoh & Toh 2008) on the EMBL-EBI online server, using default settings. Regions of ambiguous alignment were identified and excluded with GBlocks v0.91b (Talavera & Castresana 2007), with the least restrictive settings. Indels (insertion-deletions events) were treated as missing data. The two loci were concatenated for subsequent analyses because they are both from the chloroplast and preliminary phylogenetic analyses revealed no strongly supported conflict between them.

Phylogenetic analyses were performed using PAUP* v.4.0b10 (by D. L. Swofford, Sinauer Associates, Sunderland, MA) with maximum parsimony (MP), the PhyML v.3.0 web server (<http://www.atgc-montpellier.fr/phyml>, accessed 19 August 2021; Guindon *et al.* 2010) with maximum likelihood (ML), and MrBayes v.3.2.7 (Huelsenbeck & Ronquist 2001) for Bayesian inference (BI).

The MP analyses were performed using a heuristic search algorithm with 100 random addition sequence replicates, and tree bisection reconnection branch-swapping. Branch support was assessed using 100 bootstrap pseudoreplicates, each with 10 random addition replicates. For ML analyses the best-fit models of sequence evolution were determined with Smart Model Selection (GTR + G for *trnSGG* as well as the combined dataset, and GTR + I for *rps4-trnS*) and the Akaike information criterion (Lefort *et al.* 2017). Heuristic searches were performed with 10 random addition sequence replicates and subtree pruning-regrafting (SPR) branch-swapping. Branch support was assessed with 1000 bootstrap (BS) pseudoreplicates. For BI, two concurrent analyses were run, each with four Markov chains of 5 million generations that were sampled every 1000 generations, and with *nst* = 6, rates = invgamma, the default priors, and the substitution model parameters unlinked across



FIG. 3. — *Ptisana soluta* (Compton) Murdock & Perrie, comb. nov., stat. nov., field photos: **A**, frond with lamina 3-pinnate proximally and 2-pinnate distally. The frond at top-right is *P. attenuata* (Labill.) Murdock; **B**, stipes are greenish-brown at a distance; **C**, abaxial surface of costae and fertile lamina, showing transition from 3-pinnate to 2-pinnate; **D**, stipe greenish-brown and smooth; **E**, stipules around stipe bases. Photos: A-D, Leon Perrie from near Nouméa; E, Rémy Amice, from near Nouméa.

the two loci. Tracer v.1.7.1 (Rambaut *et al.* 2018) was used to assess stationarity, with the first 20% of samples discarded as ‘burn-in’.

Additionally, genealogical relationships among *P. attenuata* and *P. rolandi-principis* chloroplast haplotypes, and among *P. salicina*, *P. soluta* comb. nov., stat. nov., and *P. smithii*

chloroplast haplotypes, were determined using median joining networks (Bandelt *et al.* 1999) produced with PopART (Leigh & Bryant 2015). Because of the narrower focus of these analyses, new alignments were produced for each species complex, with ambiguously aligned nucleotide regions excluded as described above.

RESULTS

MORPHOLOGY

Three species of *Ptisana* are accepted here for New Caledonia: *P. attenuata*, *P. rolandi-principis*, and *P. soluta* comb. nov., stat. nov. (see Taxonomy section). Figs 1-3 are field photos of each species. They are distinguished morphologically as detailed in Table 1, although all characters should be further investigated, particularly in the field. Herbarium specimens that could be identified as one of these species with some confidence are listed in Appendix 2. The distributions of the three species are mapped in Fig. 4, based on the collections in Appendix 2, supplemented by unvouchered field observations for *P. soluta* comb. nov., stat. nov.

Ptisana rolandi-principis is easily distinguished by the small size of its fertile fronds, including the small dimensions and the lamina being only 1- or 2-pinnate. Among the other characters (Table 1), the darkness of the mid-veins may be the most reliable. The lamina of *P. rolandi-principis* is prominently serrate to doubly-serrate. Juveniles of *P. attenuata* can be similar, but their serration is generally less pronounced or irregular; they can of course be distinguished by being sterile when small.

Ptisana attenuata cannot be distinguished by its eponymous character state, as *P. soluta* comb. nov., stat. nov. can also have attenuate or acuminate apices on its pinnules. However, in the field, they are easily separated by their lamina division, and their stipe colour and texture. *Ptisana attenuata* has blackish, transversely-wrinkled stipes, and uniformly 3-pinnate lamina (except in small juveniles). By contrast, *P. soluta* comb. nov., stat. nov. has greenish, unwrinkled stipes. In *P. attenuata*, the stipules that clasp the stipe base are deeply divided to claw-like, while those of *P. soluta* comb. nov., stat. nov. are shallowly divided to nearly entire based on limited observations. The smooth, green stipes of *P. soluta* comb. nov., stat. nov. means it is easily confused with *Angiopteris evecta* at a distance. However, *P. soluta* comb. nov., stat. nov. is recognisable by the transition in its lamina from 3-pinnate proximally to 2-pinnate distally, larger pinnules that lack false veins, and synergia when fertile.

Distinguishing *Ptisana attenuata* and *P. soluta* comb. nov., stat. nov. from herbarium specimens is less straightforward. The stipe is usually not collected, and a 3-pinnate proximal portion of a frond of *P. soluta* comb. nov., stat. nov. could be mistaken for *P. attenuata*. This is the identification mistake we are most likely to have made with the specimens listed in Appendix 2, as only collections showing the 3-pinnate to 2-pinnate transition (Fig. 5) were identified as *P. soluta* comb. nov., stat. nov.

No obvious morphological differences were identified between the two genetic lineages found in *Ptisana attenuata* (see next section). It is possible that the lateral veins in the pinnules fork only rarely in the (south-)western plants, and then mostly proximally, while (north-)eastern plants have many forked lateral veins, with the forking

occurring at various distances from the mid-vein; this, however, needs further investigation, and careful field observation may yield additional distinctions.

Ptisana soluta comb. nov., stat. nov., while genetically related to *P. salicina*, differs in being 3-pinnate proximally and 2-pinnate distally, and in having sub-marginal sori. Based on the references cited above, online photos of living plants, and our own fieldwork in New Zealand, plants of *P. salicina* from Norfolk Island, New Zealand, and the Cook Islands are uniformly 2-pinnate (as is *P. smithii*), and have marginal sori. The sori of *P. soluta* comb. nov., stat. nov. are noticeably distant from the lamina margin, like those of *P. attenuata*, but not as medial as generally the case for *P. smithii*. *Ptisana soluta* comb. nov., stat. nov. is endemic to New Caledonia, where it has an area of occupancy of 60 km² and extent of occurrence of 4236 km².

DNA ANALYSES

After the exclusion of ambiguously aligned sites in Gblocks, the concatenated alignment of the *trnSGG* and *rps4-trnS* sequences for all samples was 2565 base-pairs (bp) in length. There were 161 variable characters of which 56 were parsimony-informative. The trees produced by the three analyses had similar topologies to each other and the phylogeny of Murdock *et al.* (2020). MP analysis recovered 1499002 most parsimonious trees with a length of 182 and a consistency index of 0.896. The Bayesian phylogram, with support values from all three analyses, is shown in Fig. 6.

Ptisana rolandi-principis formed a polytomy with two lineages of *P. attenuata* (0.99 posterior probability (PP) with BI, 60% bootstrap (BS) support with MP and 72% BS with ML). *Ptisana rolandi-principis* had three autapomorphic substitutions and one deletion in a mononucleotide run, all located in the *trnSGG* locus. One of the *P. attenuata* lineages comprised two newly-sequenced samples from eastern New Caledonia (*Perrie NC-2012-224* and *Perrie 8409*; Fig. 6) which shared one synapomorphic substitution in *trnSGG* and received strong to moderate support (0.98 PP, 65% MP BS and 71% ML BS). Despite the genetic distinctiveness of this lineage we found no morphological features to separate it from the remaining *P. attenuata* samples.

The remaining *Ptisana attenuata* samples formed a well-supported clade (1.00 PP, 98% MP BS and 99% ML BS) and shared three synapomorphic substitutions (one in *rps4-trnS* and two in *trnSGG*). The samples 125 and 126 shared a further two synapomorphic substitutions, both in *trnSGG*.

The samples of *Ptisana salicina*, *P. smithii*, and *P. soluta* comb. nov., stat. nov. formed a well-supported clade (1.00 PP, 98% MP BS and 93% ML BS). The two samples from New Caledonia (*Murdock 333* and *Perrie et al. 8330*) did not cluster together and the relationships between the remaining samples were also unresolved, except for a clade containing the three *P. smithii* samples from Fiji (0.96 PP, 63% MP BS and 62% ML BS).

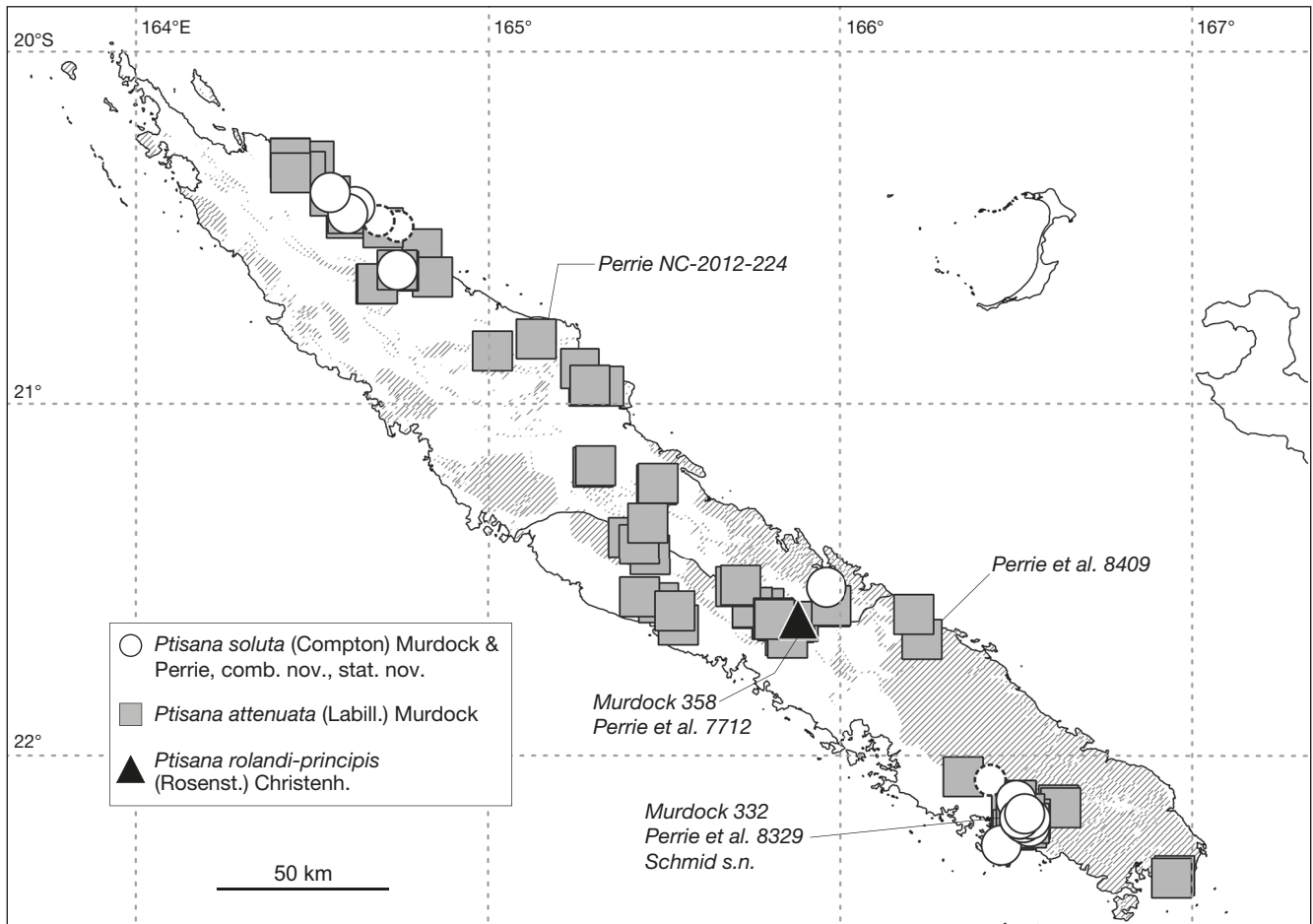


FIG. 4. — Distribution map for the New Caledonian endemic species of *Ptisana attenuata* (Labill.) Murdock (■), *P. rolandi-principis* (Rosenst.) Christenh. (▲), and *P. soluta* (Compton) Murdock & Perrie, comb. nov., stat. nov. (○, with unvouchered field observations indicated by a broken outline). Shaded areas are ultramafic substrates. The collecting sites of the sequenced *P. attenuata* samples are indicated.

The alignment comprising only the *Ptisana attenuata* and *P. rolandi-principis* sequences, with ambiguously aligned regions excluded, was 2536 bp in length and contained 27 variable characters, of which 12 were parsimony-informative. Each of the six *P. attenuata* specimens exhibited a unique chloroplast haplotype, which differed by one to 19 substitutions (Fig. 7). The haplotype sequenced from the *P. rolandi-principis* specimen differed from the closest *P. attenuata* haplotype by five substitutions.

The alignment comprising only the *Ptisana salicina*, *P. smithii*, and *P. soluta* comb. nov., stat. nov. sequences, with ambiguously aligned regions excluded, was 2507 bp in length and contained 18 variable characters, three of which were parsimony-informative. There were seven haplotypes detected amongst the 11 samples and these differed by one to nine substitutions. The median-joining network was star-like with a central haplotype that was detected in two of three *P. smithii* specimens from the Solomon Islands, the *P. salicina* specimen from the Cook Islands (Rarotonga) and one of the *P. soluta* comb. nov., stat. nov. specimens from New Caledonia (Fig. 7). The second and newly sequenced sample of *P. soluta* comb. nov., stat. nov. from New Caledonia differed from this central haplotype by a single substitution.

DISCUSSION

RECOGNITION OF *PTISANA ROLANDI-PRINCIPIS*

We believe that the current understanding of morphological and genetic variation in New Caledonian *Ptisana* is best reflected taxonomically by the recognition of three species: *P. attenuata*, *P. rolandi-principis*, and *P. soluta* comb. nov., stat. nov. All three are endemic to New Caledonia, but *P. attenuata* and *P. rolandi-principis* are comparatively closely related. They are not reciprocally-monophyletic in phylogenetic analyses of the chloroplast DNA sequence data, with the haplotype found in *P. rolandi-principis* forming a polytomy with the two lineages found in *P. attenuata*. Nevertheless the haplotype of *P. rolandi-principis* is quite distinct from those of *P. attenuata*. Importantly, they are also morphologically distinct, with *P. rolandi-principis* being easily recognised by the small size at which it produces spores and its irregular lamina serration. Furthermore, this morphological and genetic distinctiveness is maintained in sympatry, and justifies recognition of *P. rolandi-principis* as a separate species. The small size of adult *P. rolandi-principis* may be the result of pedomorphic-like evolution.



FIG. 5. — The holotype of *Ptisana soluta* (Compton) Murdock & Perrie, comb. nov., stat. nov. (Compton 1674, Ignambi, 1914, BM[BM000787128]) showing how the lamina transitions from 3-pinnate proximally to 2-pinnate distally. CC BY The Trustees of the Natural History Museum, London.

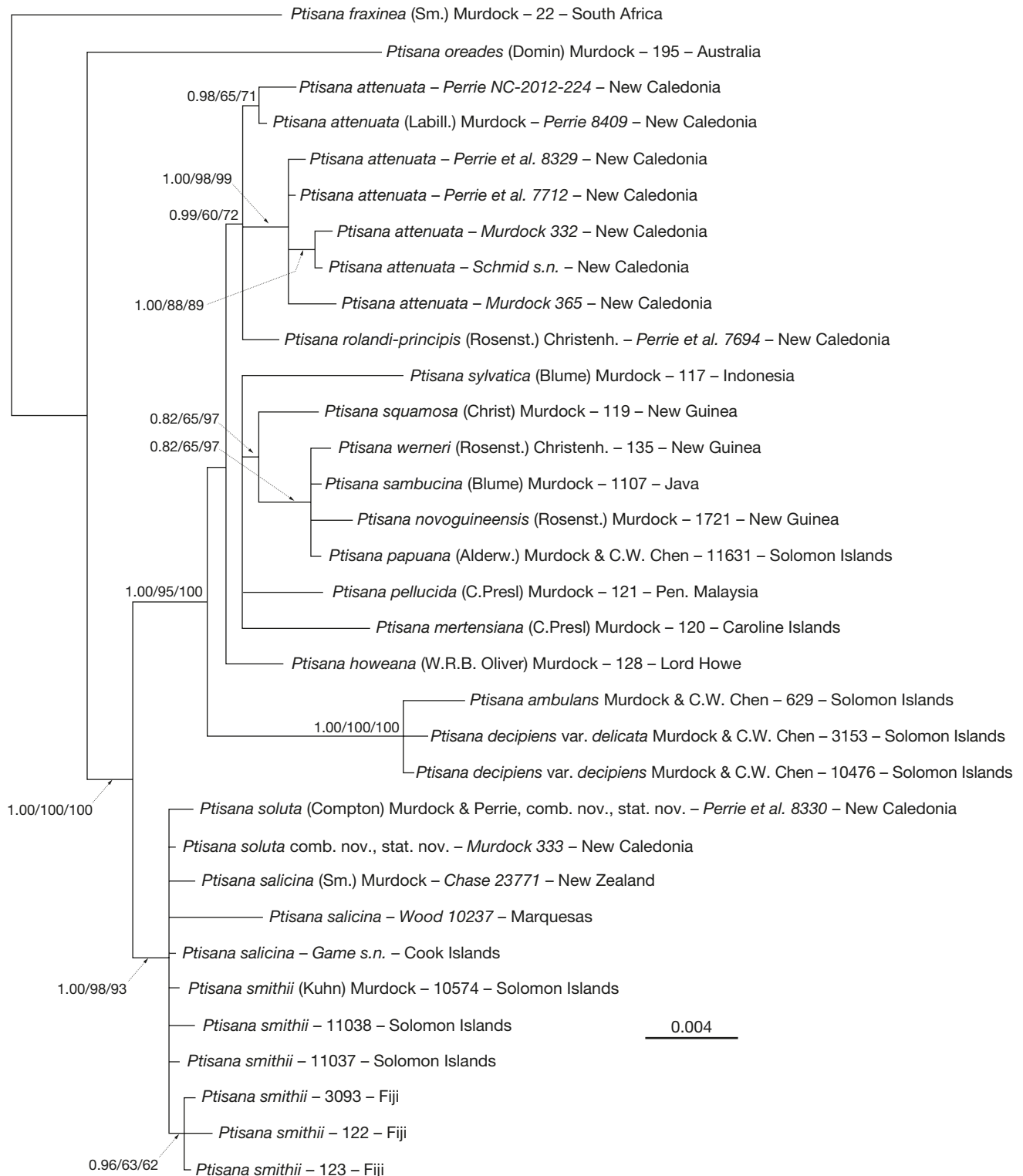


FIG. 6. — Phylogram from the Bayesian phylogenetic analysis of the chloroplast DNA sequence data for *Ptisana* Murdock. Support values for branches are given in the order of Bayesian inference posterior probability; maximum parsimony bootstrap support; and maximum likelihood bootstrap support. Only values >0.80 PP and 60% BS are shown.

Ptisana rolandi-principis is confined to a small area on Plateau de Dogny. This area is a 'Hotspot of Narrow Plant Endemism' (Wulff *et al.* 2013) containing a number of rare species including *Psychotria gateblei* Barrabé ined. (Rubiaceae; Endemia Red List

Authority 2022), *Paphia neocaledonica* (Guillaumin) P.F.Stevens (Ericaceae; Endemia Red List Authority 2022) and the recently-described fern *Lastreopsis abscondita* Perrie & Amice (Dryopteridaceae; Perrie *et al.* 2021a). Plateau de Dogny is unusual

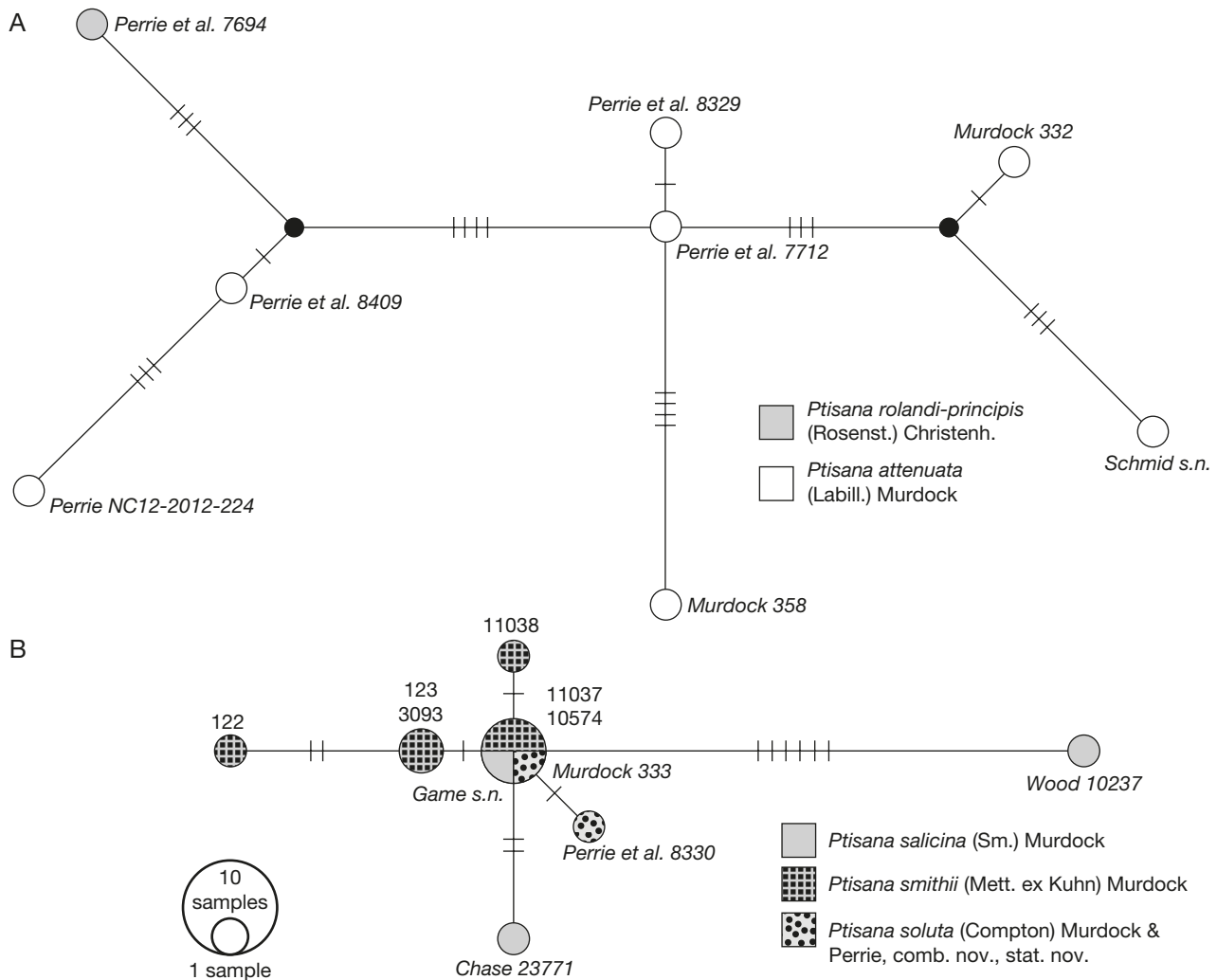


FIG. 7. — Median-joining networks based on *trnSGG* and *rps4-trnS* sequences: **A**, the *Ptisana attenuata* clade; **B**, the *P. salicina*/*P. soluta* comb. nov., stat. nov./*P. smithii* clade. The size of each circle is proportional to the haplotype frequency. Undetected intermediate haplotypes on nodes are shown as black circles and hatch marks represent mutational steps separating haplotypes.

amongst other New Caledonian hotspots because it is located on volcanic-sedimentary substrate, rather than ultramafic (Wulff *et al.* 2013). Despite its high diversity, Plateau de Dogny is not in a protected area and, although it is not at risk from mining, the vegetation there could be susceptible to fire (Wulff *et al.* 2013) and at least the lower slopes are heavily browsed (pers. obs.).

HIGH GENETIC DIVERSITY IN *PTISANA ATTENUATA*

As noted, our phylogenetic analyses of chloroplast DNA sequences did not recover *Ptisana attenuata* as monophyletic. The two eastern *P. attenuata* samples among our newly-sequenced samples formed a well-supported lineage that was as distinct from the remaining *P. attenuata* samples, as was *P. rolandi-principis*. However, we found no obvious morphological differences between our eastern and western samples. This result mirrors the findings from a study of *Ptisana* in the Solomon Islands, where genetic and morphological divergence were found in some instances to be uncoupled (Murdock *et al.* 2020). The two chloroplast DNA lineages in *P. attenuata*, which are allopatric on present understanding, could represent intraspecific varia-

tion, or they could be indicative of two separate evolutionary lineages that might warrant taxonomic recognition. Resolving these two hypotheses requires more detailed study with broad geographic sampling and, preferably, nuclear markers such as ddRADSeq loci (e.g., Shepherd *et al.* 2019), which could also elucidate past hybridisation events. For now, we circumscribe *P. attenuata* on morphological grounds.

Regardless of whether the chloroplast diversity detected within *Ptisana attenuata* represents a species complex or intraspecific variation, it may be useful for examining spatial patterns of genetic variation (phylogeography). Few phylogeographic studies have been published for New Caledonian plants (Pillon *et al.* 2021) and none for ferns. However, high levels of genetic structuring have been detected from the plants that have been examined to date; e.g., Bottin *et al.* (2005), Kurata *et al.* (2008), Poncet *et al.* (2013), Wulff *et al.* (2017). Although ferns generally have high dispersability owing to their wind-blown spores, some ferns from elsewhere are known to exhibit high intraspecific diversity and phylogeographic structuring; e.g., Shepherd *et al.* (2007), Ohlsen *et al.* (2020), Wei & Zhang (2022).

RECOGNITION OF *PTISANA SOLUTA* COMB. NOV., STAT. NOV. New Caledonian plants previously ascribed to *Ptisana salicina* – or *Marattia smithii* (Compton 1922), or *M. mertensiana* (Copeland 1929) – clearly represent an additional species within the territory, being both genetically and morphologically distinct from *P. attenuata* and *P. rolandi-principis*.

With phylogenetic analyses of chloroplast DNA sequences, the New Caledonian plants fall within a clade of samples identified as *P. salicina* and *P. smithii*. While there is genetic diversity in this clade, we were not able to clearly resolve the relationships of the taxa within this clade based on the loci that were sequenced. However, the proximally 3-pinnate laminae of New Caledonian plants distinguishes them morphologically from both *P. salicina* from its type locality and elsewhere and from *P. smithii*, which are 2-pinnate. New Caledonian plants additionally differ from *P. salicina* in having their synangia further from the margin (although not as medial as usually the case for *P. smithii*), their darker and slightly-wider scales on the abaxial lamina, and perhaps also in the lateral veins of their pinnules being at least sparsely scaly whereas those of *P. salicina* are almost glabrous. The synangia of New Caledonian plants may generally be slightly longer than those of *P. salicina*, but their ranges overlap substantially.

Compton (1922) recognised this New Caledonian form as *Marattia smithii* Mett. forma *soluta* Compton. Following current practices in Marattiaceae where clearly distinct morphological forms with disjunct ranges are recognised at the species level even when the phylogenetic relationships remain unresolved (e.g., Senterre *et al.* 2014, Murdock *et al.* 2020), we are recognising the New Caledonian form here at the species level: *Ptisana soluta* (Compton) Murdock & Perrie, comb. nov., stat. nov. Compton's labels on specimens that he collected on the same trip as the holotype and notes with the protologue suggest that *P. soluta* comb. nov., stat. nov. may sometimes be fully 2-pinnate. But, as his notes sometimes seem inconsistent, this needs verification, particularly in the populations where Compton collected.

We anticipate that other regional segregates from the *P. salicina* clade will also be recognised as species upon further study in island groups across the South Pacific. The transitioning lamina of *P. soluta* comb. nov., stat. nov. may reflect a hybrid origin between 3-pinnate *P. attenuata* and 2-pinnate *P. salicina* or *P. smithii*. *Ptisana soluta* comb. nov., stat. nov. is clearly linked to the latter pair by chloroplast sequences, but the shape of its pinnules are similar to *P. attenuata*.

In the following Taxonomy section, additional details are given for *Ptisana soluta* comb. nov., stat. nov. since this is the first time it has been distinguished as a separate species. Because it is easily recognised in the field, we anticipate botanists in New Caledonia will find more populations, possibly many more. Such success will enable a better understanding of its ecology, and may require revision of its morphological description and provisional Vulnerable conservation status. Nevertheless, all Marattiaceae in New Caledonia remain susceptible to damage by introduced deer and pigs.

SYSTEMATICS

Family MARATTIACEAE Kaulf.

Genus *Ptisana* Murdock

Ptisana attenuata (Labill.) Murdock
(Fig. 1)

Taxon 57: 746 (Murdock 2008a). — *Marattia attenuata* Labill., *Sertum Austro-Caledonicum*: 9, t. 13, 14. (Labillardière 1824). — Type: **New Caledonia**. *Labillardière s.n.* (lecto-, designated here, P[P00518397]!; isolecto-, P[P00518392, P00518393, P00518394, P00518395, P00518396, P00518398, P01646579]!; B[B-W-19456]!; BM[BM000787118]!; FI[FI004197]!). — Note: The specimen in FI bears Labillardière's own description and would have been our first choice for a lectotype. However, Brownlie (1969) made a first-step lectotypification restricting the choice to a specimen in P.

Marattia acuminata Willd. Ex Kaulf., *Enumeratio Filicum*: 33, t. 1, f. 2. (Kaulfuss 1824). — Type: **New Caledonia**. *Labillardière s.n.* (lecto-, designated here, B[B-W 19456]!; isolecto-, P[P00518392, P00518393, P00518394, P00518395, P00518396, P00518397, P00518398, P01646579]!; BM[BM000787118]!; FI[FI004197]!). — Note: the specimen from Willdenow's herbarium is selected as lectotype.

Marattia cooperi T.Moore, *The Florist and Pomologist* 2: 149 (Moore 1863). — Type: **New Caledonia**. ex hort Veitch (lecto-, designated here, K[K001057733]!). — Note: described from a juvenile plant in cultivation.

Ptisana rolandi-principis (Rosenst.) Christenh.
(Fig. 2)

Phytotaxa 19: 22 (Christenhusz *et al.* 2011). — *Marattia rolandi-principis* Rosenst., *Repertorium Specierum Novarum Regni Vegetabilis* 10: 162 (Rosenstock 1911). — Type: **New Caledonia**. Plateau de Dogny, La Foa, 900 m, 2.II.1911, *Franc 1441* (lecto-, designated here, P[P00522618]!; isolecto-, P[P00522616, P00522617, P00522619, P00522620]!; B[B200090293]!; BISH[BISH1000382 BISH1006653, BISH1006604, BISH1011969]!; BM[BM000787115, BM000787116]!; K[K000229608]!; NOU[NOU082755]!; US[US00134432]!). — Note: as with *P. attenuata*, a statement by Brownlie (1969) is a first-step lectotypification restricting the choice to a specimen in P bearing Franc's number.

Ptisana soluta (Compton)
Murdock & Perrie, comb. nov., stat. nov.
(Figs 3; 5)

Ptisana soluta (Compton) Murdock & Perrie comb. nov., stat. nov. differs from *Ptisana attenuata* (Labill.) Murdock in bearing leaves with smooth, mottled green-brown stipes, and laminae that are 3-pinnate proximally, 2-pinnate distally, and differs from *Ptisana salicina* (Sm.) Murdock in bearing synangia that are removed from the margin, and laminar division as previously described.

Marattia smithii Mett. ex Kuhn forma *soluta* Compton, *Journal of the Linnean Society, Botany* 45: 456 (Compton 1922). — Type: **New Caledonia**. Ignambi, 1500 ft., 4.VIII.1914, *Compton 1674* (holo-, BM[BM000787128]!).

ETYMOLOGY. — Compton (1922) originally described this species as *Marattia smithii* Kuhn forma *soluta* Compton and noted the lamina character that distinguishes this taxon. The Latin “*soluta*” means “separate from adjacent parts, breaking up”, presumably in reference to its transition between 2- and 3-pinnate states.

HABITAT AND DISTRIBUTION. — Based on available collections, *Ptisana soluta* comb. nov., stat. nov. is endemic to New Caledonia, where it is widespread but uncommon on Grande Terre. It is known from Mt. Ignambi and Mt. Panié in the northeast, near Canala in the central-east, and near Nouméa in the southwest (Fig. 4). One collection from Sommet Arago (Compton 1442, BM) may be this species, but was described as being from a population of 2-pinnate plants; this requires further investigation. Several collections note a (rain-) forest and/or mountain habitat, with recorded elevations ranging from 200 m to 800 m. Based on Fig. 4, it seems to be on non-ultramafic substrates, although it may come at least close to ultramafics on Koghis. At Koghis, *P. soluta* comb. nov., stat. nov. grows intermixed with *P. attenuata* and *Angiopteris evecta*. Additional study of the ecological range of *P. soluta* comb. nov., stat. nov., and how it may differ from *P. attenuata*, is needed.

CONSERVATION ASSESSMENT. — We suggest that *Ptisana soluta* comb. nov., stat. nov. be ranked as Vulnerable (VU B1ab(i,i iii,iv,v)+2ab(i,ii,iii,iv,v), IUCN 2012), with this provisional until verified by the New Caledonia Plants Red List Authority. The estimates of 60 km² for area of occupancy and 4236 km² for extent of occurrence are well under the thresholds for criterion B of the Vulnerable category. The subcriteria 1b and 2b are met because of ongoing, substantive predation by rusa deer and feral pigs, as is the case with *P. attenuata* (Endemia Red List Authority 2022). The subcriteria 1a and 2a both invoke “no more than 10 locations”. The exact number of locations is unclear, particularly with the imprecision of earlier collections,

but given the mobility of the deer and pig threats, known locations could be defined as: 1-2 in the southwest, one in the central-east, and 2-4 in the northeast (see Fig. 4). *Ptisana soluta* comb. nov., stat. nov. is unprotected by legislation, but occurs within reserves at Thy Valley and Mt. Panié. The priority for its management should be searching for new sites and surveying known localities, particularly the accessible Koghis and also Ig-nambi, where Compton (1922) said this form was “abundant”.

DESCRIPTION

Fronds 3-pinnate proximally, transitioning to 2-pinnate distally, at least 4 m long, bearing 4-6 pairs of opposite pinnae on mature fronds, the terminal pair forking at the frond apex. Stipe circular in cross-section, smooth, mottled green-dark brown, subtended by paired stipules, round, shallowly divided to nearly entire with ragged margins. Swollen pulvini present at the base of all segments, green, smooth. Ultimate segments 35-104 mm long × 6.5-19.1 mm wide on 3-pinnate portions, 163-295 mm long × 13.7-35.6 mm wide on 2-pinnate portions, oblong with acuminate apices. Laminae dark green above, lighter below, herbaceous-coriaceous, with occasional ciliate scales abaxially along veins and midribs. Veins free, *c.* 2 mm apart, occasionally dividing once. Leaf margin sub-entire-minutely serrate, more clearly serrate near apex. Synangia green when immature, tan-brown after opening, one per vein, submarginal, set back from leaf margin by 1-3 mm, 2-3.5 mm long × *c.* 1 mm wide, longer and with more locules on larger segments, receptacles bearing short, branched, uniseriate hairs.

KEY TO NEW CALEDONIAN *PTISANA* MURDOCK

1. Mature plants < 50 cm long, sori produced on fronds as small as 14 cm long *P. rolandi-principis* (Rosenst.) Christenh.
— Mature plants bearing fronds up to several metres in length, sori not produced until fronds > 100 cm long 2
2. Stipes purplish-black, wrinkled; laminae of mature plants uniformly 3-pinnate, pinnules with serrate margins, often doubly serrate toward the apex with 2-3 veins per tooth *P. attenuata* (Labill.) Murdock
— Stipes mottled green-brown, smooth; laminae of mature plants 3-pinnate proximally but 2-pinnate distally, pinnules with sub-entire or minutely serrate margins, 1 vein per tooth (rarely more) *P. soluta* (Compton) Murdock & Perrie, comb. nov., stat. nov.

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APPENDIX 1. — Collection details for the *Ptisana* samples included in the phylogenetic analyses of chloroplast DNA sequences. GenBank numbers are given in the order *rps4-trnS*, *trnSGG*, with sequences novel to this study underlined.

Ptisana ambulans Murdock & C.W. Chen: **Solomon Islands**, New Georgia, (629), Voucher: *C.-W. Chen & T.-C. Hsu SITW00629* (TAIF, TNM, BSIP), GenBank: MW051627, MW051612.

Ptisana attenuata (Labill.) Murdock: **New Caledonia**. Massif de Leunes, 12.X.2012, *Perrie NC-2012-224* (NOU084834, WELT P026579), GenBank: OM296023, OM296032; Plateau de Dogny, 26.IX.2016, *Perrie et al. 7712* (WELT P028628), GenBank: OM296026, OM296029; Thio, 26.X.2019, *Perrie et al. 8409* (WELT P030390), GenBank: OM296025, OM296033; Koghis, 20.X.2019, *Perrie et al. 8329* (NOU090682, WELT P030313), GenBank: OM296027, OM296030; Koghis, *Murdock 332* (UC), GenBank: EU439125.1, EU439206.1; Koghis, *Schmid s.n.* (UC), GenBank: EU439126.1, EU439207.1; Plateau de Dogny, *Murdock 358* (UC), GenBank: EU439127.1, EU439208.1).

Ptisana decipiens var. *decipiens* Murdock & C.W. Chen: **Solomon Islands**. San Jorge, *10476*, Voucher: *SITW10476* (TAIF, TNM, BSIP), GenBank: MW051626, MW051611.

Ptisana decipiens var. *delicata* Murdock & C.W. Chen: **Solomon Islands**. Vangunu, *Wade3153*, Voucher: *SITW03734* (TAIF, TNM, BSIP), GenBank: MW051623, MW051608.

Ptisana fraxinea (Sm.) Murdock: **South Africa**. 22, GenBank: EU439131.1, EU439212.1.

Ptisana howeana (W.R.B. Oliver) Murdock: **Lord Howe Island**. 128, GenBank: EU439128.1, EU439209.1.

Ptisana mertensiana (C.Presl) Murdock: **Caroline Islands**. 120, GenBank: EU439120.1, EU439201.1.

Ptisana novoguineensis (Rosenst.) Murdock: **New Guinea**. Z:Karger 1721, GenBank: NC_051980.1.

Ptisana oreades (Domin) Murdock: **Australia**. 195, GenBank: EU439130.1, EU439211.1.

Ptisana papuana (Alderw.) Murdock & C.W. Chen: **Solomon Islands**. Guadalcanal, *11631*, Voucher: *SITW11631* (TAIF, TNM, BSIP), GenBank: MW051635, MW051620.

Ptisana pellucida (C.Presl) Murdock: **Malaysia**. 121, GenBank: EU439121.1, EU439202.1.

Ptisana rolandi-principis (Rosenst.) Christenh.: **New Caledonia**. Plateau de Dogny, 26.IX.2016, *Perrie et al. 7694* (WELT P028627), GenBank: OM296024, OM296031.

Ptisana salicina (Sm.) Murdock: **New Zealand**. Chase 23771 (K), GenBank: EU439113.1, EU439195.1; Marquesas, *Wood 10237* (PTBG), GenBank: EU439114.1, EU439196.1; Cook Islands, Rarotonga, *Game s.n.* (UC), GenBank: EU439115.1, EU439197.1).

Ptisana sambucina (Blume) Murdock: **Java**. 1107, Voucher: *Wade1107* (TAIF), GenBank: MW051634, MW051619.

Ptisana soluta (Compton) Murdock & Perrie, comb. nov., stat. nov.: **New Caledonia**. Koghis, 20.X.2019, *Perrie et al. 8330* (NOU090683, WELT P030314), GenBank: OM296022, OM296028; Koghis, *Murdock 333* (UC), GenBank: EU439124.1, EU439205.1).

Ptisana smithii (Mett. ex Kuhn) Murdock: **Fiji**. 122, GenBank: EU439122.1, EU439203.1; 123, GenBank: EU439123.1, EU439204.1; 3093, Voucher: *Wade3093* (TAIF), GenBank: MW051628, MW051613.

Solomon Islands, Vanikoro, *10574*, Voucher: *SITW10574*, (TAIF, TNM, BSIP), GenBank: MW051630, MW051615; Vanikoro, *11038*, Voucher: *SITW11038* (TAIF, TNM, BSIP), GenBank: MW051631, MW051616; Vanikoro, *11037*, Voucher: *SITW11037* (TAIF, TNM, BSIP), GenBank: MW051629, MW051614.

Ptisana squamosa (Christ) Murdock: **New Guinea**. 119, GenBank: EU439119.1, EU439200.1.

Ptisana sylvatica (Blume) Murdock: **Indonesia**. Sulawesi, 117, GenBank: EU439117.1, EU439198.1.

Ptisana wernerii (Rosenst.) Christenh.: **New Guinea**. 135, GenBank: EU439134.1, EU439214.1.

APPENDIX 2. — Herbarium collections identified by us as each of the three New Caledonian species of *Ptisana*. For *P. attenuata*, only collections with localities that can be georeferenced, at least approximately, are listed.

Ptisana attenuata (Labill.) Murdock

Allard 39, Koghis, 7.V.2005, NOU[NOU031151]; *Balansa 801a*, Sommet du Nékou, 3.IV.1859, P[P00518386]; *Bamps 5838*, Canala-La Foa, 25.XI.1977, P[P01365735], NOU[NOU056673], BM[BM000785890]; *Bamps 5854*, Bourail-Houailou, 29.XI.1977, P[P01365729], NOU[NOU056679]; *Baumann-Bodenheim 5394*, Col d'Amieu, 13.VIII.1950, P[P00518383]; *Baumann-Bodenheim & Guillaumin 7231*, Rivière de la Thio, 23.X.1950, P[P00518382]; *Baumann-Bodenheim & Guillaumin 8615*, Mé Amméri, 27.XI.1950, P[P00518381]; *Bernardi 9615*, Col d'Amieu, 13.VII.1965, P[P00518400]; *Blanchon 1148*, Rivière Blanche, 17.XI.1964, P[P01365663], NOU[NOU056680]; *Brinon 265*, Thy, 1.V.1978, NOU[NOU056676, NOU056677]; *Brousmitche 132*, Mt. Koghi, 12.VIII.1882, P[P00518376]; *Brownsey NC 59*, Col d'Amieu, 9.IX.1974, WELT[P010087, P010088]; *Carlquist 15306*, Col d'Amieu, 29.VII.1977, P[P00518399], NOU[NOU056678]; *Compton 201*, Ermitage Stream [Koghis], 29.I.1914, BM[BM000785887]; *Compton 1451*, Mont Arago, 18.VII.1914, BM[BM000785885]; *Compton 1490*, Ignambi, 29.VII.1914 BM[BM000785886]; *Compton 1770*, Mont Panié, 24.VIII.1914, BM[BM000785898]; *Coulerie 21*, Dogny, 14.V.2009, NOU[NOU050814]; *Cribbs 375*, Nessadiou, X.1900, P[P00518373, P00518374]; *de Labillardière s.n.*, no locality or date, P[P00518392, P00518393, P00518394, P00518395, P00518396, P00518397, P00518398, P01646579], B[B-W-19456], BM [BM000787118], FI[FI004197] [type collection]; *de Labillardière s.n.*, no locality, 1824, P[P00518396]; *de Pompéry s.n.*, Pic des Trois-Frères, VIII.1881, P[P00522774]; *Foster 143*, Col de Parari, 11.VI.1956, P[P00518371], UC[UC1078341]; *Foster 75*, Dogny, V.1956, P[P00518372], UC[UC1078297]; *Franc 142 bis*, Yahoué, I.1907, P[P00518363, P00518364], UC[UC393195]; *Franc 142*, Yahoué, IV.1909, P[P00518365]; *Franc 20 bis*, Mont Mou, VIII.1906, P[P01365732]; *Franc 632*, Koghi, 2.II.1909, P[P00518362], BM[BM000785903]; *Franc 632*, Mont Mou, 1907, BM[BM000785894]; *Franc 653*, Mt. Koghi, VI.1913, UC[UC392872]; *Franc 653*, L'Hermitage [Koghis], XI.1911, P[P00518360, P00518361, P01365211, P01365212, P01365213, P01365666], NOU[NOU050736]; *Franc 653*, Monts Koghis, 25.VII.1912, P[P00518358, P00518359, P01365256]; *Franc 653*, Monts Koghis, 8.I.1911, P[P00518355], BM[BM000785900, BM000785901]; *Franc s.n.*, Mont Koghi, III.1911, P[P00518367, P00518368]; *Franc s.n.*, Mont Koghi, IX.1906, P[P00518369]; *Franc s.n.*, Yahoué, X.1905, P[P00518366]; *Fukuoka 481*, Koghis, 30.VIII.1976, NOU[NOU056661]; *Graive 19*, Vallée de la Conception, 1895, P[P01365731]; *Guillaumin & Baumann-Bodenheim 8662*, Mé Amméri, 27.XI.1950, P[P00522611]; *Hürlimann 2000*, Ignambi, 15.VIII.1951, P[P00518353]; *Layard s.n.*, Mt. Kogi, no date, UC[UC679495]; *Le Rat 2413*, entre Bourail et Houailou, VII.1904, P[P00522798]; *LeMieux 2040b*, Dogny, 4.II.2000, UC[UC2082856]; *MacKee 18076*, Canala, 5.XII.1967, P[P00522795, P01365215], NOU[NOU056664]; *MacKee 26688*, Poindimié, 14.V.1973, P[P01222461, P01222462], NOU[NOU056669], UC[UC1978013]; *McPherson 1595*, Thy River valley, 4.V.1979, P[P01365744], NOU[NOU056681]; *Munzinger 1502 et al.*, Col d'Amoss, 13.XI.2002, P[P00354489, P00477918], NOU[NOU056672]; *Munzinger et al.* 4622, Dogny, 26.X.2007, NOU[NOU030725]; *Musselman 5293*, Coula, 20.V.1977, NOU[NOU056671], UC[UC1422383]; *Nonnea s.n.*, Mont Koghii, IV.1906, UC[UC810836]; *Perrie et al.* 7712, Dogny, 26.IX.2016, WELT[P028628]; *Perrie et al.* 8329, Koghis, 20.X.2019, WELT[P030313], NOU[NOU090682]; *Perrie et al.* 8409, Forêt de Saille, 26.X.2019, WELT[P030390]; *Perrie NC-2012-224*, Tiwaé, 12.X.2012, WELT[P026579], NOU[NOU084834]; *Pignal et al.* 5190, Bopope, 29.X.2017,

P[P01073043, P01073153, P01073154], MPU[MPU091657, MPU091658], NOU[NOU091710, NOU091711]; *Sarasin 185*, Ignambi, 4.X.1911, P[P00522772]; *Sarasin 67*, Tao, 27.VI.1911, P[P00522773]; *Schlechter 15050*, Yaouhé, 15.X.1902, P[P00522769, P00522770, P00522771], BM[BM000785904]; *Schmid 1204*, Piste de Wayagette, 17.IV.1966, P[P01365703], NOU[NOU056665]; *Schmid 2556*, Haute Boghen, 13.XII.1967, P[P01365704, P01365705], NOU[NOU056682]; *Schmid 2663*, Port Boisé, 6.II.1969, P[P01365667], NOU[NOU056663]; *Schmid & Phillips 3027*, Mt. Koghi, 16.VII.1978, P[P01222220, P01222221]; *Schmid 338*, Monts Koghis, 18.VI.1965, NOU[NOU056666]; *Schmid s.n.*, Mt. Koghi, I.1978, UC[UC1616126, UC1616127]; *Stone 14737*, Mont Koghi, 4.VIII.1981, NOU[NOU056657]; *Swenson 628 et al.*, Mt. Colnett, XI.2004, P[P01365255], NOU[NOU006631]; *Thorne 28300*, Col des Roussettes, 26.X.1959, P[P00522768]; *Thorne 28497*, Mt. Koghi, 4.XI.1959, P[P00522767]; *van der Werff & McPherson 15894*, 28.X.1999, NOU[NOU033625]; *van der Werff 15911 & McPherson*, Mont Panié, 23.X.1999, NOU[NOU056684], UC[UC1740299]; *Veillon 1782*, Mont Arago, 22.II.1968, P[P01365706], NOU[NOU056683]; *Veillon 2743*, Aoupinié, 29.VIII.1972, P[P01365745, P01365746], NOU[NOU056667]; *Veillon 2971*, Ouégoa, 31.VII.1973, P[P00522766], NOU[NOU056670]; *Vieillard 1680*, Ponébo, I.1861, P[P01365214, P01365711, P01365730]; *Vieillard 1680*, Wagap, 1864, P[P01566107, P06243329]; *Vieillard 1682*, Balade, no date, P[P00522749, P00522750, P00522751, P00522752, P00522753, P01365743]; *Vieillard s.n.*, Wagap, 1864, P[P00522754, P00522755, P00522756, P00522757]; *Viroit 738*, Mt. Mi, VIII.1942, P[P00522748, P01365257], NOU[NOU053412]; *Webster & Hildreth 14894*, Col d'Amieu, 19.VIII.1968, P[P00522747].

Ptisana rolandi-principis

Le Rat 849, Plateau de Dogny, IX.1909, P[P00522799]; *Franc 1411*, Plateau de Dogny, I.1911, P[P00522612, P01365761] [syntypes]; *Franc 1411*, 2.II.1911, P[P00522616, P00522617, P00522618, P00522619, P00522620], B[B200090293], BISH[BISH1000382 BISH1006653, BISH1006604, BISH1011969], BM[BM000787115, BM000787116], K[K000229608], NOU[NOU082755], US[00134432] [lectotype and isoelectotypes]; *Franc s.n.* [Rosenstock 121a], Dogny, 2.II.1911, P[P00522607, P00522608, P00522609, P00522610], BM[BM000786144, BM000787117], K[K000229609], GH[GH00021620], MICH[MICH1286092], NY[NY00127426], UC[UC352579] [syntypes]; *Franc s.n.* [Rosenstock 121], Dogny, 2.II.1911, P[P00522613, P00522614, P00522615], BM[BM000787114], S[S-P-2194] [syntypes]; *Munzinger et al.* 4855, Plateau de Dogny, XI.2007, P[P00758375], NOU[NOU030696]; *Perrie et al.* 7694, Plateau de Dogny, 26.IX.2016, WELT[P028627].

Ptisana soluta comb. nov., stat. nov.

Balansa 1559, Canala, 20.XI.1869, P[P00522621, P00522622, P00522623, P00522624, P00522625, P00522626]; *Braithwaite 559*, no locality or date, NOU[NOU056668, NOU056674, NOU056675]; *Buchholz 1230*, Thy River, 20.X.1947, P[P00518375], UC[799340]; *Compton 1674*, Ignambi, 1914, BM[BM000787128] [holotype of *Marattia smithii* f. *soluta*]; *Foster 156*, Ignambi, 12.VI.1956, UC[UC1053924]; *Franc 1911* [sic] (Rosenstock 122), no locality or date, P[P01365760]; *Franc 2376*, Monts Koghis, 6.X.1929, P[P00522537]; *Franc 2377*, Monts Koghis, 6.X.1929, P[P00518354]; *Franc 749*, Mts Koghis, IV.1912, P[P01365700, P01365758, P01365759]; *Franc 749*, Monts Koghis, 25.VII.1912, P[P00522537, P0522637, P01365699]; *Franc 749*, no locality or date, UC[UC392870]; *Franc s.n.*, Mont Koghi,

Appendix 2. — Continuation.

IV.1911, P[P00522539, P00522540, P0522541, P0522542]; *MacKee* 4795, Mt Ignambi, 12.VI.1956, P[P00522796]; no collector, locality, or date, P[P00522786]; *Pancher s.n.*, Montrouzier, 1855, P[P00518388]; *Perrie et al.* 8330, Koghis, 20.X.2019, WELT[P030314], NOU[NOU090683, NOU106931]; *Pinard s.n.*, Nord, 1856, P[P00522776]; *Schmid* 17, Koghis, 14.I.1965, NOU[NOU056662]; *van der Werff & McPherson* 15907, Mt. Panié, 23.X.1999, NOU[NOU056685], UC[UC1740300]; *Vieillard* 1681, Balade, no date, P[P0522758, P00522759, P01365709]; *Vieillard* 1681, Pouébo, no date, BM[BM000785905].

Possible *P. soluta* comb. nov., stat. nov. (not mapped)

Balansa 1560, Canala, 20.XI.1869, P[P00522544, P00522545]; *Balansa* 801, Mont Mi, 16.III.1869, P[P00522546, P00522547]; *Compton* 1442, Mont Arago, 14.VII.1914, BM[BM000785888]; *MacGillivray* 29, no locality, VI.1858, P[P01646578]; *MacGillivray* 729, no locality, VIII.1858, P[P00522642, P00522797], BM[BM000785896]; *Pancher* 1680, no locality or date, P[P00522781]; *Pancher s.n.* no locality, 1870, P[P00522534, P00522536]; *Pancher s.n.*, no locality or date, P[P00522459, P00522780, P00522782, P00522783]; *Suprin* 1481, Thy, 20.XI.1981, P[P01365254].