



An account of the Cunoniaceae in the Solomon archipelago and Vanuatu

H. C. F. Hopkins¹, J. C. Bradford² & Y. Pillon³

Summary. Five genera of the largely southern hemisphere family Cunoniaceae occur in the Solomon archipelago (Solomon Islands plus the Autonomous Region of Bougainville, Papua New Guinea): *Geissois*, *Pterophylla* (previously *Weinmannia p.p.*), *Spiraeanthemum*, *Schizomeria* and *Ackama* (including *Spiraeopsis*) (total of 12 species); the first three genera are also found in Vanuatu (total of four species). None of the genera is endemic to these two archipelagos although more than half the species are and *Spiraeanthemum macgillivrayi* Seem. is the only species common to both island groups. Along with keys to the genera and species, accounts are given for *G. denhamii* Seem. (throughout Vanuatu), *G. pentaphylla* C.T.White (restricted to the island of Vanikoro, Solomon Islands), and *P. makiniae* H.C.Hopkins, J.Bradford & Pillon sp. nov., from Vangunu and Kolombangara in the Solomon Islands. Most of the remaining taxa have been revised for generic treatments or flora accounts and for these, only a synopsis is given with notes on types for some names. Provisional conservation assessments are provided, with ecological summaries. Generic diversity in the Cunoniaceae decreases eastwards across the Pacific Ocean to the Marquesas and Austral Islands. The islands in the western Pacific have surprisingly few genera in common with Australia, and, compared with New Caledonia, Fiji or the Solomon archipelago, Vanuatu has fewer taxa than might be predicted from its location and size, presumably because of its young geological age.

Key Words. Bougainville, logging, new species, Solomon Islands, South-west Pacific, taxonomy, Vanikoro.

Introduction

Treatments of the Cunoniaceae have been published relatively recently for Fiji, Malesia and New Caledonia (Hopkins & Hoogland 2002; Hopkins *et al.* 2014; Smith 1985). This paper provides an account of the family in the Solomon archipelago and Vanuatu to fill the geographical gap between these other island groups.

Cunoniaceae is a largely southern hemisphere family with a total of 27 genera and c. 335 species (Pillon *et al.* 2021a). Common though not universal characters include opposite or whorled decussate leaves that are simple or compound, the blades generally having toothed margins; stipules present and commonly interpetiolar; flowers poly-symmetric and hypogynous, with or without petals and having as many styles (stylodia) as carpels; and small capsular fruits containing winged or hairy seeds (Bradford *et al.* 2004). The greatest generic diversity is in eastern Malesia (nine genera in New Guinea), the islands of the south-west Pacific (11 genera) and eastern Australia (15 genera), with marked species richness in the Andes and Madagascar.

A recent phylogenetic study by Pillon *et al.* (2021a) indicated that changes should be made to generic limits affecting the names of two of the genera discussed

here. *Weinmannia* L., the largest genus in the family, was shown to be polyphyletic and so was divided into two: *Weinmannia* s.s. is now confined to the Americas, including the islands of the Caribbean, plus the Mascarene islands (Indian Ocean); the remaining species, from Madagascar, Malesia and the islands of the western and central Pacific Ocean, were transferred to the resurrected genus *Pterophylla* D.Don. This study also found that the species previously placed in *Spiraeopsis* Miq. (Philippines to Solomon Islands) were nested within *Ackama* A.Cunn. (Australia and New Zealand) and so were transferred to the latter.

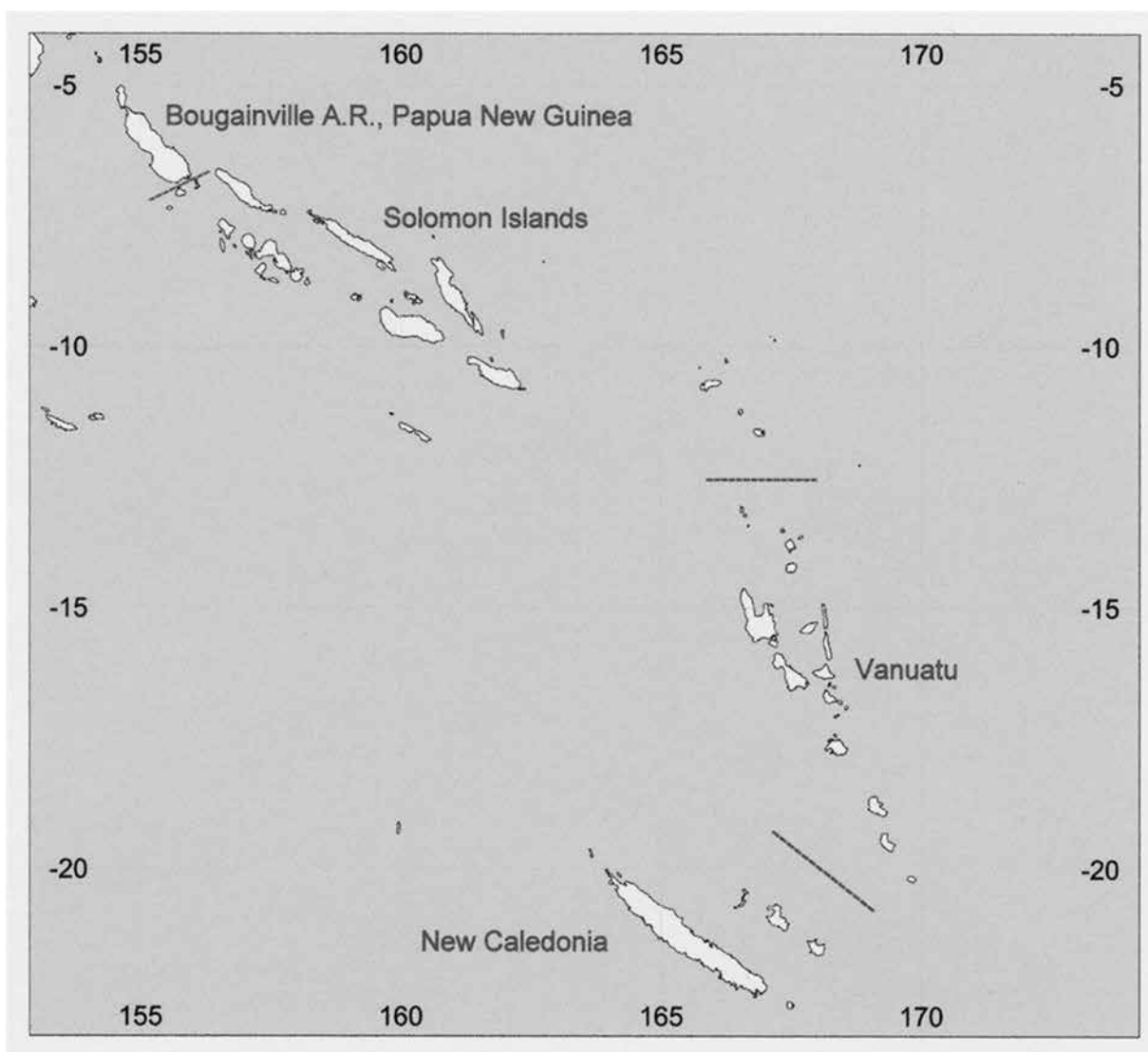
The area dealt with here comprises the Autonomous Region (A. R.) of Bougainville, which is politically part of Papua New Guinea, plus the Solomon Islands, which together form the Solomon chain or archipelago (sometimes referred to below just as “Solomons”), and Vanuatu (Map 1). Five genera of Cunoniaceae occur in the region, *Ackama*, *Geissois* Labill., *Pterophylla*, *Schizomeria* D.Don and *Spiraeanthemum* A.Gray, with a total of 15 species, 12 in the Solomon archipelago and four in Vanuatu (Table 1).

Bougainville A. R., previously known as North Solomons or Bougainville Province of Papua New Guinea, comprises the northernmost large island in

¹ Herbarium, Royal Botanic Gardens, Kew, Richmond TW9 3AE, UK. e-mail: h.fortune-hopkins@kew.org

² Corvallis, Oregon, USA

³ LSTM, IRD, INRA, CIRAD, Institut Agro, Univ. Montpellier, Montpellier, France



Map 1. Archipelagos in the southwest Pacific Ocean.

the Solomon chain (Bougainville), the small island of Buka immediately to its north and a few remote atolls. It was not included in the area covered by *Flora Malesiana*, which extends east only to New Britain and New Ireland in the Bismarck archipelago. The checklist by Foreman (1971) included seven names in Cunoniaceae and cited collections but is now considerably out of date.

A brief treatment of the family in the Solomon Islands (excluding Bougainville) by Whitmore (1966a) recognised eight species, including one in *Pullea* Schltr. and he omitted *Spiraeanthemum* (Hoogland 1979: 504) — apparently a simple case of mistaken identity. The checklist of Hancock & Henderson

(1988) recorded 12 species but included some synonyms. Relatively recent collections of Cunoniaceae include those by Bradford in 1997 and by a consortium of institutions from the Solomon Islands, Taiwan and Japan, especially from 2013 to 2015 (Flora of Solomon Islands, online). However, the main publication from this project (Chiou *et al.* 2016) does not include any members of this family.

For Vanuatu, formerly the New Hebrides, notes on several species were published by Guillaumin (1931, 1935, 1937), and Guillaumin (1948) listed nine taxa of Cunoniaceae although five of these names are now considered synonyms. Brief descriptions with illustrations were provided by Wheatley

Table 1. Species of Cunoniaceae in the Solomon archipelago and Vanuatu, plus those from the Bismarck archipelago for comparison. Authors are given only for species not discussed in the text.

Bismarck archipelago: New Britain [NB], New Ireland [NI] and Manus [M]	<i>Ackama celebica</i> [NB, NI] <i>Ceratotalum succinbrum</i> C.T.White [NB] <i>Opocunonia nymanii</i> (K.Schum.) Schltr. [NB] <i>Pterophylla croftii</i> [NB, M] <i>Pterophylla fraxinea</i> [NB & NI] <i>Schizomeria serrata</i> [NB] <i>Spiraeanthemum macgillivrayi</i> subsp. <i>kajewskii</i> [NB & NI]
Solomon archipelago: Bougainville A. R.	<i>Ackama celebica</i> <i>Pterophylla purpurea</i> <i>Pterophylla</i> sp. (Solomons B) <i>Schizomeria serrata</i> <i>Spiraeanthemum bougainvillense</i> <i>Spiraeanthemum macgillivrayi</i> subsp. <i>kajewskii</i>
Solomon archipelago: Solomon Islands	<i>Ackama celebica</i> <i>Geissois pentaphylla</i> <i>Pterophylla croftii</i> <i>Pterophylla fraxinea</i> <i>Pterophylla makiniae</i> <i>Pterophylla purpurea</i> <i>Pterophylla ysabelensis</i> <i>Schizomeria ilicina</i> <i>Schizomeria serrata</i> <i>Spiraeanthemum macgillivrayi</i> subsp. <i>kajewskii</i>
Vanuatu	<i>Geissois denhamii</i> <i>Pterophylla denhamii</i> <i>Pterophylla macgillivrayi</i> <i>Spiraeanthemum macgillivrayi</i> subsp. <i>macgillivrayi</i>

(1992) and Ramon & Sam (2015) for both *Pterophylla denhamii* (Seem.) Pillon & H.C.Hopkins (as *Weinmannia*) and *Geissois denhamii* Seem. Recent collections from Vanuatu include those by members of the French expedition to Santo in 2006 (Bouchet *et al.* 2011) and by staff from NY, from 2014 onwards, as part of an ethnobotanical study in Tafea Province (Tanna, Erromango and Aneityum (= Anatom)) (<https://forestry.gov.vu/projects/project-2-new-york-botanical-garden/> accessed Sept. 2021) (and see Plunkett *et al.* 2022).

Methods and Organisation of the Paper

For all genera, material at BM, K and P was seen, including many early BSIP (British Solomon Islands Protectorate) collections at K, plus some material from CANB, G, L, LAE, and NOU. For *Pterophylla* and *Schizomeria*, the herbaria consulted were given in the revisions cited. Images in the following online databases were also reviewed: Harvard University Herbaria (A), Bishop Museum (BISH), Naturalis (L, U), Linnean Collections — Smith Herbarium (LINN-SH), Tropicos (MO), C. V. Starr Virtual Herbarium (NY), Muséum National d’Histoire Naturelle (P), Flora of Solomon Islands (TNM, only includes

material from their recent expeditions), Taiwan Forestry Research Institute (TAIF), and the National Museum of Nature and Science, Japan (TNS). Some additional types were seen in Jstor Global Plants (online). Databases for the national herbaria of Papua New Guinea (LAE) (Conn *et al.* 2004 onwards) and Vanuatu (PVNH) (Flora of Vanuatu online; and see Vanuaflora online) list some additional collections but lack images. The National Herbarium of the Solomon Islands (BSIP) does not currently have an online database.

Within genera and sections, species are treated alphabetically irrespective of island group. The format for each genus varies according to what has been published elsewhere but for most taxa, only a synopsis is given. Except for basionyms, synonyms are listed only if the type is from the present region. When information on types is repeated from previous publications, herbarium barcodes have been added. All material cited has been seen, either in the herbarium or as an image, unless indicated “n.v.”. Dimensions of leaves and other vegetative characters are taken primarily from fertile shoots; leaves on sterile collections are generally more variable in size, shape and indumentum. For species with unisexual flowers, m. = male, f. = female. When indicating the

phenological state of specimens, yfr. = young fruit. Map outlines were made using Simplemapp (Short-house 2010, online). Under vernacular names, the local name has been taken from specimen field notes. This name is followed by the name of the language or tribal group, if known, in parentheses, and finally the collector's name and number of the specimen from which the information came.

Notes on Typification

For the new taxa of Cunoniaceae in Papua published by Perry (1949) (*Spiraeanthemum kajewskii* L.M.Perry, *Weinmannia purpurea* L.M.Perry, *W. ysabelensis* L.M.Perry), she stated that her paper was based on material at A and indicated certain collections as types. If only a single sheet of these collections is known at A, it is cited as the holotype.

Seemann (1865 – 1873) published the names of four species of Cunoniaceae from Vanuatu in his *Flora vitiensis* and cited the collection(s) on which each name was based although he did not mention the word “type”. Three of the names are followed by the phrase “Seem. mss. in Herb. Mus. Brit.” (once omitting “Herb.”). For *Geissois denhamii* and *Spiraeanthemum macgillivrayi*, he mentioned only a single collection and the sheet at BM is cited here as the holotype. His other names, *Weinmannia denhamii* Seem. and *W. macgillivrayi* Seem., were lectotypified elsewhere.

Further notes on types are given in some species accounts.

Notes on Conservation Assessments

Conservation assessments using the IUCN Categories and Criteria (IUCN 2019, online) are based on the entire distribution of species. GeoCAT (online; Bachman *et al.* 2011) was used to derive the area of occupancy (AOO) and extent of occurrence (EOO), and to suggest the Red List category for some species, but not in cases where large areas of sea would have been included in the EOO; a measurement of AOH (area of habitat) would be more appropriate in these cases (Brooks *et al.* 2019). For calculating the EOO of widespread taxa in Vanuatu, a land surface area of 12190 km² for the archipelago was taken from World Bank data (online).

Assessments are preliminary for several reasons. First, some collections are old and their localities may now be of historical interest only due to habitat destruction, even though under criterion B this is not taken into account. Second, data on the distribution of less common species may not be comprehensive because of under-collecting on some islands. Third, local knowledge about the current

extent of habitat loss and the ability of species to persist in secondary and logged forests is needed to make more meaningful assessments. Some Cunoniaceae have weedy tendencies and selective logging and small-scale habitat disturbance could result in population increases, though this is unlikely to be true in all cases.

Bougainville has been less affected by deforestation than many other parts of the region, partly because of its involvement in a civil war from 1988 to 1998, but several logging operations are planned or in progress (e.g. PNGexposed Blog 2014; Papua New Guinea Mine Watch 2018). The degree to which any Cunoniaceae are affected by this activity will depend on the type, extent and elevation of the logging. Mining for copper has also caused habitat destruction. No areas of forest on Bougainville currently have legal protection (UNEP-WCMC 2019).

Slash and burn agriculture has had a marked effect on the vegetation of the Solomon Islands over several centuries (Whitmore 1969), land has also been cleared for the cultivation of cash crops such as oil palm and cocoa, and considerable areas have been logged commercially. This continues at levels well above what is considered sustainable and at current rates of felling, commercially viable areas of forest are expected to be exhausted by 2036 (Global Witness 2018; Solomon Islands Government 2014). Logging makes a major contribution to the economy and, even if large-scale mining plays an increasing role in the future (Porter & Allen 2015), logging is likely to continue. Much current activity is for the export of round logs to China and some is said to be illegal and unmonitored (REDD in Solomon Islands 2014; Global Witness 2018). The proportion of forest selectively logged varies amongst the islands (Katovai *et al.* 2015: fig. 4) but on some, the lowland forest has already gone and so any large tree species is likely to have suffered a significant reduction in population and genetic diversity. Although a system of marine protected areas exists in the Solomon Islands, very little of the terrestrial environment has formal protection (UNEP-WCMC 2019).

Vanuatu has had relatively low forest loss compared with other countries in the region (REDD in Vanuatu 2013). However, significant areas of forest were lost on Santo when land was cleared for crops during WW2 and then subsequently for cattle raising (Pineda 2011). Widespread logging with some extensive forest degradation occurred from 1980 to 1998, when an export ban on round logs was introduced (King 2007); the islands most affected were Santo and Tanna (Herold *et al.* 2007: fig. 5). Although Vanuatu has a number of forest conservation areas, they cover < 5% of the land surface (UNEP-WCMC 2019).

Taxonomic Treatment

Key to the genera (and some species) of Cunoniaceae in the Solomon archipelago and Vanuatu

1. Leaves simple (or rarely unifoliolate).....2
- 1'. Leaves compound.....4
2. Flowers in racemes (partial inflorescences), several together forming a terminal, sparsely branched inflorescence; calyx lobes imbricate in bud (Solomons).....**3.7. Pterophylla purpurea**
- 2'. Flowers in well-branched thyrses, these terminal or lateral/axillary; calyx lobes valvate in bud.....3
3. Plants dioecious (in this area); in female flowers, ovary apocarpous; fruit composed of a number of small follicles, each dehiscent from the apex and containing numerous small seeds; petals absent (Solomons, Vanuatu).....**5. Spiraeanthemum**
- 3'. Plants bisexual or andromonoecious; in female and bisexual flowers, ovary syncarpous; fruit a drupe, endocarp containing 1 (– 3) seeds; petals lacinate, generally 3-toothed (Solomons).....**4. Schizomeria**
4. Leaves palmately compound, leaflets 3 – 5 (in this region); flowers bright red, in axillary or ramiflorous racemes; petals absent; stamens far exceeding the sepals (Solomons [Vanikoro], Vanuatu).....**2. Geissois**
- 4'. Leaves pinnately compound (trifoliolate or imparipinnate); flowers white, cream or pale pink, in racemes or thyrses, not ramiflorous; petals elliptic and membranous; stamens shortly exceeding the perianth.....5
5. Inflorescence a much-branched axillary thyrse; sepals valvate in bud; indumentum including stellate hairs and orange peltate “glands”; seeds small, flattened, winged (Solomons).....**1.1. Ackama celebica**
- 5'. Inflorescence consisting of several racemes or pseudoracemes (partial inflorescences), several together in various arrangements, usually on a common peduncle, forming a sparsely branched inflorescence that may be terminal, axillary or a combination; sepals imbricate in bud; indumentum of simple hairs only; seeds small, ellipsoid, usually comose (Solomons, Vanuatu).....**3. Pterophylla**

1. Ackama *A.Cunn.* (Cunningham 1839: 358); Bradford *et al.* (2004: 106); Pillon *et al.* (2021a: 1196).

Spiraeopsis Miq. (Miquel 1856: 719); Perry (1949: 145); Hopkins & Hoogland (2002: 128); Bradford *et al.* (2004: 106).

Trees or sometimes *shrubs*. Indumentum of simple hairs and in some, stellate trichomes and almost spherical orange peltate “glands” on leaves and inflorescences. *Stipules* interpetiolar, 1 pair per node. *Leaves* opposite and decussate, imparipinnate, commonly 2 – 4-jugate or trifoliolate, petiolate, leaflet margins toothed to sub-entire; domatia frequently present. *Inflorescences* many-flowered, axillary, cone-shaped thyrses. *Flowers* sessile to shortly pedicellate, bisexual (perhaps strongly protandrous in some, see Hopkins & Hoogland 2002) or possibly sometimes unisexual; sepals 4 – 5 (– 6), valvate in bud; petals 4 – 5 (– 6), elliptic; stamens 8 or 10 (12); disc annular to distinctly lobed; gynoecium of 2 – 5 carpels, fused to almost free, locules and styles 2 – 5; ovules 4 – 16 per locule, arranged in 2 rows. *Capsules* dehiscent; valves boat-shaped, as many as carpels, sometimes margins of each partially detaching to form a persistent replum. *Seeds* several, small, either spindle-shaped and glabrous with a small wing at either end or ellipsoid and pubescent.

Ten species in the Philippines, Sulawesi, the Moluccas, New Guinea, New Britain, New Ireland, the Solomon archipelago, Australia and New Zealand; one species in the Solomon archipelago.

1.1. Ackama celebica (Blume) Pillon & H.C.Hopkins (in Pillon *et al.* 2021a: 1197). *Cunonia celebica* Blume (1826: 868). *Dirhynchosia celebica* (Blume) Blume (1855: 6). *Spiraeopsis celebica* (Blume) Miq. (Miquel 1856: 719). *Caldcluvia celebica* (Blume) Hoogland (1979: 485). Type: [Indonesia, N Sulawesi], Lukon and Rumagang Mts, Reinwardt 1549 (lectotype of Hoogland (1979): L [L0019901, buds]; isolectotypes: L [L0019902, fr.]; U [Reinwardt s.n., U0094967, buds]). See Hopkins & Hoogland (2002: 133) for additional synonymy and distribution map, under *Spiraeopsis celebica*.

Tree 10 – 20 (– 40) m high. *Leaves* imparipinnate, lateral leaflets 1 – 4 pairs, oblong to obovate-oblong or ovate-oblong, 8 – 15 (– 25) × 4 – 7 (– 12) cm, apex acute or slightly acuminate, base acute and decurrent to rounded; upper surface sparsely short-hirsute, glabrescent; lower surface glabrous or with sparse to closed tomentum of short lanose hairs plus longer hirsute hairs, plus numerous orange peltate “glands”.

Inflorescence axes densely hairy. *Flowers* yellowish-green, pale green with white stamens or white, scented, c. 1 mm long plus styles 1 mm; ovary densely hairy, 2 (3)-carpellate. *Fruits* shortly hairy, ripening brown or with a deep reddish tinge, valves 4 – 5 mm long plus styles 1 – 2 mm. Fig. 1B (and see Koorders 1918: fig. 7a – b, under *Spiraeopsis celebica*).

DISTRIBUTION. Philippines; Indonesia (Sulawesi, Molucas, western New Guinea); Papua New Guinea (mainland, New Britain, New Ireland, Bougainville); Solomon Islands (Kolomobangara, Malaita, Santa Isabel, Guadalcanal).

REPRESENTATIVE SPECIMENS. PAPUA NEW GUINEA. Bougainville A. R.: Bougainville: Panguna ridge, lower slopes, track to Pankiranku valley and Barapinang, 6°20'S 155°30'E, 10 April 1965 (fl.), *Cole* s.n. (K ×2); Mt Balbi, on saddle between two peaks, 1900 m, 8 May 1988 (fl.), *Gideon et al.* LAE 78568 (LAE ×3); Kupei Gold Field, 1000 m, 14 April 1930 (fr.), *Kajewski* 1715 (BM, P); Pavairi, 6°15'S 155°30'E, 550 m, 25 Jan. 1967 (fr.), *Lavarack & Ridsdale* NGF 31203 (L ×2); vicinity of Koniguru I village, 18 km N of Buin patrol post, 275 m, 21 July 1964 (fr.), *Schodde & Craven* 3615 (K); SW of Crown Prince Range, 600 m, 3 Feb. 1936 (buds), *Voyce* B6 (K ×2); Iru, 670 m, 28 Sept. 1931 (fr.), *Waterhouse* 555 [555 – B] (K); Paramoni, Maisua, Sept. 1932 (fl.), *Waterhouse* 738 [K.738 & B.738] (K ×3, L). **SOLOMON ISLANDS. Western Prov.: New Georgia Group: Kolomobangara:** end of logging road NNW of Ringi Cove and S of Mt Rano, 8°03'S 157°04'E, 390 m, 18 Nov. 1997 (old infruct.), *Bradford* 834 (K ×2, MO); Mt Duke, S of Mt Tapalamenggututu and N of Vila R., 7°38'S 157°06'E, 960 m, 20 Nov. 1997 (buds), *Bradford* 840 (K, MO); Kokove Area, 900 m, 21 Jan. 1968 (buds), *Mauriasi & collectors* BSIP 7645 (K, L). **Guadalcanal Prov.: Guadalcanal:** SW, Duidui Area, 100 m, 7 Oct. 1968 (yfr.), *Farodo & collectors* BSIP 12015 (K, L); W coast, Alidavata (Talise) Kiki Ridge, Duidui, 250 m, 13 June 1968 (fl.), *Sirute'e & collectors* BSIP 10070 (K, L). **Malaita Prov.: Malaita:** trail from Matakualao to Malu'u, 8 April 1966 (fr.), *Kondo* 418 (BPBM Acc. No. 6977) (L). **Isabel Prov.: Santa Isabel:** Tiratona, 600 m, 26 Nov. 1932 (fr.), *Brass* 3214 (BISH, BM, L); nr Maringe Lagoon, Mt Sasari, 790 m, 26 Oct. 1963 (buds), *Whitmore* BSIP 2431 (K, L).

HABITAT AND ECOLOGY. *Ackama celebica* occurs in wet primary forest, including mossy montane forest, and in tall secondary or disturbed forest, as well as old gardens (Whitmore 1966a), on steep slopes and ridge tops, commonly on well drained sites, at 100 – 960 m. The field notes of *Cole* s.n. state that on Bougainville, this species formed a monospecific community over a copper anomaly and those of *Whitmore* BSIP 2318 that on Santa Isabel, it is found on limestone.

CONSERVATION STATUS. Least Concern (LC), based on its wide distribution (Philippines to Solomon Islands) and ability to grow in disturbed sites.

VERNACULAR NAMES. Bougainville: Dognai, fide *Waterhouse* 555. Domorai, fide *Voyce* B6. Donai, fide *Waterhouse* 738. Tomuri, fide *Kajewski* 2113 (P). **Solomon Islands:** Ngangalau, Ngwangalau Nguangalau, Ngwanga Lau (Kwara'ae name): numerous collections, especially from Guadalcanal. Aitootoo (Kara'ae name), fide *Sirute'e et al.* BSIP 10074. Potafeo, fide *Brass* 3214. Wangalau (Kwara'ae name), fide *Whitmore* BSIP 2318, BSIP 2337, BSIP 2431.

NOTES. This is the only one of the six species of *Ackama* that occurs in New Guinea whose distribution extends beyond that island. Amongst the Cunoniaceae in the Solomon archipelago, *A. celebica* is unique in having a combination of a thyrsoid inflorescence and imparipinnate leaves, as well as stellate hairs and orange peltate “glands” on the leaves and inflorescence. Very young leaves and inflorescences also have tiny, dark red, globose structures amongst the dense indumentum.

The protologue of *Cunonia celebica* (Blume 1826) did not cite collections but stated “Crescit: in montanis insulae Celebes”. Besides the lectotype and isolectotypes cited above, a series of microscope slides at L prepared from *Reinwardt* 1549 also form part of the type material. Two lectoparatypes (L0019903, L0019904) have printed labels (“Typ. Dupl.”) plus “*Cunonia celebica*” in Hoogland's hand.

2. Geissois *Labill.* (*Labillardière* 1825: 50); Smith (1985: 12); *Bradford et al.* (2004: 105); *Hopkins* (2006: 311); *Pillon* (2011: 93); *Hopkins et al.* (2014: 194).

Trees or sometimes *shrubs*. Indumentum of simple hairs, often with some minute curled trichomes and minute, red, spherical, “glandular” trichomes. *Stipules* intrapetiolar, 1 pair per node. *Leaves* opposite and decussate, petiolate, palmately compound; leaflets 3, 5, 7 or 9 (or rarely an even number), margins in adult plants entire or rarely toothed (not this region), in juvenile and shade foliage margins occasionally toothed; domatia sometimes present. *Inflorescences* ramiflorous or sometimes axillary, many-flowered, racemose, usually a monad (a single unbranched raceme on a peduncle) or rarely a triad (3 racemes on a common peduncle). *Flowers* pedicellate, bisexual; calyx 4-lobed, valvate in bud, bright red; corolla absent; stamens numerous (11 – 28), in a single whorl, filaments bright red, extending far beyond calyx; disc annular, often yellow; gynoecium of 2 carpels, fused at level of ovary; locules and stylodia 2; ovules numerous, arranged in 2 rows in each locule. *Capsules* usually cylindrical (rarely ovoid, not this region), tapering towards and dehiscent from the apex; seeds numerous small, flat, winged.



Fig. 1. Flowers and foliage of Cunoniaceae from the Solomon Islands. **A** *Pterophylla croftii*; **B** *Ackama celebica*, flowers in young bud; **C, D** *Pterophylla fraxinea*; **E** forest on Vangunu, 650 m. Vouchers: **A** Bradford 811; **B** Bradford 840; **C, D** Bradford 830. PHOTOS: JASON C. BRADFORD.

About 18 species, in the Solomon Islands (Vanikoro), Vanuatu, New Caledonia and Fiji; one species in the Solomon Islands and one in Vanuatu. For generic distribution maps see Hoogland (1984: no.

263, excluding Australia) and Hopkins *et al.* (2013: fig. 5). *Karrabina* Rozefelds & H.C.Hopkins accommodates two Australian species at one time included in *Geissois* (Hopkins *et al.* 2013).

Key to the species of *Geissois* in the Solomon Islands and Vanuatu

1. Leaflets 3 per leaf; young stems and petioles usually densely to sparsely pubescent, rarely pruinose; ovary often densely hairy (rarely almost glabrous) (Vanuatu)..... **2.1. *G. denhamii***
 1'. Leaflets usually 5 per leaf (occasionally some leaves with 3 or 4 leaflets); young stems and petioles usually glabrous and pruinose; ovary glabrous or rarely with a few hairs only Solomon Islands, Vanikoro)..... **2.2. *G. pentaphylla***

2.1. *Geissois denhamii* Seem. (Seemann 1866: 109), “*denhamii*”; Guillaumin (1931: 251); Wheatley (1992: 74, fig. p. 75). Type: New Hebrides [Vanuatu], Aneiteum [sic], 1854 (fl. & yfr.), *MacGillivray* s.n. (holotype: BM [BM000600409]; possible isotype: K [K000739695, no. 927, Nov. 1853, fl. & yfr.).

Geissois parviflora Guillaumin (1937: 287). Type: [Vanuatu], Erromango, versant W du massif occupant le N de l'île, cote 390, 2^{ème} voyage 1935–1936, 19 Feb. 1936 (buds), *M. et Mme Aubert de la Rüe* s.n. (lectotype of Hopkins (2006): P [P00641896]; probable isotype P [P00641897]).

Small or medium-sized *tree*, 5–15 (–25) m tall, trunk to 70 cm diam., or sometimes a *shrub* (3 m). Young stems markedly flattened, densely to sparsely pubescent (and then older stems glabrous) or occasionally glabrous, older stems lenticellate; axillary buds golden-hirsute. *Stipules* in dormant buds ± ligulate-triangular (rarely ovate), 5–10 × 2–3 mm, glabrous to densely hairy, not swollen over apical bud; after separating 20–27 (–45) × 4–6 (–12) mm, adaxial surface ± glabrous except around yellow-felty margins, caducous or briefly persistent at subdistal nodes. *Leaves* 3-foliolate, variable in size but often rather small on fertile twigs; petiole 0.7–5 cm long, densely pubescent to glabrous. Median leaflet: petiolule 0.3–2 cm long, glabrous to densely pubescent; blade elliptic to obovate, (3–) 7–16 (–20) × (1.5–) 3–7.5 (–8.5) cm, narrowly cuneate to decurrent at base, acute to shortly apiculate at apex, ± chartaceous, both surfaces glabrous or sometimes strigose along either side of midrib beneath; margins entire; domatia in angle between secondary veins and midrib on under-surface of leaflets common, minute, without hairs; secondary veins 9–13 on either side of midrib, minutely prominent on lower surface. Lateral leaflets ± similar to median except unequal at base and petiolules 2/3 as long. Young leaves sparsely hairy, especially on midrib and secondary veins beneath, plus sparse red glands on lower surface of blades. *Inflorescence* of monads (or

rarely small dyads or triads), ramiflorous, solitary or 2 together, projecting; axis 6–20 cm (including peduncle 3–5 cm), glabrous or occasionally sparsely hirsute, minutely ridged, bearing 15–50 flowers. Floral bracts triangular-ovate, 1.5–2.5 × 0.5–0.7 mm, glabrous or almost so, margins sometimes ciliolate. Pedicels (2–) 4–13 mm long, glabrous or shortly hairy, articulated near mid-point. *Flowers*: calyx lobes 5.3–8 × (1.8–) 2.3–3.5 (–4.5) mm, sparsely to densely hirsute on inner surface (hairs 0.2–0.8 mm), glabrous on outer surface; stamens 8–18, filaments (10–) 12–20 mm long, anthers 1–1.3 × 0.6–1 × 0.3–0.6 mm; disc 0.6–1.2 × 0.3–0.5 mm; ovary 3–4.5 × 1.2–2 mm, usually densely hirsute (hairs 0.3–2.5 mm) or occasionally glabrous; styles 12–17 mm long, ovules 2 × 11–18 per locule. *Capsules* cylindrical, slightly curved, valves 1.2–2 (–2.5) × 0.35–0.5 cm (plus style-bases 1 mm long), glabrous to densely ± adpressed hirsute. Seeds c. 5 × 1.5 mm, including apical wing 2–2.5 mm long. Figs 2, 3H–M.

DISTRIBUTION. Endemic to Vanuatu and recorded from most of the major islands. Map 2.

REPRESENTATIVE SPECIMENS (from a total of 60 collections). **VANUATU. Torba Prov.: Banks Islands: Vanua Lava:** crête vers 500 m, 13 June 1983 (yfr.), *Veillon* 5531 (NOU, P). **Sanma Prov.: Espiritu Santo:** col sur la custom road, entre la rivière Pialapa et le village de Wunabaï, Cumberland, 1240 m, 21 March 1978 (yfr.), *Cabalion* 466 (NOU, P); Nokowoula village area, 28 Aug. 1971 (old fl.), *Gillison & Beveridge* RSNH 3529 (K, P); N, vallée de la Pialoraï, 1 Aug. 1979 (fl.), *Morat* 6454 (L, NOU, P × 4); Pénaoru Valley, 14°58'3"S 166°40'43"E, 1200 m, 10 Nov. 2006 (fl. & fr.), *Munzinger et al.* 3787 (P); Mt Tabwemasana, sommet, 15°21'49"S 166°45'06"E, 1820 m, 3 Nov. 2006 (buds), *Pillon et al.* 559 (K, P, PVNH); Cumberland, nr Camp de la Rivière Beesel (or Beetsina), rive gauche, 14°57'20"S 166°40'20"E, 650–750 m, 18 Nov. 2006 (fl. & fr.), *Pillon et al.* 589 (K, L, P); Boutmas, sentier forestier à partir de la piste carrossable Boutmas – Tatafo,



Fig. 2. *Geissois denhamii*, Espiritu Santo, Vanuatu. **A** small tree; **B** opposite trifoliate leaves and apical bud enclosed by stipules; **C** ramiflorous inflorescence; **D** flowers. Vouchers: **A, B** Pillon *et al.* 540, **C** Pillon *et al.* 589, **D** Poncy *et al.* 2382. PHOTOS: **A** – C YOHAN PILLON, **D** ODILE PONCY.

à l'E du plateau du Tanakar, 15°22'20"S 166°59'00"E, 450 m, 16 Oct. 2006 (fl.), Poncy *et al.* 2382 (P). **Penama Prov.: Pentecost:** Kumre, 600 m, 19 Dec. 1935 (seedling), Aubert de la Rüe s.n. (P); **Ambrym:** versant W du Mt Toïno, 600 m, 21 Jan. 1936 (fl.), Aubert de la Rüe s.n. (P ×2). **Malampa Prov.: Paama:** 350 m, 28 Aug. 1989 (fr.), Wheatley 632 (K). **Shefa Prov.: Efate:** Undine Bay, 300 m, 27 April 1928 (buds & fl.), Kajewski 225 (P); "Vate", 450 m, 26 May 1965 (yfr.), Schmid 246 (NOU). **Tafea Prov.: Erromango:** 11 km W of Ipota (Pouta), 28 – 31 May 1968 (fr.), Bernardi 13371 (G, K, NOU, P); S, près de Bouniakoup, 200 m, 21 Feb. 1982 (fr.), Cabalion 1486 (NOU); Lenu Hill above Port Narvinm, 20 m, 10 Aug. 1992 (fl. & fr.), Curry 594 (K); nr Nouankao camp, 18°54'S 169°11'E, 150 m, 3 Aug. 1971 (fl.), Green RSNH 1260 (K ×2, L, NOU, P ×2); peak S from Mt Gordon, Dillon's Bay, 5 Aug. 1896 (fl.), Morrison s.n. (K). **Tanna:** Pagi Yanehoop?, 500 – 590 m, 21 May 1968 (fr.), Bernardi 13101 (G, K, NOU, P); Eniou, 300 m,

14 June 1982 (yfr.), Cabalion 1567 (NOU, P); Lenakel, 200 m, 6 March 1928 (fr.), Kajewski 106 (K, P); flan E du Toukosmereu, 600 m, 7 Feb. 1978 (buds), Morat 5900 (NOU, P); N, Green Hill area, Nusemetu Conservation Area, 19°23'31"S 169°17'34"E, 400 m, 15 Nov. 2014 (fl. & fr.), Ranker *et al.* 2319 (NY); Ikouroup, 28 July 1971 (buds, fl. & fr.), Raynal RSNH 16174 (K, P, NOU). **Aneityum:** Baie de Inyeug, Feb. 1934 (buds), Aubert de la Rüe s.n. (P); NW, Anseaniplitea, 20°14'13"S 169°47'56"E, 10 m, 19 April 2016 (fl. & fr.), Balick *et al.* 4916 (NY); nr Anawounamalo towards stream Inwa Lelgey, 10 – 180 m, 5 May 1968 (fr.), Bernardi 12930 (G, K, L, NOU, P); nr Anelgaohat, 20 m, 7 Feb. 1986 (fr.), Bourdy 323 (K, NOU, P); coast to Saddle Mt, March 1955 (fl. & yfr.), Cheesman A124 (BM); Niezouma Peninsula, SE of Anelgaohat, 200 m, 19 July 1971 (buds, fl. & fr.), Chew RSNH 53 (K, L, NOU, P); summit between Anummy (spelling?) & Ithug, 700 m, 26 June 1896 (fl.), Morrison s.n. (K, P).

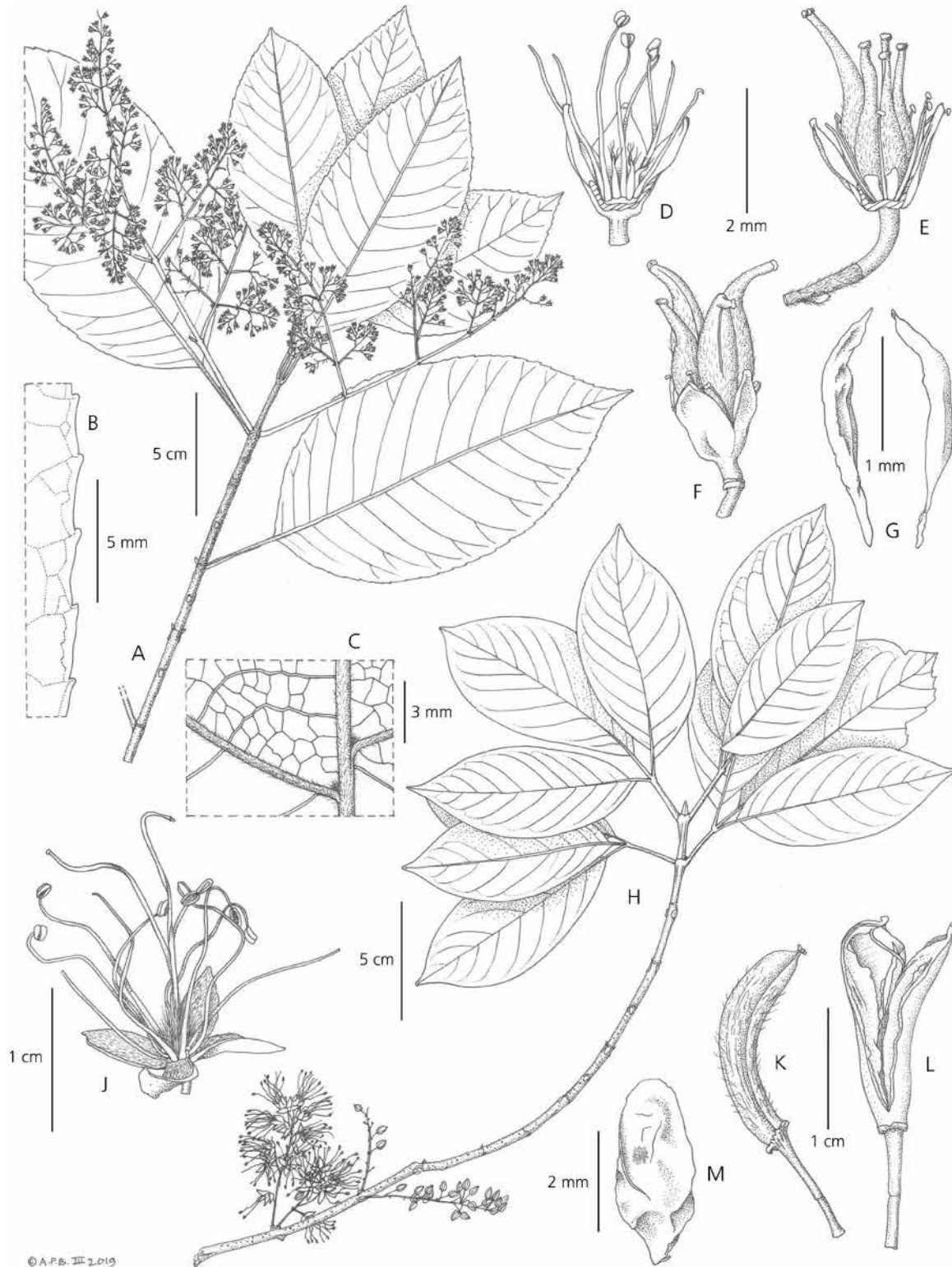


Fig. 3. **A – G** *Spiraeanthemum bougainvillense*. **A** leafy shoot with inflorescence at young fruiting stage; **B** leaf margin (adaxial surface); **C** detail of venation and domatia on abaxial surface of leaf; **D** male flower, one tepal removed; **E** female flower, one tepal removed (note reduced stamens); **F** mature fruit; **G** seed in face view (L) and side view (R). **H – M** *Geissois denhamii*. **H** leafy shoot and ramiflorous inflorescences; **J** flower; **K** young fruit; **L** mature dehiscent fruit; **M** seed. **A – C, E** Schodde et al. 3850; **D** Cole 107; **F, G** Schodde et al. 3768; **H** Wheatley 723; **J** Bernardi 12932; **K – M** Wheatley 632). DRAWN BY ANDREW BROWN.

HABITAT AND ECOLOGY. *Geissois denhamii* occurs in rain forest, moss forest, in scrub or thicket, at the forest edge, in pasture and near the strand line, from 10 – 1300 m. Chew (1975) noted that some plants in Vanuatu, including *Geissois*, occurred mainly at higher elevations in the northern islands but were more abundant at lower altitudes on the southern islands. According to Wheatley (1992 and specimen labels), this species grows in natural gaps in the canopy and is a canopy tree in old growth. It is reported as abundant on some islands and occasional or common in logged areas. Substrates include volcanic soils and rarely limestone on Santo (field notes of Pillon 531, Poncey 2382 & 2399).

CONSERVATION STATUS. LC (Least Concern). The number and distribution of collections suggests *Geissois denhamii* is widespread and relatively abundant throughout Vanuatu. It is not a significant timber species and can be found in previously logged habitats.

LOCAL NAMES (additional to those in Wheatley 1992): Aokara (Wusi-Kerepua), fide Pillon *et al.* 540. Boküet, fide Aubert de la Rüe s.n. (from Pentecost). Topnân (Butmas-Tur), fide Pillon *et al.* 531.

NOTES. The phylogenies of Pillon (2011; Pillon *et al.* 2014) placed *Geissois denhamii* in the *G. pruinosa* – *G. racemosa* clade as sister to *G. ternata* A.Gray from Fiji. These two are rather similar as both commonly have relatively small trifoliolate leaflets on fertile shoots. Leaves on sterile shoots of *G. denhamii* often have slightly larger leaflets than those on fertile shoots. The leaflets were described by Wheatley (1992) as almost silvery green below with the stipules light green and conspicuous.

Guillaumin (1937) distinguished *Geissois parviflora* by its large leaves (leaflet blades 21 × 11 cm) and small flowers (sepals 5.3 mm long; pedicels 2 – 3 mm long, articulated at or near the apex). Although the type (Aubert de la Rüe s.n.) is unusual, it is not far outside the normal range for *G. denhamii* and so *G. parviflora* is not maintained as distinct.

Variation in the density of the indumentum on the stipules and the ovary is not closely correlated (Map 2); where the indumentum is denser, the hairs are often longer. In the northern islands (Banks Isl. to Efate), the stipules are sparsely hairy, whereas in the southern islands (Erromango, Tanna, Aneityum) their indumentum is dense. Densely hairy ovaries occur in Espiritu Santo, Tanna and Aneityum, and more sparsely hairy ovaries are found in the northern islands (including Santo) and as far south as Tanna, meaning that the distributions of sparsely and densely hairy ovaries overlap. However, it is not yet confirmed that plants from the Banks Islands have sparsely hairy ovaries.

2.2. *Geissois pentaphylla* C.T.White (1950: 86); Whitmore (1966a: 59). Type: Solomon Islands, Santa Cruz Group, Vanikoro, nr Lamia R., 30 Nov. 1945

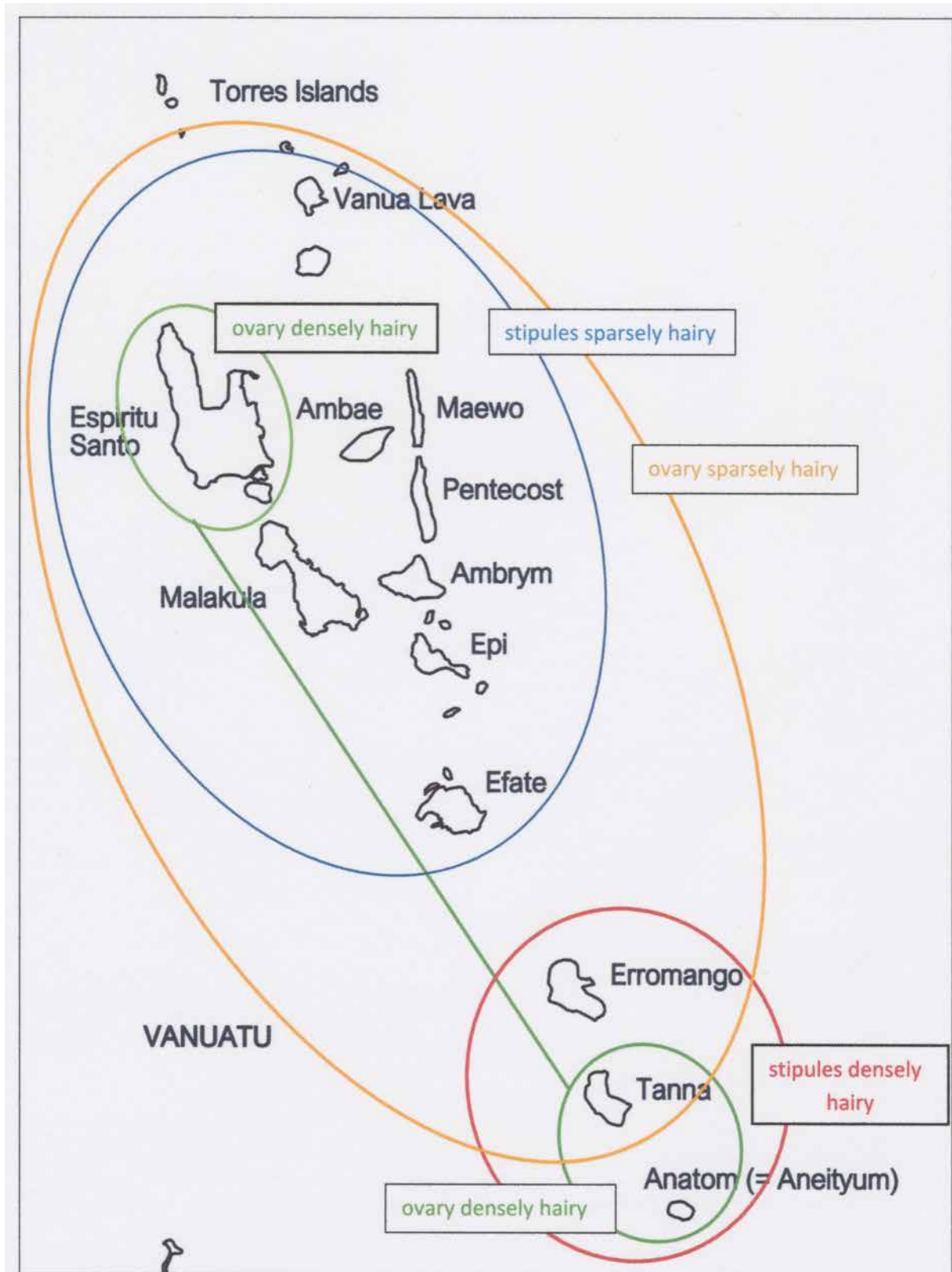
(fr.), F. S. Walker BSIP 217 (holotype: BRI ×2 [both BRI-AQ0354924]; isotypes: A, K ×2 [K000739699, K000739700], LAE n.v.).

Geissois pentaphylla C.T.White in F.S.Walker (1948: 110), *nom. invalid.*, description in English.

Tree 6 – 20 m high, trunk to 1 m girth; buttresses thin, to 1 m, or absent. Young stems markedly flattened, sometimes pruinose, glabrous or very sparsely hairy; older stems lenticellate, glabrous. *Stipules* in bud ligulate-ovate, c. 7 × 3 – 4 mm, glabrous or somewhat pubescent-hirsute with margins densely yellow-hairy, not markedly swollen over apical bud; after separating, caducous or briefly persistent, adaxial surface glabrous except for sparse orange glands and margins minutely yellow-felty with a few longer hairs. *Leaves* (3, 4) or commonly 5-foliolate; petiole 2.5 – 8 cm long, glabrous and usually pruinose (or very sparsely pubescent). Median leaflet: petiolule 1 – 3 cm long; blade elliptic, 13 – 17.5 × 5.3 – 7.3 cm, narrowly cuneate at base, acute-acuminate at apex, chartaceous, margins entire (or serrulate in type), both surfaces glabrous or with a few minute hairs along either side of midrib; secondary veins 8 – 12 on either side of midrib, minutely prominent beneath; domatia sometimes present in angle between secondary veins and midrib on lower surface, lacking hairs. In 5-foliolate leaves, inner laterals ± similar to median leaflet, with petiolules 2/3 as long, and outer laterals slightly smaller, 7.5 – 13.5 × 3 – 6 cm, asymmetric at base, with shorter petiolules. *Inflorescence* of monads, ramiflorous, projecting, solitary; axis 2 – 9 cm long, glabrous (to very sparsely hairy), bearing c. 20 – 30 flowers. Floral bracts not seen. Pedicels 4 – 8 mm long (– 10 mm in fruit), glabrous or with a few minute orange glands (at × 40), articulated at or below mid-point. *Flowers*: calyx lobes 6 – 7 × 2.5 – 3 mm, inner surface sparsely hirsute-crispate to almost glabrous, outer surface glabrous; stamens 10 – 18, filaments 15 – 18 mm long, anthers 1 × 1 mm; disc 0.5 × 0.5 mm; ovary 2 – 3 × 0.8 mm, glabrous or almost so; styles to 1.4 cm long. *Capsule* cylindrical, curved or straight, tapering towards apex, valves 2 – 3 × 0.3 – 0.5 cm (plus style bases c. 1 mm long), glabrous or sometimes with a few white hairs when immature. Seeds 5 – 6 × 1.5 mm, including apical wing 2 – 2.5 mm long. Fig. 4.

DISTRIBUTION. Endemic to Vanikoro, Solomon Islands (Map 3).

ADDITIONAL SPECIMENS EXAMINED. SOLOMON ISLANDS. Temotu Prov.: Vanikoro: environs du village de Paiou, 2 Dec. 1999 (st.), Cabalion 3338 (NOU); 300 m, 11 Dec. 1954 (fl. & fr.), Hadley 53 (BM); Ngae R., 11°36'49"S 166°49'8"E, 10 – 150 m, 20 June 2016 (fl. & fr.), Hsu *et al.* SITW10846 (BSIP n.v., TAIF, TNM); S coast at Emwa, 300 m, 8 April 1963 (fr.), Whitmore BSIP 1684 (K, L); Middle Ridge, 460 m, 23 April 1963 (fr.), Whitmore BSIP 1762 (K, L). Island not specified: E Santa Cruz,



Map 2. Variation in *Geissois denhamii* in Vanuatu based on an analysis by R. D. Hoogland (unpublished). Four possible combinations occur: densely or sparsely hairy ovaries with either densely or sparsely hairy stipules. Espiritu Santo and Tanna both have some specimens with densely hairy ovaries and others with sparsely hairy ones.

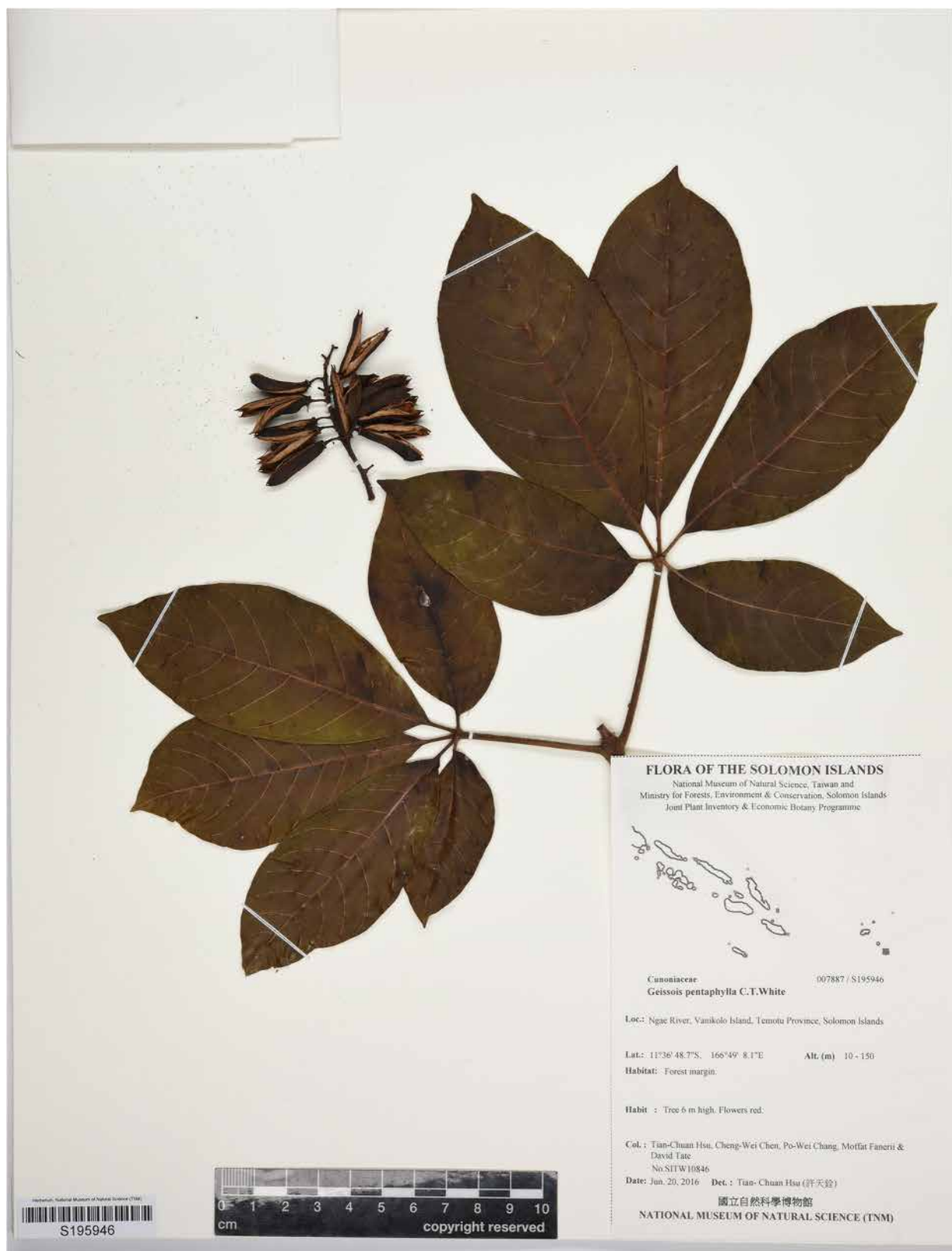


Fig. 4. *Geissois pentaphylla*, Vanikoro, Solomon Islands. Image of Hsu *et al.* SITW10846-TNM, kindly supplied by the National Museum of Natural Science, Taichung, Taiwan.

215 m, 20 Oct. 1969 (fl. & yfr.), *Mauriasi et al.* BSIP 17726 (K), 17727 (L).

HABITAT. *Geissois pentaphylla* occurs in well drained primary forest, ridge forest on deep clay and lowland rain forest on fern-covered hillsides subject to fire, as well as at the forest edge, from 100 – 460 m.

CONSERVATION STATUS. Vanikoro is the most southerly of the Santa Cruz group of volcanic islands that lie to the south-east of the main chain of the Solomon Islands. The principal island is 27 km long with an area of c. 190 km² (Pierce 2014). At its centre is the crater of Mt Banie (also called Mt Kapogo or Mt Popokio), variously reported as between 800 and 1000 m high, with densely forested slopes and surrounded by subsidiary craters. A second, smaller inhabited island (Tevai or Te Anu) plus several uninhabited islets also form part of Vanikoro although collections of *Geissois pentaphylla* are all likely to have come from the main island. Vanikoro and its forests were described by Whitmore (1966b), Hallé (2003) and Cabalion (2003, including a species list); see also Kajewski (1930) and Walker (1948).

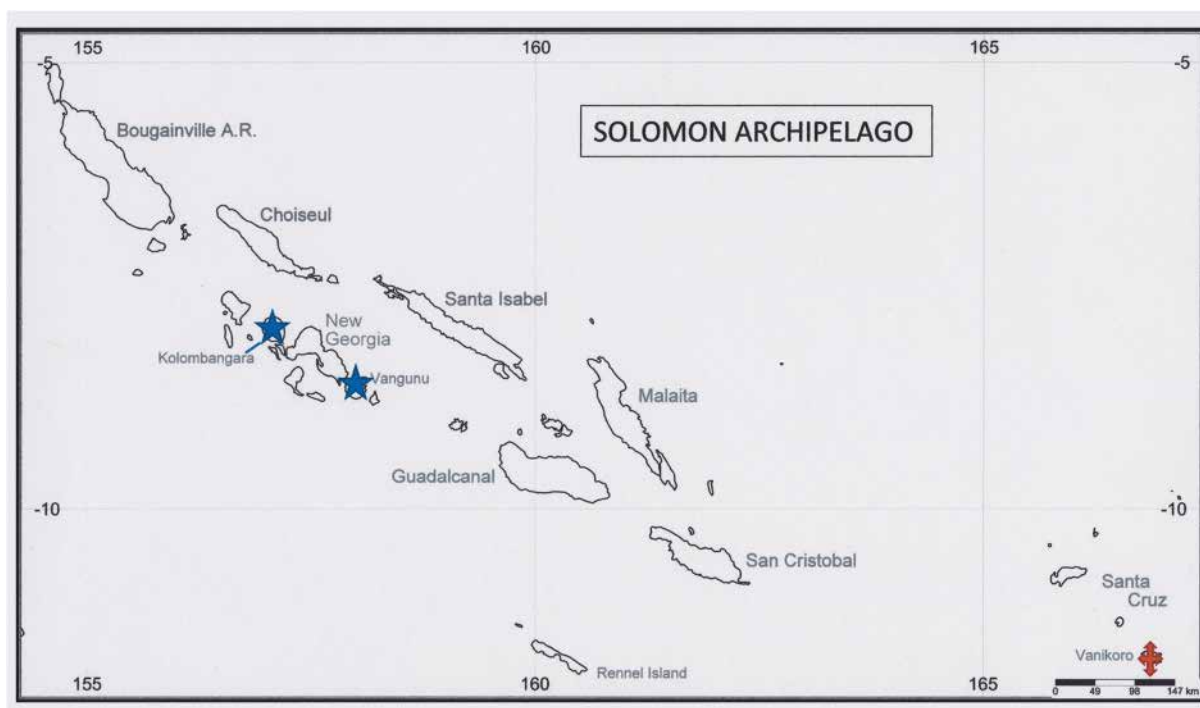
Commercial logging for Kauri (*Agathis macrophylla* Mast.) occurred on Vanikoro from 1926 to 1964 (Bennett 2000; Whitmore 1966b) and new logging licences have been granted (Dawen & Cannon 2017) although meeting with some local opposition. Habitat destruction threatens several bird and bat species that are endemic to the Santa Cruz Islands

(Pierce 2014) and no protected areas currently exist on Vanikoro. Although *Geissois pentaphylla* appears to survive in degraded habitats, the combination of its small EOO (probably < 150 km²), presence at fewer than five locations and threats from loss of habitat suggests a provisional conservation assessment of Endangered (EN B1ab(i,ii,iii)).

LOCAL NAME. Jaco wa tandoé, fide *Cabalion* 3338.

NOTES. *Geissois pentaphylla* was not included in the phylogenetic analyses of Pillon (2011; Pillon *et al.* 2014) but its morphology suggests its affinities are with *G. denhamii* in the *G. pruinosa* – *G. racemosa* clade.

The type material at K and BRI is in poor condition making it difficult to verify some of the characters in the protologue, and discrepancies exist between the descriptions of White and material collected subsequently. For these reasons, unconfirmed characters from White's accounts have been excluded from the description here. According to White (in Walker 1948), the flowers have five sepals, but like others in the genus, this species normally has four. White (1950) described the young leaves as densely pubescent but in the only specimen we have seen with young leaves, Whitmore BSIP 1762, the emerging leaves are glabrous or almost so, and when hairs are present on the petioles and petiolules in adult leaves, they are sparse. White (1950) described the stipules as 3 cm long just before falling, but in subsequent collections they are shorter; however, in several species, including *Geissois*



Map 3. The Solomon archipelago, showing the occurrence of *Geissois pentaphylla* (◆) and *Pterophylla makiniae* (★).

denhamii, the stipules appear to elongate just prior to being shed.

In addition to a few long, white, strigose hairs, the young leaf emerging from between the stipules on *Whitmore* BSIP 1762 (L) has some spherical, orange, gland-like structures, especially on the abaxial surface on either side of the prominent secondary veins. Similar but smaller structures are present on the pedicels and these “glands” occur occasionally in other species of *Geissois*.

The only collection mentioned in the protologue of *Geissois pentaphylla* was *Walker* BSIP 217 and in his introduction, *White* (1950) stated that types of his new species were at Queensland Herbarium, Brisbane, with isotypes at A, K and sometimes elsewhere. The two sheets of *Walker* BSIP 217 at BRI each have a label stating “holotype”, and either “sheet 1 of 2”, or “sheet 2 of 2”, written by A. Bolin on 15 Nov. 1983. This holotype designation was erroneously changed in *Hopkins* (2006) and is corrected here.

3. *Pterophylla* *D. Don* (1830: 93); *Pillon et al.* (2021a: 1197, q.v. for synonymy).

Trees or shrubs. Indumentum of simple hairs. Stems often slightly flattened at nodes. *Stipules* interpetiolar, 1 pair per node, usually caducous in fertile material. *Leaves* opposite and decussate (rarely whorled), simple, trifoliolate or imparipinnate, usually petiolate; in compound leaves, lateral leaflets usually opposite and sessile, sometimes asymmetric at base, terminal leaflets usually decurrent at base; margins of blades toothed or crenulate (rarely ± entire); domatia absent. *Inflorescences* many-flowered; racemes either simple and axillary (not this region) or arranged in groups on a sterile axis (peduncle), the basal segment(s) of which is either axillary or terminal, or a combination. *Flowers* bisexual, unisexual or a mixture, pedicellate, hypogynous or slightly perigynous; sepals 4–5, imbricate in bud; petals 4–5, elliptic or ovate, membranous, white to pale pink; stamens (5) 8 or 10, reduced in female flowers; disc annular or divided into lobes; gynoecium of 2 (3) carpels, united at the level of the ovary, locules and stylocidia 2 (3); ovules 8–16 per

Table 2. Species of *Pterophylla* in the Solomon archipelago and Vanuatu according to section and island group.

	Solomon archipelago	Vanuatu
sect. <i>Pterophylla</i>	<i>P. fraxinea</i> <i>P. makiniae</i> <i>P. ysabelensis</i>	<i>P. macgillivrayi</i>
sect. <i>Leiospermum</i>	<i>P. croftii</i> <i>P. purpurea</i> <i>Pterophylla</i> sp. (Solomons B)	<i>P. denhamii</i>

locule, in 2 rows, placentation axile; gynoecium reduced in male flowers. *Capsules* dehiscent from the apex, free central column often present, valves ± coriaceous, boat-shaped, calyx lobes persistent or not. *Seeds* numerous, ellipsoid, comose or occasionally hairy all over.

About 68 species in Madagascar and the Comoros, throughout Malesia and the islands of the southern Pacific as far east as the Marquesas and Austral Islands; absent from the Americas, Africa, mainland Asia (except Peninsular Thailand, Peninsular Malaysia) and Australia; six species in the Solomon archipelago and two in Vanuatu (Table 2).

Bradford (1998) divided *Weinmannia* s.l. (i.e. both New and Old World species) into five sections, four of which now comprise *Pterophylla* (*Pillon et al.* 2021a). Two sections, *Pterophylla* and *Leiospermum*, occur in the present area and the structure of the inflorescence is significant in distinguishing between them (see diagrams in *Bradford* 1998; *Hopkins & Bradford* 1998).

Some changes are made here to the species accounts in *Hopkins & Bradford* (1998) and *Hopkins et al.* (1998), including to the distribution of *Pterophylla croftii*, and we describe *P. makiniae* sp. nov. for material from the Solomon Islands previously identified as *W. exigua* A.C.Sm. Descriptions of most taxa were also given by *Bernardi* (1964, as *Weinmannia*). All species in the region have rather similar small flowers with petals 1–2 mm long, and all have similar small, brown or reddish-brown fruits, 2–4 (–6) × 1.5–2 (–3) mm (plus style remnants 1–2 mm). The specimens cited are recent collections or represent rare species.

Key to the species of *Pterophylla* in the Solomon archipelago and Vanuatu

1. Flowers grouped in small fascicles on the axis of a raceme, each fascicle in the axil of a small bract; inflorescence comprising 1 or 2 (3) pairs of opposite axillary dyads or tetrads (each formed of 2 or 4 racemes on a common peduncle) at the most distal leaf-bearing node of a shoot, i.e. inflorescence units lateral; if more than 1 pair of dyads or tetrads, these inserted in series..... sect. **Pterophylla**: 2
- 1'. Flowers inserted singly on the axis of a raceme, each flower in the axil of a small bract; inflorescence commonly a triad or pentad (each formed of 3 or 5 racemes on a common peduncle), these typically in a median position, sometimes with some additional axillary racemes at the base..... sect. **Leiospermum**: 5
2. Petiole and rachis segments very narrowly winged.....3
- 2'. Petiole and rachis segments not winged.....4

3. In fertile material, lateral leaflets in c. 8 pairs with blades elliptic to slightly obovate, 1 – 1.7 × 0.4 – 0.6 cm (Solomons: Kolombangara & Vangunu) **3.3. *P. makiniae***
- 3'. In fertile material, lateral leaflets in c. 1 – 5 pairs with blades ovate to oblong, 1.3 – 2 × 0.7 – 0.8 cm (Solomons: Isabel) **3.4. *P. ysabelensis***
4. Lateral leaflets in 4 – 10 (– 12) pairs, often with a small “ear” (an extra loose piece of leaf tissue) at the point of attachment of the leaflet to the rachis (Vanuatu)..... **3.2. *P. macgillivrayi***
- 4'. Lateral leaflets in 1 – 4 (– 6) pairs, without an “ear” at the point of attachment to the rachis (Solomons) **3.1. *P. fraxinea***
5. Leaves usually simple or unifoliolate, sometimes a few leaves trifoliolate (Solomons: Bougainville, Guadalcanal) **3.7. *P. purpurea***
- 5'. Leaves usually compound.....6
6. Leaves trifoliolate or imparipinnate with 2 pairs of lateral leaflets (Solomons)..... **3.5. *P. croftii***
- 6'. Most leaves imparipinnate, with 1 – 12 pairs of lateral leaflets7
7. Lateral leaflets in 1 – 12 pairs, 1.1 – 3 (– 4.8) × 0.3 – 1.1 (– 1.5) cm (Vanuatu)..... **3.6. *P. denhamii***
- 7'. Lateral leaflets in 2 – 5 pairs, 0.7 – 1.9 × 0.4 – 0.7 cm (Solomons: Bougainville)..... **3.8. *Pterophylla* sp. (Solomons B)**

sect. *Pterophylla*

Weinmannia L. sect. *Fasciculatae* Bernardi ex Hoogland & H.C.Hopkins (in Hopkins & Bradford 1998: 21, as “Fasciculata”).

3.1. *Pterophylla fraxinea* D.Don (1830: 93). *Weinmannia fraxinea* (D.Don) Miq. (Miquel 1856: 718). Type: [Indonesia, Moluccas], Honimoam, April 1797 (fl.), C. Smith s.n. (holotype: LINN-HS [LINN-HS 695.7]).

Tree to 25 (– 40) m high, often with buttresses. *Leaves* imparipinnate, rachis terete; lateral leaflets in 1 – 4 (– 8 elsewhere) pairs, usually narrowly ovate, sometimes lanceolate, narrowly elliptic or ovate, commonly 4.2 – 9 × 1.2 – 3.5 cm, with base rounded to cuneate and asymmetric, apex acute to acuminate; terminal leaflet often larger than largest laterals. *Inflorescence* usually well developed. *Flowers* bisexual in Solomon Islands. Fig. 1C – D (and Hopkins & Bradford 1998: fig. 7).

DISTRIBUTION. Thailand (Peninsular), Malaysia, Indonesia (not Sulawesi), Brunei, Papua New Guinea (mainland, New Britain, New Ireland, not Manus or Bougainville), Solomon Islands (Choiseul, New Georgia Group [Vella Lavella, Kolombangara, New Georgia, Vangunu], Santa Isabel, Malaita, Small Malaita, Guadalcanal). 31 collections from the Solomon Islands.

SPECIMENS EXAMINED (additional to Hopkins *et al.* 1998). **SOLOMON ISLANDS. Western Prov.: New Georgia Group: Vangunu:** NW of Vura, along ridge to Mt Olasana, 08°42'S 158°01'E, 370 m, 15 Nov. 1997 (st.), Bradford 829 (MO); **Kolombangara:** end of logging road NNW of Ringi Cove and S of Mt Rano, 8°03'S 157°04'E, 400 m, 18 Nov. 1997 (fl.), Bradford 830 (K, MO).

HABITAT. Reported from rain forest, sometimes wet and mossy, from 10 – 600 m in the Solomon Islands.

CONSERVATION STATUS. Overall LC (Least Concern); in the Solomon Islands, DD (Data Deficient). Despite the high level of logging in the Solomon Islands, the wide distribution of this species and the relatively large number of collections over its entire range suggest that it may not be threatened. It demonstrates weedy tendencies in Borneo, sometimes growing abundantly in roadside cuttings (Hopkins & Bradford pers. obs. 1996) and so can probably regenerate in gaps when forest is selectively logged.

NOTES. The most widespread species of *Pterophylla* in Malesia and the Solomon Islands, *P. fraxinea* was reported by Whitmore (1966a, as *Weinmannia blumei* Planch.) as encountered occasionally in the Solomon Islands. Taken over its range as a whole, it is polymorphic, with variation in the size, thickness and number of leaflets per leaf (Hopkins & Bradford 1998).

The field notes of Bradford 830 reported that the flowers have a pale green calyx with the petals and filaments white and the nectary yellow, and the carpels and styles are white; the flowers are slightly sweetly fragrant and visited by bees.

3.2. *Pterophylla macgillivrayi* (Seem.) Pillon & H.C.Hopkins (in Pillon *et al.* 2021a: 1198). *Weinmannia macgillivrayi* Seem. (Seemann 1866: 109). Type: New Hebrides [Vanuatu], Aneiteum [sic], HMS Herald 1854 (fl.), Milne 277 (lectotype of Hopkins *et al.* 1998) K [K000739831]).

Shrub or *tree* to 20 m tall. *Leaves* imparipinnate, rachis terete, densely hairy on upper surface, segments not winged; lateral leaflets 4 – 10 (– 12) pairs, narrowly ovate to lanceolate, 2.2 – 4.6 × 0.6 – 1.3 cm, with base asymmetric, obtuse to rounded and apex acute, blades of the proximal 1 – 3 pairs distinctly shorter than the distal ones, often with small, free ‘ear’ at the base.

Flowers unisexual or rarely bisexual and plants polygamodioecious. Fig. 5 (and Hopkins *et al.* 1998: fig. 7).

DISTRIBUTION. Restricted to Vanuatu and known principally from Aneityum (13 collections) and also collected rarely on Espiritu Santo (*Cabalion* 880, *Veillon* 3992 (P)) and Erromango (*Cabalion* 1716). All except one of the collections listed below were determined by G. Plunkett.

SPECIMENS EXAMINED (additional to Hopkins *et al.* 1998).

VANUATU. Sanma Prov.: Espiritu Santo: 1 Aug. 1979, *Cabalion* 880 (PVNH n.v.). **Tafea Prov.: Erromango:** 22 June 1982, *Cabalion* 1716 (PVNH n.v.). **Aneityum:** behind Unameij, Anuwunamlau [sic], 20°13'47"S 169°46'45"E, 30 m, 16 April 2016 (fl.), *Balick et al.* 4874 (NY, PVNH n.v.); road past Anepancat swamp towards Mt Inrero, 0.4 km NE of Anelgauhat village, 20°13'50"S 169°47'01"E, 11 m, 5 Dec. 2016 (fr.), *Plunkett et al.* 3582 (NY n.v., PNVH n.v.); Anuwuncamlau area of Anelcauhahat, 20°13'51"S 169°46'41"E, 19 m, 11 Dec. 2019 (fl.), *Plunkett et al.* 5301 (NY n.v., PNVH n.v.).

HABITAT. Recorded from c. 10 – 300 m in rain forest, scrub, open secondary forest, forest remnants and forest on ridges. Described as common in the field notes of *Kajewski* 735.

CONSERVATION STATUS. DD (Data Deficient). The small volcanic island of Aneityum, where most collections of *Pterophylla macgillivrayi* have been made, has an area of c. 160 km². Based on this population only, the species would have a provisional conservation assessment of EN (Endangered) according to criterion B1. The sparsity of collections from other islands, including Santo which has been well collected for Cunoniaceae in general, suggests

that *P. macgillivrayi* is rare elsewhere. These other populations might change the conservation status, perhaps to VU (Vulnerable), but more information is needed on its abundance on these other islands.

NOTES. *Pterophylla macgillivrayi* is less widely distributed in Vanuatu than the more common *P. denhamii*. It appears closely related to *P. fraxinea* but is distinguished by its more numerous and smaller leaflets and by the “ears” that are frequent on the leaf rachis at the point of insertion of the lateral leaflets; in both species, the upper surface of the leaf rachis is often densely hairy.

3.3. *Pterophylla makiniae* H.C.Hopkins, J.Bradford & Pillon, sp. nov. Type: Solomon Islands, Western Prov., New Georgia Group, Vangunu Isl., inland from Merusu Islet, crater rim, 600 m, 10 Dec. 1962 (fl.), *Whitmore* BSIP 995 (holotype: K [K001235503]; isotype: L [L0332015]).

<http://www.ipni.org/urn:lsid:ipni.org:names:77317210-1>

Shrub or tree to 15 m high, dbh to 50 cm. Young twigs sericeous, older twigs pubescent with pale lenticels, eventually glabrescent; expanding leaves on either side of apical bud hairy abaxially. *Stipules* almost circular with shortly cuneate base, to 7 × 6 mm, abaxially sericeous, adaxially glabrous, usually present only at growing tips in fertile material, fugaceous, leaving a shallowly inverted U-shaped scar, exposing a sericeous apical bud with an axillary bud on either side and a

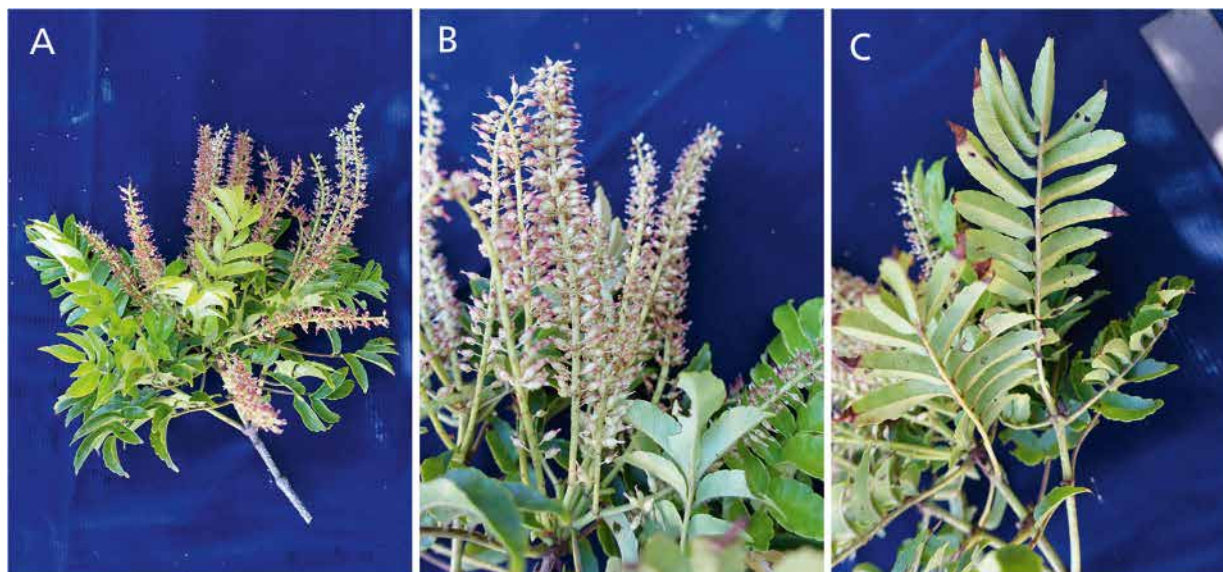


Fig. 5. *Pterophylla macgillivrayi*, Aneityum, Vanuatu. **A – B** twig with leaves and very young fruits, infructescence composed of bidens visible in B; **C** under-surface of leaves, note rachis unwinged. Voucher: *Balick et al.* 4874. PHOTOS: MICHAEL J. BALICK.

row of minute, finger-like, purple colleters; in sterile material especially, distal part of stipules sometimes reflexed. *Leaves* imparipinnate, to 6 cm long; petiole c. 8 mm long; rachis segments 4–7 mm long, each minutely winged distally (just below insertion of leaflets), densely hairy along midline on upper surface (hairs 0.5 mm, straw-coloured), almost glabrous to somewhat hairy on lower surface, glabrous laterally; in fertile material lateral leaflets c. 8 pairs, opposite (or basal pairs subopposite), $1 - 1.7 \times 0.4 - 0.6$ cm, distal ones slightly larger than proximal ones, elliptic to slightly obovate, base acute and \pm symmetric to asymmetric, apex acute; terminal leaflet scarcely longer than largest laterals, more narrowly acute at base; blades glabrous above and beneath or with a few hairs on midrib beneath; margins flat, teeth 3–5 on either side; secondary veins ending in the sinus of a tooth; under-surface sometimes with scattered raised dots (remains of hair bases?); in sterile material, leaves to 8.5 cm long with up to 13 pairs of lateral leaflets. *Inflorescence* a tetrad (composed of 2 opposite dyads, each dyad consisting of 2 racemes on a common peduncle), each common peduncle arising at the shoot apex in a leaf axil; apical bud of stem (between bases of peduncles) and minute bud at apex of each peduncle (between bases of racemes) sericeous; common peduncle of dyad 6–10 mm long, racemes to 5 cm long; axes puberulent. *Flowers* in fascicles, bisexual; pedicel 1 mm long; calyx lobes 4, triangular, 0.6 mm long; petals 4, 1–1.4 mm long, elliptic-oblong, round or notched at apex, membranous, whitish; stamens 8, filaments 3 mm long, anthers 0.3×0.3 mm, connective shortly extended; disc segments peg-like, 0.3 mm long, alternating with stamens, dark purplish when dry; ovary (in very young fruit) ovoid to orbicular, 0.5 mm long, densely hairy (hairs to 0.2 mm, golden); styles 2 mm long, dark purplish. *Mature fruits* not seen. Fig. 6.

RECOGNITION. Similar to *Pterophylla exigua* (A.C.Sm.) Pillon & H.C.Hopkins from Fiji but the lateral leaflets are more numerous (c. 8 pairs per leaf in fertile specimens, vs (0) 1–4 pairs in *P. exigua*) and the segments of the leaf rachis are very narrowly winged (vs distinctly winged in *P. exigua*). Also similar to *P. urdanetensis* (Elmer) Pillon & H.C.Hopkins from the Philippines and New Guinea but the leaflets in *P. makiniae* are glabrous or almost so (vs leaflets usually densely hairy on the under-surface in *P. urdanetensis*) and the rachis segments of the leaf are minutely winged (vs unwinged in *P. urdanetensis*).

DISTRIBUTION. Solomon Islands (Western Province) (Map 3).

SPECIMENS EXAMINED. SOLOMON ISLANDS. Western Prov.: New Georgia Group: Vangunu: NW of Vura along ridge to Mt Olasana, $8^{\circ}42'S$ $158^{\circ}01'E$, 680 m, 14 Nov. 1997 (st.), *Bradford* 814 (K \times 2, MO); *ibid.*, $8^{\circ}42'S$

$158^{\circ}01'E$, 840 m, 15 Nov. 1997 (st.), *Bradford* 827 (K, MO); inland from Merusu Islet, crater rim, 600 m, 10 Dec. 1962 (fl.), *Whitmore* BSIP 995 (type, K, L). **Kolombangara:** Mt Duke, S of Mt Tapalamenggututu and N of Vila R., $7^{\circ}58'S$ $157^{\circ}06'E$, 1130 m, 20 Nov. 1997 (st.), *Bradford* 835 (K, MO); Camp 2, $7^{\circ}58'56"S$ $157^{\circ}05'35"E$, 1300 m, 9 Aug. 2014 (st.), *Song et al.* SITW06037 (TAIF, TNM).

HABITAT. Found in mossy montane forest where it is a canopy tree on ridges with a deep humus layer. Collected between 600–1300 m and sometimes common (field notes of *Bradford* 814).

CONSERVATION STATUS. *Pterophylla makiniae* is known only from two small volcanic islands in the Solomon Islands. Vangunu has an area of 509 km² but was reported by Lavery & Judge (2017) to have only 80 km² of forest habitat remaining, with logging ongoing. Kolombangara is almost circular with a diameter of 30 km, giving it a surface area of c. 700 km². It is said to be one of the most intensively logged in the Solomon Islands with < 10% of the primary forest outside the central crater of Mt Veve (1770 m) remaining intact (Katovai *et al.* 2012). Long term plots here have provided data on forest dynamics (Burslem *et al.* 2000; Whitmore 1989) and the vegetation here (and presumably also on Vangunu) is subject to cyclones so trees that survive must be capable of regenerating after major disturbances; however, we have no specific information about regeneration in *P. makiniae*. The combined EOO for both islands is a maximum of 1200 km², and together with the potential threat from continued logging, suggests a provisional conservation assessment of Endangered (EN B1ab(i,ii,iii)).

ETYMOLOGY. Named for the Solomon Islands' poet, writer and activist for women's rights, Jully Makini, who was born in Western Province.

LOCAL NAME. Angula (Kwara'ae), fide *Whitmore* BSIP 995.

NOTES. Whitmore (1966a) recorded *Pterophylla urdanetensis* (as *Weinmannia urdanetensis* Elmer) from the Solomon Islands, based on *Whitmore* BSIP 995, now the type of *P. makiniae*. *Pterophylla urdanetensis*, from the Philippines and New Guinea, has leaflets similar in size and shape to those of the Whitmore collection but although the range in leaflet shape overlaps, those of *P. urdanetensis* are usually more oblong and the leaf rachis is terete and hairy all round (hairs straw-coloured, to 1 mm long), rather than very narrowly winged and often hairy only on the upper surface (*P. makiniae*). The young twigs in *P. urdanetensis* are typically densely hairy, as is the under-surface of the leaflets, especially the midrib, whereas in *P. makiniae* young twigs have a finer indumentum and the leaflets are glabrous or almost so.

Hopkins *et al.* (1998) equated *Whitmore* BSIP 995 with *Weinmannia exigua* from Fiji (see description in

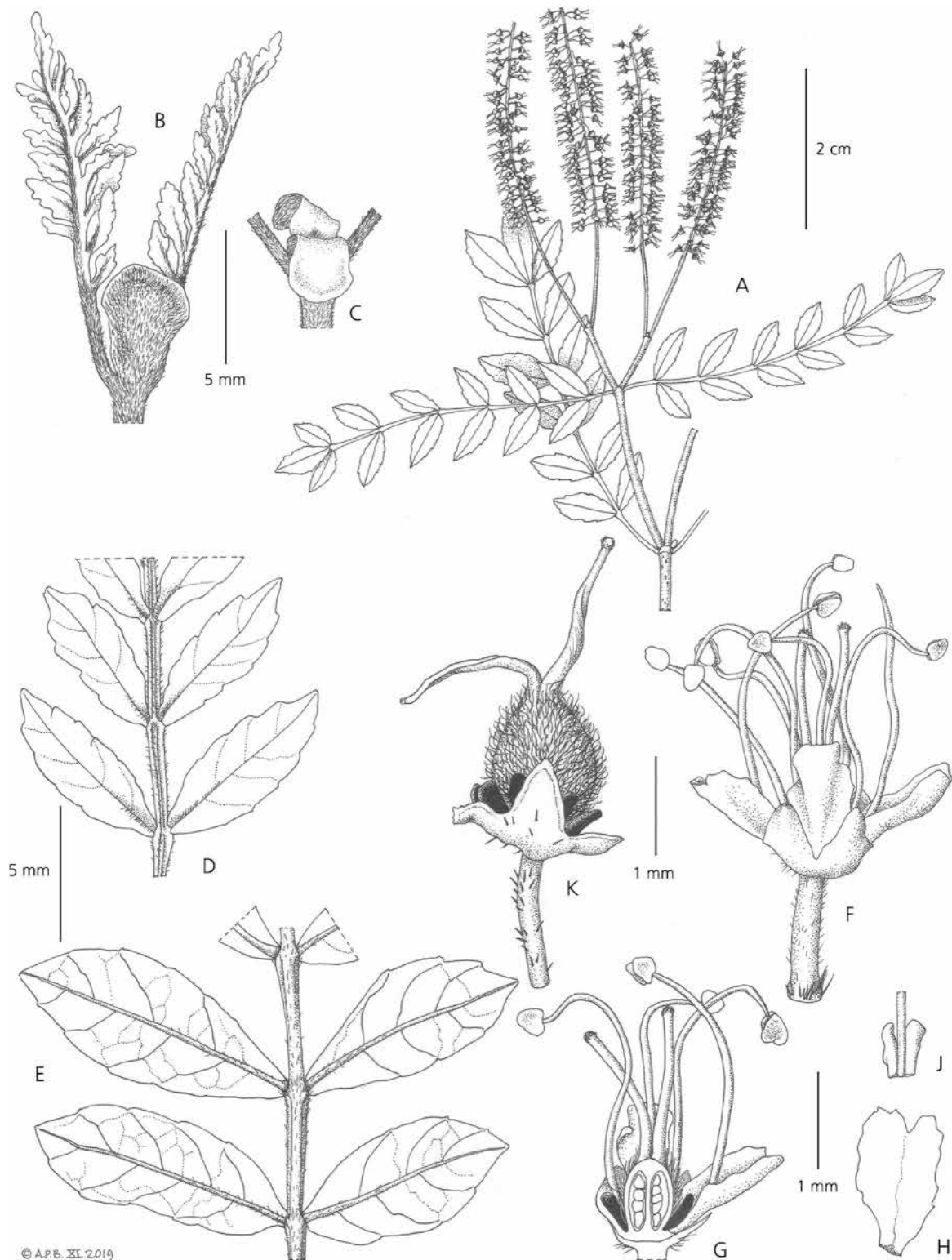


Fig. 6. *Pterophylla makiniae*. **A** leafy shoot and inflorescence at young fruiting stage; **B** apex of a shoot, showing a pair of young leaves and the outer, hairy surface of a stipule; **C** apex of another shoot, showing opposite petioles and recurved stipules (note adaxial surface glabrous); **D** part of a leaf, adaxial surface, note very narrowly winged rachis; **E** part of a larger leaf, abaxial surface; **F** flower, lateral view; **G** half-flower; **H** petal, flattened: note that not all petals are notched; **J** two disc segments, one on either side of the base of a filament; **K** young fruit. **A – K** Whitmore BSIP 995. DRAWN BY ANDREW BROWN.

Smith 1952: 137), which at the time was known only from two collections, the type (*Horne* 632, Fiji, Vanua Levu, between Waiwai and Lomaloma, May 1878 (fl. & yfr.), K000739828) and *Rangagone* in *Howard* 89 (Fiji, Vanua Levu [BISH, K: “*Pauliasi Rayaqona* H.89”). Similarities between the Whitmore collection and those from Fiji included leaves with small leaflets and the rachis segments narrowly winged, although those in Whitmore’s material are more narrowly winged than those of *Horne* 632. Now the species from Fiji is represented by a further collection (*Barrabé et al.* 1132, Taveuni [K, P]), it is clear that Whitmore’s specimen does not belong to the Fijian species and collections from the Solomon Islands by Bradford and Song *et al.*, although sterile, confirm this. The other species of *Pterophylla* known from Kolombangara and Vangunu, *P. croftii*, has fewer, considerably larger leaflets that differ in shape from those of *P. makimiae* (compare Figs 6 and 7) and has an inflorescence structure typical of sect. *Leiospermum* rather than sect. *Pterophylla*. *Pterophylla exigua* should now be considered endemic to Fiji.

3.4. *Pterophylla ysabelensis* (*L.M.Perry*) *Pillon & H.C.Hopkins* (in *Pillon et al.* 2021a: 1198). *Weinmannia ysabelensis* *L.M.Perry* (1949: 162). Type: Solomon Islands, Ysabel [sic], Tiratona, 600 m, Nov. 1932 (fl. & yfr.), *L. J. Brass* 3215 (holotype: A [A00043376]; isotypes: BISH [BISH1001197], BM [BM000565637], BRI [BRI-AQ0332038], BO, G [G00357656], L [L0062691], SING).

Tree 25 m tall. *Leaves* imparipinnate, rachis semi-terete, hairy along upper mid-line, distal rachis segments minutely winged; lateral leaflets in 1 – 5 pairs, ovate to oblong, 1.3 – 2 × 0.7 – 0.8 cm, with base somewhat asymmetric and apex broadly acute; terminal leaflet markedly larger than laterals (3 – 4.4 × 1 – 1.3 cm). *Flowers* bisexual. Illustration: *Hopkins et al.* (1998: fig. 6).

DISTRIBUTION. Solomon Islands (Santa Isabel), known only from the type.

HABITAT. Occurs in montane forest at 600 m and described as common.

CONSERVATION STATUS. DD (Data Deficient). Further information is needed on distribution and abundance, as well as on its relationship with *Pterophylla fraxinea*. Large parts of Santa Isabel have been logged (*Katovai et al.* 2015: fig. 4), which is likely to have reduced the habitat available.

NOTES. *Pterophylla ysabelensis* is similar to *P. fraxinea* but has much smaller leaflets. Although Whitmore (1966a) included them as two separate taxa in his key, he went on to imply they might be synonymous. Until we have more material from Santa Isabel, *P. ysabelensis* is maintained as distinct.

sect. *Leiospermum* (*D.Don*) *Engl.*

3.5. *Pterophylla croftii* (*H.C.Hopkins*) *Pillon & H.C.Hopkins* (in *Pillon et al.* 2021a: 1198). *Weinmannia croftii* *H.C.Hopkins* (in *Hopkins et al.* 1998: 76). Type: Papua New Guinea, Madang Prov., Kar Kar Island, 4°40'S 145°57'E, 914 m [3000 ft], 22 Jan. 1968 (fl. & yfr.), *C. E. Ridsdale* NGF 36706 (holotype: L [L0062690]; isotypes: A [A00066043], BISH [BISH1001181], CANB [CANB194320], K [K000739855]).

Weinmannia sp. (Solomons A) of *Hopkins et al.* (1998: 84).

Tree or *shrub*, 2 – 20 m high (to 10 m with trunk up to 1 m dbh in Solomons). *Leaves* trifoliolate or imparipinnate; petiole and rachis winged; lateral leaflets 1 – 3 pairs (usually 1 – 2 pairs in Solomons), lanceolate to narrowly elliptic, 2 – 6.7 × 0.5 – 1.7 cm (commonly 2 – 4 × 0.5 – 1.5 cm in Solomons, proximal leaflets slightly smaller than distal ones), with base asymmetric and apex acute; terminal leaflet somewhat longer and broader than largest laterals. On sterile shoots, lateral leaflets commonly in 3 pairs and slightly larger than on fertile shoots. *Flowers* unisexual and plants dioecious. Figs 1A, 7.

DISTRIBUTION. Papua New Guinea (Manus, Karkar, New Britain, New Ireland; not mainland or Bougainville) and Solomon Islands (Kolombangara, Vangunu, Guadalcanal).

SPECIMENS EXAMINED. SOLOMON ISLANDS. Guadalcanal Prov.: Guadalcanal: Popomanasiu, 2130 m, 23 Oct. 1965 (fl.), *Cornier* RSS 89 (K, L). **Western Prov.: New Georgia Group: Vangunu:** NW of Vura along ridge to Mt Olasana, 8°42'S 158°01'E, 700 m, 14 Nov. 1997 (fl.), *Bradford* 811 (K × 2, MO); *ibid.*, 8°42'S 158°01'E, 810 m, 15 Nov. 1997 (fr.), *Bradford* 822 (K × 2, MO). **Kolombangara:** Mt Duke, S of Mt Tapalamenggututu and N of Vila R., 7°58'S 157°06'E, 1220 m, 20 Nov. 1997 (st.), *Bradford* 836 (MO); *ibid.*, (fr.), *Bradford* 837 (K, MO); 1675 m, 2 Sept. 1965 (st.), *Cornier* RSS 1188 (K); *Weinmannia* cf. *croftii*: **Guadalcanal:** Popomanasiu, 2130 m, 5 Nov. 1965 (st.), *Hill* RSS 9011 (K, L).

HABITAT AND ECOLOGY. In the Solomon Islands, *Pterophylla croftii* is found on extinct volcanic mountains in wet, mossy montane forest, often on ridges, at 700 – 2150 m. The field notes of *Bradford* 811 and 822 report it as common.

CONSERVATION STATUS. Overall probably LC (Least Concern) although it may be under some threat locally as it has been found on only three of the Solomon Islands, all of which have been subject to logging. It appears to be quite common on Vangunu and Kolombangara, and the threats from logging may be mitigated by its occurrence on ridges at relatively high elevation and its tolerance of disturbance.

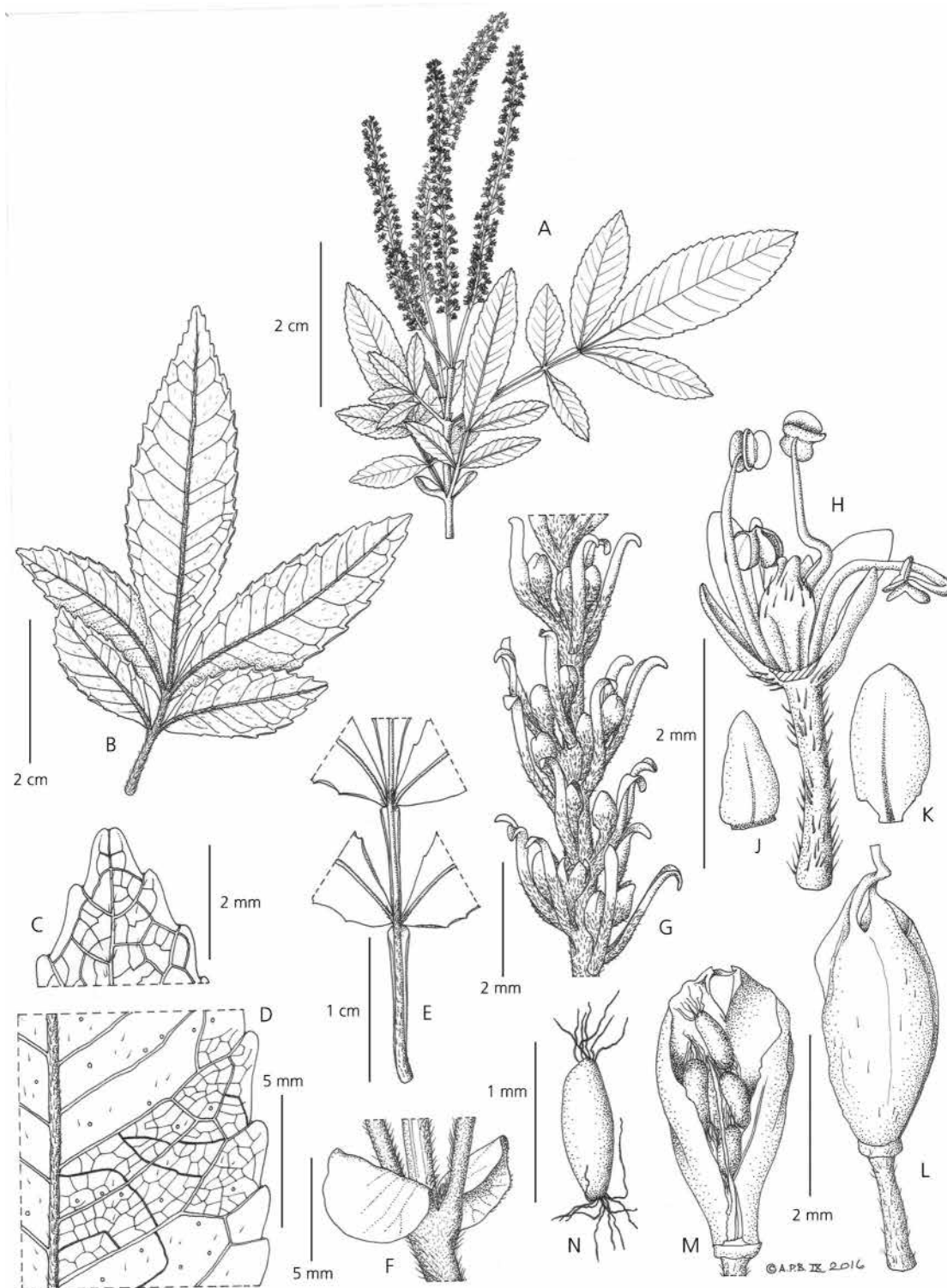


Fig. 7. *Pterophylla croftii*. **A** leafy shoot with inflorescence (triad) and part of another inflorescence behind it; **B** small leaf, abaxial surface, note that unusually, the rachis is unwinged; **C** tip of leaflet, abaxial surface; **D** abaxial surface of leaflet showing venation, sparse indumentum and "red dots" (hair bases?); **E** abaxial surface of larger leaf showing typical winged rachis; **F** stem with opposite petioles, base of median inflorescence axis and a pair of stipules; **G** part of a young inflorescence, note each flower is subtended by a bract; **H** flower, with 2 sepals, 2 petals and 4 stamens removed; **J** sepal; **K** petal; **L** mature fruit just starting to dehisce; **M** one half of a dehiscent fruit with seeds in situ; **N** seed. **A – F, H – K** Bradford 811; **G** Corner RSS 89; **L – N** Bradford 822. DRAWN BY ANDREW BROWN.

NOTES. Hopkins *et al.* (1998) suggested that the Corner and Hill specimens from Kolombangara and Guadalcanal might either represent a new species (*Weinmannia* sp. (Solomons A)) or belong to *P. croftii*, but of the three collections then known, only Corner RSS 89 was fertile and sterile material of *Pterophylla* is notoriously variable. However, the subsequent collections by Bradford cannot be distinguished from *P. croftii* although the leaflets are slightly smaller than typical. Hill RSS 9011 has rounder, broader leaflets (laterals 3 – 3.3 × 1.8 – 2 cm) and may be from an immature plant.

The field notes of Bradford 811 reported that the calyx was pale green, the petals and filaments white, the anthers dull yellow and that the flowers were barely fragrant; young foliage was pink to red, as commonly seen in *Pterophylla*.

3.6. *Pterophylla denhamii* (Seem.) Pillon & H.C.Hopkins (in Pillon *et al.* 2021a: 1198). *Weinmannia denhamii* Seem. (Seemann 1866: 109) as “*denhami*”. Type: New Hebrides [Vanuatu], Aneiteum, Feb. 1859 (fl.), (*MacGillivray*) 45 (lectotype of Hopkins *et al.* (1998): K [K000739834]; isolectotypes: BM [BM000565635], G [G00357649], P ×3 [P00641908, P00641909, P05552899]).

Weinmannia kajewskii Guillaumin (1931: 250). Type: New Hebrides [Vanuatu], Eromanga [sic] Is., Dillon Bay, 400 m, 28 May 1928 (fr.), *S. F. Kajewski* 317 (lectotype, **designated here**: P [P00641907]; isolectotypes: A [A00066044], BISH, K [000739836], NY [NY00356112]).

Weinmannia tannaensis Guillaumin (1931: 251). Type: New Hebrides [Vanuatu], Tanna Is., Mt Tokosh Meru, 1000 m, 15 March 1928 (buds), *S. F. Kajewski* 151 (lectotype, **designated here**: P [P00641903]; isolectotypes: BISH, K [K000739835], NY [NY00356116]).

Weinmannia kajewskii Guillaumin var. *ambrymensis* Guillaumin (1935: 349), *nom. illegit.*, no Latin description. Material cited: New Hebrides [Vanuatu], Ile Ambrym, grande plateau de scories à proximité du volcan actif, cote 600 – 700, Aug. 1934 (fl. & fr.), *E. Aubert de la Rüe* s.n. (A, L, P ×3 [P00641904, P00641905, P00641906]).

Tree or shrub 2 – 20 m high. *Leaves* imparipinnate, rachis and petiole flattened above with a narrow central ridge, segments winged; lateral leaflets in 1 – 12 pairs, lanceolate, elliptic or ovate, 1.1 – 3 (– 4.8) × 0.3 – 1.1 (– 1.5) cm, with base asymmetric and apex acute, proximal ones often shorter than more distal ones; terminal leaflet often slightly larger than laterals. *Flowers* unisexual and plants dioecious or polygamodioecious. Fig. 8.

DISTRIBUTION. Endemic to Vanuatu (Vanua Lava, Espiritu Santo, Ambae, Pentecost, Ambrym, Epi, Efate, Erromango, Tanna, Aneityum). Known from 42 collections.

REPRESENTATIVE SPECIMENS EXAMINED (and see Hopkins *et al.* 1998). **VANUATU. Sanma Prov.: Espiritu Santo:** Pénaoru Valley, 14°58'00"S 166°39'22"E, 900 m, 12 Nov. 2006 (fr.), *Munzinger et al.* 3885 (P); *ibid.*, 14°58'17"S 166°40'33"E, 1350 m, 12 Nov. 2006 (fr.), *Munzinger et al.* 3937 (P); Mt Tabwémassana, summit, 15°21'49"S 166°45'06"E, 1850 m, 3 Nov. 2006 (fl.), *Pillon et al.* 558 (K, MO, NOU, P, PVNH, SUVA); Cumberland, nr Camp de la Rivière Beesel (or Beetsina), 14°57'16"S 166°40'04"E, 700 m, 20 Nov. 2006 (fl.), *Pillon et al.* 601 (K ×2, MO, NOU, P, PVNH, SUVA). **Tafea Prov.: Tanna:** SW, Mt Tukosmera area, upper slopes, 19°34'36"S 169°23'16"E, 1086 m, 25 April 2016 (fl.), *Plunkett et al.* 3298 (NY); Central, nr Mt Lowanialu, road from Lenakel to Yasur, 6.8 km SE of Lamnatu, 19°30'20"S 169°21'15"E, 468 m, 20 June 2014 (fr.), *Ranker et al.* 2263 (NY).

HABITAT AND ECOLOGY. *Pterophylla denhamii* is found in both open habitats and in forest, and has been reported from riverine forest on basalt, open woodland with tree ferns, bracken-covered ridge grazed by bullocks, open scrub with *Acacia* Mill., open secondary forest, and deforested areas with ferns (*Pteridium* Gled. ex Scop. and *Gleichenia* Neck.). At higher elevations it occurs in dwarf montane forest on exposed crests and ridges. Wheatley (1992) described it as a canopy species of upper middle and high elevation forest and co-dominant with *Metrosideros* Banks ex Gaertn. over large areas. Soil types include volcanic cinders and lava, and young brown andosol. It belongs to a small clade of species including *P. croftii* and *P. vitiensis* Seem. that are often found on volcanic soils.

The overall elevational range is 120 – 1800 m but the lowest recorded altitude varies by island. *Pterophylla* (as *Weinmannia*, species not indicated but likely to be this one) was another of the plants that Chew (1975) reported as occurring mainly at higher elevations in the northern islands of Vanuatu and at lower altitude in the southern islands.

CONSERVATION STATUS. LC (Least Concern). The EOO is less than 20000 km² which could indicate a status of Vulnerable. However, this species is known from numerous herbarium collections and from almost all the larger islands of Vanuatu. Wheatley (1992) reported it from various secondary and disturbed habitats, indicating that it is able to persist or regenerate after selective logging and so LC is given for the present.

NOTES. The leaves of *Pterophylla denhamii* are quite variable in the number of pairs of leaflets and their size and shape; when the leaflets are few, they are usually lanceolate and when numerous, they are shorter and

relatively broader (Fig. 8). Specimens with the fewest leaflets are from Efate, Santo and Aneityum, and those with the most from Tanna and Ambae. On Santo, leaflets are smaller and stiffer with increasing elevation (Pillon pers. obs. 2006).

Hopkins *et al.* (1998) stated that the types at P for the names *Weinmannia kajewskii* and *W. tannaensis* were holotypes. However, as Guillaumin (1931) did not specify this and several duplicates are known, these designations are amended here to lectotypes.

3.7. *Pterophylla purpurea* (L.M.Perry) Pillon & H.C.Hopkins (in Pillon *et al.* 2021a: 1198). *Weinmannia purpurea* L.M.Perry (1949: 159). Type: [Papua New Guinea], Bougainville Is., Kupei Gold Field, 1000 m, 17 April 1930, S. F. Kajewski 1738 (lectotype, designated here: A [A00043371, fr.]; isolectotypes: A [A00043372, fl.], BM [BM000565639], BRI [BRI-AQ0340997], G [G00357678], L [L0062694], LE [LE00013435], P [P00697297], S [S08-7408], SING, US [US00097293]).

Tree 20 m high. *Leaves* usually simple or unifoliolate (rarely trifoliolate); petiole narrowly winged; blade broadly lanceolate to narrowly ovate, (3 –) 4.2 – 18 × 1.3 – 5 cm, with base attenuate to decurrent and apex acute to caudate. *Flowers* unisexual, only female ones known. Illustration: Hopkins *et al.* (1998: fig. 6).

DISTRIBUTION. Papua New Guinea (Bougainville only: type) and Solomon Islands (Guadalcanal only: SW, Duidui area, 730 m, 9 Oct. 1968 (fl. & yfr.), *Maurias* BSIP 12092 (K, L)).

HABITAT. Reported from rain forest, including well drained primary forest on a ridge top, at 730 – 1000 m.

CONSERVATION STATUS. Collected only twice, this species has a very small AOO and although its potential EOO is much larger (c. 14000 km²) if it were to occur throughout Bougainville and Guadalcanal, this may be misleading as the more recent of the collections was made more than 50 years ago. Although described as common in the field notes of *Kajewski* 1738, the lack of herbarium material probably indicates that it is in fact rare and likely to be threatened by habitat destruction. Clearly more information is needed but a provisional status of Vulnerable is assigned (VU B1a,b(i,ii,iii)).

NOTES. Hopkins *et al.* (1998) stated that the holotype of *Weinmannia purpurea* was at A but as two sheets of *Kajewski* 1738 are shown on the Harvard University Herbaria website (online), the name is lectotypified here. Both sheets have good leaf material and the one chosen as the lectotype, with fruits, has previously been labelled as the holotype.

3.8. *Pterophylla* sp. (Solomons B).

Weinmannia sp. (Solomons B) of Hopkins *et al.* (1998: 84).

Tree 5 m tall. *Leaves* imparipinnate, to 5 cm long; rachis hirsute especially on upper surface, segments narrowly winged; lateral leaflets in 2 – 5 pairs, elliptic, 0.7 – 2 × 0.4 – 0.7 cm, with base acute and apex broadly acute; terminal leaflet slightly larger than largest laterals. Flowers seen in bud only. Fruits unknown.

DISTRIBUTION. Papua New Guinea (Bougainville), known from a single locality.

SPECIMENS EXAMINED. PAPUA NEW GUINEA. Bougainville A. R.: Bougainville: Mt Balbi, summit, 2400 m, 8 May 1988 (buds & old fr.?), *Gideon* LAE 78577 (K, LAE n.v.); Mt Balbi (“Bolbi”), 2440 m, Oct. 1963 (buds), *Parker* 6 (CANB, LAE n.v.).

HABITAT. Reported as growing in forest, on the rim of an old volcanic crater. Said to be common as a canopy tree, reaching 5 m (field notes of *Gideon* LAE 78577). The elevation suggests montane forest.

NOTES. This undescribed material has markedly smaller leaflets than other species in sect. *Leiospermum* in the region. *Pterophylla croftii*, which has not been collected on Bougainville, also has leaves with winged rachis segments and also grows on volcanic substrates but it typically has fewer, larger leaflets although they are sometimes similar in shape (e.g. *Isles et al.* NGF 34406, New Britain, 2000 m [A, BISH, K, L]). Although both collections of *Pterophylla* sp. (Solomons B) are from high elevation and there is a correlation in several Cunoniaceae between decreasing leaf(let) size and increasing elevation, it seems unlikely that this material is conspecific with *P. croftii*. However, further collections are needed to determine the range of variation in leaf characters before this taxon is described.

4. *Schizomeria* D.Don (1830: 94); Perry (1949: 151); Hopkins & Hoogland (2002: 117); Bradford *et al.* (2004: 103); Hopkins (2018).

Trees or rarely *shrubs*. Indumentum of simple hairs and sometimes hemispherical gland-like trichomes (not this region). *Stipules* interpetiolar, 1 pair per node, usually caducous in fertile material leaving a scar. *Leaves* opposite and decussate, simple, petiolate; margins toothed or crenate (rarely entire); domatia absent. *Inflorescence* a many-flowered thyrse, terminal, pseudo-terminal or axillary. *Flowers* shortly pedicellate or almost sessile, bisexual or male; calyx lobes 4 – 6, valvate in bud; petals 4 – 6, lacinate, usually with 3 teeth, usually white; stamens 8, 10 or 12; disc annular, deeply incised into lobes; gynoecium of 2 – 3 carpels, united at level of ovary, locules and stylodia 2 – 3; ovules ± pendulous, 2 – 4 (– 6) per locule, arranged in 2 rows. *Drupes* spherical to ellipsoid, minute remnants



Fig. 8. *Pterophylla denhamii*, Espiritu Santo, Vanuatu. **A** tree in forest; **B – C** foliage (note short leaflets and winged rachis), plus buds and flowers, inflorescence composed of triads; **D** foliage with longer leaflets and flowers in bud. Vouchers: **A – C** Pillon *et al.* 558, **D** Pillon *et al.* 601. PHOTOS: YOHAN PILLON.

of calyx persisting at base; epicarp smooth or warty, white, yellowish or brownish; mesocarp fleshy or granular/fibrous; endocarp very hard, often with deep indentations, these sometimes containing resinous material; locules 1 (– 3); seeds 1 (– 3) per fruit.

About 10 species from the Moluccas, New Guinea, the Bismarck archipelago, the Solomon archipelago and eastern Australia (Hopkins 2018: map 1); two species in the Solomon archipelago.

Key to the species of *Schizomeria* in the Solomon archipelago

1. Leaves coriaceous, leaf blades commonly elliptic with rounded apex, 1.7 – 11.5 × 1 – 7 cm overall; 3 – 5.5 × 1.5 – 2.5 cm in Solomon Isl.; secondary veins commonly at a wide angle to the midrib, especially towards the base of the blade; ovary glabrous (> 1750 m on Guadalcanal).....**4.1. *S. ilicina***
 1'. Leaves chartaceous to coriaceous, leaf blades rather variable in shape, generally ovate with apex acute or obtuse, 8.5 – 22.5 × 3.3 – 9.5 cm; secondary veins typically arcuate; ovary usually densely hairy (low to mid-elevation, Bougainville south to Makira).....**4.2. *S. serrata***

4.1. *Schizomeria ilicina* (Ridl.) Schltr. (Schlechter 1918: 194); Engler (1928: 248); Perry (1949: 155). *Cremnobates ilicina* Ridl. (Ridley 1916: 41). Type: [Indonesia, Papua Prov.], Wollaston Expedition, Camp VIC, 1524 m, [Kloss] s.n. (BM?, specimen not found; lectotype of Hopkins (2018): Ridley (1916): pl. 3, figs 56 – 63; pl. 4, fig. 55).

Shrub 3 – 10 m tall on Guadalcanal (tree or shrub in New Guinea). *Leaves* ± erect, blades stiff, the sides often recurved. *Inflorescence* terminal, often compact, robust, with (sparsely) pubescent axes. *Flowers* usually bisexual, < 5 mm long; petals cream-white, stamens and disc yellow, ovary red (Corner RSS 88). *Fruits* (on Guadalcanal) c. 1 × 0.8 cm, with pericarp brownish ochre or brownish-red, slightly pulpy and ripening creamy fawn (Corner RSS 88, Dennis BSIP 508). Illustration: Hopkins & Hoogland (2002: fig. 26).

DISTRIBUTION. Indonesia (western New Guinea), Papua New Guinea (mainland, New Britain?), and Solomon Islands (Guadalcanal, known from a single locality).

SPECIMENS EXAMINED. SOLOMON ISLANDS. Guadalcanal Prov.: Guadalcanal: Mt Popomanaseu (“Popomansiu”), 2130 m, 23 Oct. 1965 (fl. & fr.), Corner RSS 88 (K, L); *ibid.*, 2285 m, 9 Nov. 1962 (fr.), Dennis BSIP 508 (K, L).

HABITAT. On Guadalcanal, the elevation at which *Schizomeria ilicina* grows suggests montane forest and it was reported as a common bushy or gnarled and probably wind-damaged tree from the summit ridge and plateau of Mt Popomanaseu, occurring from 1750 m (field notes of Corner RSS 88) to 2285 m, and upwards towards the summit (at 2335 m). In New Guinea, this species is widespread in mixed montane forest from (850 –) 1200 – 3200 (– 3500) m.

CONSERVATION STATUS. Overall, LC (Least Concern). Although it is known from only a single locality in the Solomon Islands, it was reported to be quite common (field notes of Corner RSS 88) and the elevation may be too high to be affected by logging, so that its population on Guadalcanal may not be declining. Should this population be demonstrated to be genetically distinct from that in New Guinea its status will need to be re-assessed.

NOTES. Material with small leaflets from Guadalcanal is equated here with *Schizomeria ilicina* but the fruits (1 × 0.8 cm) are smaller than typical for New Guinea (usually 1.6 – 3 × 1.3 – 2.5 cm); however, we do not know if the fruits on the material currently available from the Solomon Islands are mature. The inflorescence axes in the only flowering specimen, Corner RSS 88, are more sparsely hairy than usual for this species but the flowers have the typical glabrous ovaries. Both *S. ilicina* and *S. serrata* have terminal inflorescences and glabrous leaves and in New Guinea, *S. ilicina* replaces *S. serrata* at high elevations (Hopkins 2018: table 4) and it appears that the same occurs on Guadalcanal. However, it would be interesting to know whether plants of *S. ilicina* from Guadalcanal are genetically close to similar material from New Guinea or whether their characters of small leaves and glabrous ovaries have evolved independently in situ.

4.2. *Schizomeria serrata* (Hochr.) Hochr. (Hochreutiner 1907: 118); Whitmore (1966a: 60; 1967: 5); Hopkins (2018). *Acronychia serrata* Hochr. (Hochreutiner 1904: 49). Type: [Indonesia, Java, cultivated], Hort. Bogor, Ile d’Amboine (fl. & fr.), Hochreutiner 103 (lectotype of Hopkins (2018): G [G00357640]; isolectotypes: B [B100249823, Hochreutiner s.n.], BO n.v., G, K ×2 [K000739809, K000739811], L ×4 [L0019948, L0019949, L0019950, L0019951]).

Tree 8 – 45 m high, often with buttresses. *Leaf-blades* not especially stiff nor recurved along the sides. *Inflorescence* terminal, often well developed, not congested, flowering profusely, with axes pubescent to almost glabrous. *Flowers* usually bisexual, < 5 mm long, white, cream or yellow, reported as scented or not. *Fruits* subglobose or somewhat ellipsoid, 1 – 1.8 (– 2.5) × 1 – 1.5 (– 2) cm. Illustration: Hopkins (2018: fig. 8).

DISTRIBUTION. Indonesia (Moluccas, Aru Islands, western New Guinea), Papua New Guinea (mainland, Louisiade Archipelago, New Britain, Bougainville), and Solomon Islands (most of the large islands including Choiseul, the New Georgia Group, Santa Isabel, Malaita, Guadalcanal, Makira, plus some smaller islands).

SPECIMENS EXAMINED. 74 collections from Bougainville A. R. and the Solomon Islands; selected material cited in Hopkins (2018).

HABITAT. In the Solomon archipelago, *Schizomeria serrata* is commonly reported from well drained mixed primary rain forest on hillsides and ridges, extending upwards into mossy montane forest, and occasionally growing on coastal ridges or in secondary and disturbed primary forest. The field notes of Corner RSS 2710 ([Isabel Prov.], San Jorge, Astrolabe Bay [K, L]) reported it from *Casuarina* forest on ultramafic soil. It is sometimes described as dominant or co-dominant, and according to Whitmore (1966a, 1969), it is the only member of the Cunoniaceae that is a common, large tree in the Solomon Islands where it is said to be one of the 12 commonest species that reach the top layer of the canopy in lowland forests. It is found in similar habitats in New Guinea although it does not appear to be as abundant there. Burslem & Whitmore (1996) described seedling demography and the growth and mortality rates of adults on Kolombangara.

Schizomeria serrata has been collected across a wide range of elevations in the Solomon archipelago (3 – 1200 m), with the highest records from Kolombangara and Guadalcanal (both 1200 m), followed by Bougainville (730 m), Vangunu (670 m) and Makira (610 m).

CONSERVATION STATUS. Overall, LC (Least Concern). It is widely distributed and common in lowland forest in the Solomon Islands although continued logging must have reduced the number of mature individuals. An assessment of NT may be appropriate locally. **NOTES.** Whitmore (1967) described *Schizomeria serrata* as polymorphic, showing variation in the size and shape of the leaves and to a lesser extent, the fruits.

5. *Spiraeanthemum* A. Gray (May 1854: 128; June 1854: 666) & *Atlas* (1856: t. 83A); Hoogland (1979: 501); Smith (1952: 119; 1985: 6); Hopkins & Hoogland (2002: 127); Bradford *et al.* (2004: 101); Pillon *et al.* (2009: 146), Hopkins *et al.* (2014: 372).

Trees or shrubs. Indumentum of simple hairs; red dots (apparently secretory glands) on under-surface of leaves in some species. *Stipules* interpetiolar, the

number per node equal to the number of leaves. *Leaves* opposite and decussate, or whorled (not this region), simple, petiolate, margins entire or crenate-serrate; domatia often present. *Inflorescences* many-flowered, axillary thyrses. *Flowers* pedicellate, either unisexual and then species dioecious, or bisexual (not this area), c. 2 mm long. Sepals 3 – 5 (– 6), commonly 4, valvate in bud; petals absent; stamens 6, 8 or 10 (12), reduced in female flowers; disc lobed, the lobes often united in pairs; ovary absent in male flowers, in female and bisexual ones apocarpous, carpels 2 – 5 (– 6), if more than 2 then number usually equal to that of sepals, ovoid, hairy; ovules 1 – 4 (– 6) per carpel. *Fruit* of 2 – 5 (– 6) follicle-like fruitlets, each dehiscent with boat-shaped valves, horned at apex. *Seeds* 1 – 4 per carpel, glabrous, spindle-shaped or ellipsoid (and then with a tail at either end) or flattened and bearing a small membranous wing.

Nineteen species, from the Moluccas, New Guinea, the Bismarck and Solomon archipelagos, Vanuatu, New Caledonia, Fiji, Samoa and north-eastern Australia (see Pillon *et al.* 2009: fig. 2); two species in the Solomon archipelago, one of which is also found in Vanuatu.

Based on DNA sequence data and morphology, Pillon *et al.* (2009) recognised three monophyletic groups within *Spiraeanthemum* s.l. and both *S. bougainvillense* Hoogland and *S. macgillivrayi* Seem. belong to *Spiraeanthemum* s.s. This group occurs in the Bismarck and Solomon archipelagos, Vanuatu, Fiji and Samoa and its members are all dioecious with opposite leaves, usually with toothed margins, ovate-elliptic stipules, hairy apical buds, and usually four free carpels in the female flowers, each of which contains two ovules that develop into spindle-shaped/ellipsoid seeds (Pillon *et al.* 2009: table 2).

The species concepts here follow Hoogland (1979), who recognised two species in the present region. The names of others, from Fiji and Samoa, have sometimes been used on herbarium specimens as their leaves are quite similar. Keys for Fiji and Samoa were provided by Smith (1952, 1985) but a comprehensive key to the species of *Spiraeanthemum* s.s. is lacking.

Key to the species and subspecies of *Spiraeanthemum* in the Solomon archipelago and Vanuatu

1. Twigs with a dense, whitish or straw-coloured, pubescent to hirsute tomentum (hairs up to 1 mm long), usually quite persistent; similar indumentum also present on the petioles and midrib of the leaf (on lower leaf surface and upper surface at least towards the base of the blade); leaf blades 8 – 19 × 5 – 9.5 cm; domatia in the form of pockets or pouches with a tuft of longish hairs (Bougainville only)..... **5.1. *S. bougainvillense***
- 1'. Twigs glabrous or with a thin, open, pale tomentum (soon glabrescent); petiole and midrib on lower surface of leaves glabrous or with a few scattered hairs, midrib on upper surface glabrous; leaf blades c. 5 – 12 × 2 – 7

- cm; domatia in the form of a hollow pit or “igloo” with a few very short hairs at most at the mouth (Solomon archipelago & Vanuatu) **5.2. *S. macgillivrayi*: 2**
2. Leaf blades usually quite broad, 5 – 12 × 2.5 – 7 cm (length/width ratio 1.75); secondary veins (5 –) 7 – 9 (– 10) (Vanuatu)..... **5.2a. *S. macgillivrayi* subsp. *macgillivrayi***
- 2'. Leaf blades usually relatively narrow, 5 – 11 × 2 – 4.5 cm (length/width ratio 2.25); secondary veins more numerous, (7 –) 10 – 14 (– 16) (Solomon archipelago)..... **5.2b. *S. macgillivrayi* subsp. *kajewskii***

5.1. *Spiraeanthemum bougainvillense* Hoogland (1979: 501). Type: [Papua New Guinea], Bougainville, lower S slopes of Lake Loloru crater, c. 28 km [17 ml] N of Buin, 780 m [2600 ft], 6 Aug. 1964 (buds, fl. – f. & fr.), *Schodde (& Craven)* 3768 (holotype: CANB ×4 [CANB143113, CANB143114, CANB143115, CANB143116]; isotypes: A [00043342], BISH [BISH1001175], BRI [BRI-AQ0334698], E [E00317582], G ×2 [G00357637 + 1 other], K [K001193787], L [L0019953], LAE n.v., MEL [MEL568236], P [P00641892], TNS, US [US00170059]).

Tree 10 – 30 m. Young twigs bearing dense pale indumentum, especially at nodes, slowly glabrescent. *Stipules* broadly ovate, to 10 × 9 mm, with dense pale indumentum on both surfaces. *Leaves*: petioles 1.7 – 3 cm long; blades ovate or ovate-elliptic, base broadly cuneate to slightly decurrent, apex broadly acute, margins crenulate; venation ± craspedodromous; domatia in angle between secondary veins and midrib, and sometimes also where secondary veins split. *Inflorescences* 12 – 17 cm long, axes densely pubescent. *Flowers* creamy white, cream-green in bud. *Fruits* red-brown. Fig. 3A – G.

DISTRIBUTION. Papua New Guinea, restricted to Bougainville.

ADDITIONAL SPECIMENS EXAMINED. PAPUA NEW GUINEA.

Bougainville A. R.: Bougainville: Panguna ridge, slope leading down to Pankiranku Creek, 6°20'S 155°30'E, 14 April 1965 (fl. – m.), *Cole* 107 (K ×2); Lake Loloru crater, lower slopes, 24 km N of Buin, 730 m, 30 July 1964 (fl. – f.), *Craven & Schodde* 127 (K, L); Koniguru, Buin, 950 m, 13 Aug. 1930 (buds), *Kajewski* 2082 (L, P); Maide R. gorge, lower slopes of Lake Loloru crater, 24 km N of Buin, 700 m, 15 Aug. 1964 (fl. – f.), *Schodde & Craven* 3850 (K, L).

HABITAT. Lower montane primary rain forest, from 700 – 950 m, sometimes reported as common.

CONSERVATION STATUS. *Spiraeanthemum bougainvillense* is known from five gatherings but these represent only two or possibly three collection sites. If this plant were present throughout the forest south of Panguna and above c. 700 m, it would have an EOO no more than 1000 km², which together with plans for logging on Bougainville, would suggest a status of Endangered (EN B1ab(i,ii iii)).

VERNACULAR NAME. Tetarome, fide *Kajewski* 2082.

NOTES. Hoogland (1979) distinguished *Spiraeanthemum bougainvillense* by the dense, rather persistent indumentum on the twigs, stipules (both surfaces), petioles and inflorescence axes. All the collections cited here are types or paratypes and no more recent material is listed at LAE (Conn *et al.* 2004 onwards).

In the protologue, Hoogland (1979) stated that the “type” was at CANB with numerous isotypes elsewhere. Jstor Global Plants (online) shows four sheets at CANB that each bear a printed holotype label and another label stating “sheet 1 of 4”, “sheet 2 of 4” etc., showing that all four sheets together constitute the holotype.

5.2. *Spiraeanthemum macgillivrayi* Seem. (Seemann 1866: 111). Type: New Hebrides [Vanuatu], Aneiteum [sic], May 1859 (fl. – m.), *J. MacGillivray* 59 (holotype: BM [BM000600413]; isotypes: G ×2 [G00357635 + 1 other], P ×3 [P00641884, P00641885 (fragment), P00641886]).

Tree or shrub 3 – 12 (– 20) m. Young twigs glabrous or almost so. *Stipules* ovate, to 10 × 5 mm, adaxial surface glabrous, abaxial surface with sparse white indumentum. *Leaves*: petioles 1.5 – 3 cm long; blades ovate or narrowly ovate, rather variable in size, base cuneate to broadly cuneate, apex acute, both surfaces glabrous, margins toothed, tips of teeth conspicuous and drying dark (glandular when young?); venation craspedodromous; domatia in angle between secondary veins and midrib, and sometimes also where secondary veins split, drying dark. *Inflorescences* to 16 × 10 cm but often smaller, axes glabrous to sparsely hairy. *Flowers* white, pale green, yellowish, yellow-green or pale pink, with white stamens, scented. *Fruits* brown or red-brown. Fig. 9.

DISTRIBUTION. Papua New Guinea (New Britain, New Ireland, Bougainville) and the Solomon Islands (subsp. *kajewskii*), and Vanuatu (subsp. *macgillivrayi*).

5.2. *Spiraeanthemum macgillivrayi* Seem. subsp. *macgillivrayi*

Spiraeanthemum rui Guillaumin (1937: 286). Type: New Hebrides [Vanuatu], Ambrym, grand plateau autour du Mont Marum, 650 m, 9 Jan. 1936 (fl. – m.),



Fig. 9. *Spiraeanthemum macgillivrayi* subsp. *macgillivrayi*, Espiritu Santo, Vanuatu. **A** small tree in open habitat; **B** foliage and fruits. Voucher: *Pillon et al.* 570. PHOTOS: YOHAN PILLON.

E. Aubert de la Rüe s.n. (lectotype of Hoogland (1979): P [P00641887]).

DISTRIBUTION. Restricted to Vanuatu where it occurs on most of the larger islands.

REPRESENTATIVE SPECIMENS (from a total of 45 collections). **VANUATU. Torba Prov.: Banks Islands: Vanua Lava:** 550 m, 18 April 1989 (fr.), *Wheatley* 341 (K). **Sanma Prov.: Espiritu Santo:** Patmoru, W of Fortsenale village, 970 m, 12 Dec. 1994 (fl. – f.), *Berry* 17 (K); N, Valleé de la Pialoraï, 600 – 800 m, 1 Aug. 1979 (fr.), *Morat* 6463 (P ×3); Boutmas, contrefort du Plateau de Tankara, 15°22'33"S 166°58'03"E, 600 – 680 m, 26 Oct. 2006 (st., regrowth shoot), *Pillon et al.* 525 (P); Mt Tabwémasana, 15°20'10"S 166°43'40"E, 1000 m, 6 Nov. 2006 (fr.), *Pillon et al.* 570 (K, P); Pénaoru Valley, 14°58'4"S 166°38'42"E, 600 – 900 m, 27 Nov. 2006 (fl. – m.), *Tuiwawa et al.* 3026 (P); crête NE direction du Voutmele, 1300 m, Aug. 1979 (fr.), *Veillon* 4045 (P). **Penama Prov.: Pentecost:** 500 m, 17 Jan. 1989 (buds, fl. – f. & fr.), *Wheatley* 132 (K ×2). **Shefa Prov.: Efate:** 450 m, 26 May 1965 (fl. – m.), *Schmid* 247 (P). **Tafea Prov.: Erromango:** de Happy Land ad orientem montis Nompoun-Oumpan, 400 – 450 m, 7 June 1968 (buds), *Bernardi* 13324 (K, P); 10 km WSW of Ipota, 18°53'S

169°12'E, 180 m, 9 Aug. 1971 (buds), *Beveridge* RSNH 3009 (K, P); summit of Rantop, 860 m, 22 July 1983 (fl. – m.), *Cabalion* 2112 (K, P); summit of Traitor's Head, 20 July 1896 (fr.), *Morrison* s.n. (K). **Tanna:** nr Lamwinaoura, 1 – 2 May 1968 (fl. – f. & yfr.), *Bernardi* 12912 (K, P); Mt Tukosmea area, 19°34'46.5"S 169°22'46"S, 872 m, 25 April 2016 (fl. – f.), *Plunkett et al.* 3321 (NY); Ikouroup, 28 July 1971 (buds, fl. – f. & fr.), *Raynal* RSNH 16173 (K, P). **Aneityum:** Anumy Valley, W side, 25 June 1896 (fr.), *Morrison* s.n. (P); Hills SW of Ithug, 26 June 1896 (fl. – m.), *Morrison* s.n. (K); Mt Inrerow, Atamein, 20°11'04"S 169°47'25"E, 850 m, 20 April 2016 (fl. – m.), *Plunkett et al.* 3265 (NY).

HABITAT & ECOLOGY. Found in forest including secondary growth and at the forest edge, low-growing in dwarf montane forest and shrubby or grassy vegetation on ridges and summits, reaching a larger size below the ridges; also found in old growth and on river banks; recorded from virgin Kauri forest (field notes of *Beveridge* RSNH 3009) and once on limestone (Pleistocene reef) (field notes of *Pillon et al.* 525). Elevational range (c. 100 –) 400 – 1500 m. Various descriptions as local, locally abundant or frequent in the field notes of *Green* RSNH 1250, *Pillon et al.* 570 and *Bernardi* 13158 respectively.

CONSERVATION STATUS. The EOO is less than 20000 km², which could indicate a status of Vulnerable but because of its wide distribution within Vanuatu, its ecological range and the number of collections, LC (Least Concern) appears to be more appropriate.

VERNACULAR NAME. Seova (Fortsenale language), fide *Berry* 17.

NOTES. Guillaumin (1937) cited material from “Ambrym : grand plateau autour du Mont Marum, 650-700 m” after the description of *Spiraeanthemum ruei* in his account of the plants collected by M. and Mme Aubert de la Rüe on their second voyage to the New Hebrides in 1935 – 1936; specimens from this expedition lack collection numbers. The lectotype designated by Hoogland (1979) has male flowers and gives this locality plus “cote 650” and “9 janvier 1936”, and has the word “type” in Guillaumin’s hand. Two other sheets at P, labelled by Hoogland as syntypes, are from the same locality but their details differ slightly: P00641888 (“cote 700, 9 – I – 1936”, fl. – m) and P00641889 (“Plateau 650 – 800 m, 8 – II janvier 1936”, buds). Further sheets collected by Aubert de la Rüe, at A, BM, L and NY (all n.v.), were also listed by Hoogland as syntypes and are probably lectoparatypes although it is not clear how many separate gatherings are represented by this material.

5.2b. *Spiraeanthemum macgillivrayi* Seem. subsp. *kajewskii* (L.M.Perry) Hoogland (1979: 504). *Spiraeanthemum kajewskii* L.M.Perry (1949: 139). Type: [Papua New Guinea], Bougainville, Kupei Gold Field, 1000 m, 14 April 1930 (fl. – f. & fr.), *S. F. Kajewski* 1700 (holotype: A [A00043343]; isotypes: BISH n.v., BM [BM000600414], BO n.v., BRI [BRI-AQ0340984], G ×2 [G00357638 + 1 other], L [L0019954], P [P00641883]).

For description, see Hopkins & Hoogland (2002: 128).

DISTRIBUTION. Papua New Guinea (New Britain, New Ireland, Bougainville A. R.) and Solomon Islands (Kolombangara, Vangunu, Guadalcanal, Santa Isabel). **SPECIMENS EXAMINED. PAPUA NEW GUINEA. Bougainville A. R.: Bougainville:** ridge S of Panguna, 6°20'S 155°30'E, 1070 m, 5 Oct. 1971 (buds – m.), *Argent* NGBF 1227 (K, L); Mt Balbi, on saddle between two peaks, 1900 m, 8 May 1988 (buds), *Gideon et al.* LAE 78569 (K). **SOLOMON ISLANDS. Western Prov.: New Georgia Group: Vangunu:** crater rim, inland from Merusu Islet, 700 m, 10 Dec. 1962 (buds), *Whitmore* BSIP 1209 (K). **Kolombangara:** summit, 1680 m, 31 Aug. 1965 (fl. – f.), *Hunt* RSS 2469 (K); Camp 2, 7°58'57"S 157°05'35"E, 1300 m, 8 Aug. 2014 (st.), *Song et al.* SITW06030 (TNM). **Guadalcanal Prov.: Guadalcanal:** Popomanasiu, 2130 m, 23 Oct. 1965 (buds), *Corner* RSS 93 (K, P); Vulolo, Tutuve Mt, 1200 m, 17 April 1931

(buds – f.), *Kajewski* 2533 (BM, L, P); S coast (Duidui), Kolotsiri Ridge, 1040 m, 17 June 1968 (fr.), *Sirute'e & collectors* BSIP 10173 (K). **Isabel Prov.: Santa Isabel:** nr Maringe Lagoon, Mt Sasari, 800 m, 26 Oct. 1963 (fr.), *Whitmore* BSIP 2430 (K).

Spiraeanthemum cf. *macgillivrayi* subsp. *kajewskii*: **SOLOMON ISLANDS. Vangunu:** NW of Vura along ridge to Mt Olasana, 8°42'S 158°01'E, 870 m, 15 Nov. 1997 (st.), *Bradford* 824 (K, MO); **Kolombangara:** Mt Duke, along main ridge to summit, S of Mt Tapalamenggutu and N of Vila R., 7°58'S 157°06'E, 1270 m, 20 Nov. 1997 (old fr.), *Bradford* 838 (K ×2, MO).

HABITAT. Common in mossy montane forest and tall forest on ridges, in the understorey and canopy, at 700 – 2280 m.

CONSERVATION STATUS. This taxon has a relatively wide distribution, occurring on five islands, but nevertheless its EOO is estimated to be less than 5000 km². It is not clear whether it could be under-collected because the flowers are relatively inconspicuous; if so, its EOO may in fact be greater. It occurs over a wide elevational range and at least some collections are from high elevation where the effects of logging are likely to be low. For these reasons, despite the low EOO, a conservation status of Vulnerable is assigned (VU B1a,b(i,ii,iii)).

VERNACULAR NAMES. Ban walli, fide *Kajewski* 2533. Fatafata, fide *Corner* RSS 93.

NOTES. The leaves of *Whitmore* BSIP 2430 from Santa Isabel approach those of subsp. *macgillivrayi* in shape. The sterile sheets of *Bradford* 824 and 838 at K have leaves that are more hirsute than is typical in foliage associated with flowers and fruits.

Discussion

Although no genus is confined to either the Solomon archipelago or Vanuatu (Table 3), more than half the species of Cunoniaceae in these two island groups are endemic. The non-endemics are *Ackama celebica*, *Pterophylla croftii* and *P. fraxinea*, *Schizomeria ilicina* and *S. serrata*, and *Spiraeanthemum macgillivrayi*, which are also found in New Guinea, or the Bismarck archipelago, or both. The only species common to both Vanuatu and the Solomon archipelago is *Spiraeanthemum macgillivrayi*, which is represented by a different subspecies in each island group. Additional collections would be useful for some of the less common species and from some of the less visited islands (e.g. Choiseul, Santa Isabel, Bougainville) to aid understanding of the variation, delimitation, distribution and abundance of some taxa.

Comparison with other island groups in the western Pacific

Good (1969) and Thorne (1969) found that the flora of the Solomon Islands in general had its affinities with New Guinea, no doubt due to their geographical

proximity and the presence of similar habitats. However, the flora of New Guinea is more closely allied with that in the rest of Malesia, rather than with the Bismarck archipelago and the Solomon Islands (Marsh *et al.* (2009).

Among the genera of Cunoniaceae in the Solomon Islands and Bougainville, four are shared with the Bismarck archipelago (Table 1) and New Guinea. Both *Ackama* and *Schizomeria* have their greatest number of species in New Guinea and both also occur in eastern Australia. *Schizomeria* reaches its eastern limit in the Solomon Islands while *Ackama* extends south to New Zealand. Conversely, five genera that are found in New Guinea (Hopkins & Jennings 2021) are absent from the Solomon chain (*Aistopetalum* Schltr., *Ceratopetalum* Sm., *Gillbeea* F.Muell., *Opocunonia* Schltr., *Pullea*). Among these, *Pullea* has a curious disjunct distribution being found in eastern Malesia (Moluccas, New Guinea), north-eastern Australia and Fiji, but it is absent from the Bismarck and Solomon archipelagos and Vanuatu (map in Hoogland 1984).

Geissois is the only genus present in the Solomon Islands that does not also occur in New Guinea. Its greatest species richness is in New Caledonia and its northern limit is Vanikoro, at the southern edge of the Solomon Islands, with Fiji marking the eastern extent of its range. Vanikoro is closer to Vanua Lava (c. 250 km), the more northerly of the two largest Banks Islands in Vanuatu, than it is to any of the large islands of the Solomon group, the nearest of which is Makira (= San Cristobal), about 500 km distant, and this may be a factor in why *Geissois* does not occur further north despite its wind-dispersed seeds.

Within the Solomon archipelago, Bougainville has the same four genera that are found on the other large islands. At species level, notable absences are *Pterophylla fraxinea*, which is found throughout much of Malesia, including New Guinea, New Britain and New Ireland, and on several of the large islands of the Solomon group, and *P. croftii*, which is known from the Bismarck archipelago and a few of the Solomon Islands. Endemic to Bougainville are *Spiraeanthemum bougainvillense* and *Pterophylla* sp. (Solomons B).

With only four species, the Cunoniaceae of Vanuatu are depauperate compared with other island groups in the western Pacific. Their affinities are largely with the Solomon Islands and/or Fiji, and only to a lesser extent with Vanuatu's close neighbour New Caledonia. As mentioned above, *Geissois denhamii* belongs to the *G. pruinosa* – *G. racemosa* clade, which is well represented in New Caledonia (Pillon 2011; Pillon *et al.* 2014), but the taxa of *Spiraeanthemum* and *Pterophylla* in Vanuatu are not especially closely related to their congeners in New Caledonia (Bradford 1998; Pillon *et al.* 2009).

Spiraeanthemum s.s., to which the species from both the Solomon archipelago and Vanuatu belong, is often

associated with quite recent volcanic substrates and the lack of these in New Caledonia may be a factor in the absence of *Spiraeanthemum* s.s. from that island. The other two groups in the genus, whose members were previously placed in *Acsmithia* Hoogland, are the “densiflorum” group (Moluccas, New Guinea, north-eastern Australia, New Caledonia), and the “brongniartianum” group (New Caledonia, Fiji) (Pillon *et al.* 2009). Only Fiji and New Caledonia have representatives of more than one species group.

Pterophylla has the largest number of species of any of the genera in the present region. Two of its four sections occur here, sect. *Leiospermum*, which is largely confined to Pacific islands plus some volcanic islands off the north coast of New Guinea, and sect. *Pterophylla*, which is largely Malesian but extends into the Pacific as far east as Fiji (Hopkins & Bradford 1998: fig. 1). The members of both sections from the Solomon chain and Vanuatu are all morphologically typical of their sections whereas at least three of the four species from New Caledonia appear to form a unique group within sect. *Leiospermum* (Bradford 1998).

Compared with the Cunoniaceae found in the Solomon archipelago and Vanuatu, the family forms a distinctive and abundant element in the flora in New Caledonia, where it comprises some 90 species in seven genera, with three of the genera and all the species being endemic (Hopkins *et al.* 2014). Four genera from New Caledonia are absent from Vanuatu (*Codia* J.R.Forst. & G.Forst., *Cunonia* L., *Hooglandia* McPherson & Lowry, *Pancheria* Brongn. & Gris) and these four plus *Pterophylla* are also absent from Australia.

The marked difference in generic and species richness between Vanuatu and New Caledonia is likely to be the result of differences in geological age, history and substrates. The “high” islands of Vanuatu are largely composed of Tertiary volcanics (Oligocene to Quaternary, according to island) with some limestone, especially on Santo (Mallick 1975: fig. 1), and a few volcanoes are still active (including Mt Yasur on Tanna). Most of the current land mass of Vanuatu emerged from beneath the sea only in the last 2 million years (Mallick 1975: fig. 2) although small areas of land have been above sea level from the end of the Oligocene. The recent origin of Vanuatu as an archipelago no doubt accounts for, or contributes to, the small number of species of Cunoniaceae found there. In contrast, the main island of New Caledonia is a much older and more geologically complex land mass (Pillon *et al.* 2021b) and about half the Cunoniaceae there occur on ultramafic substrates (mostly peridotites) (Hopkins *et al.* 2014).

Fiji has a relatively large number of species of Cunoniaceae (13) in four genera (*Geissois*, *Pterophylla*, *Pullea*, *Spiraeanthemum*; Smith 1985), which, except for *Pullea*, all occur in Vanuatu and the Solomon archipelago.

Table 3. Generic distributions of Cunoniaceae worldwide. Endemic genera are indicated by a spot (•) in main part of table, and by the number in parentheses in the line labelled “No. of genera”. Most figures are from Pillon et al. (2021a).

Genus	Total no. spp.	Americas incl. Caribbean	South-Africa	Madagascar & Comoros Isl.	Mascarene Isl.	W. Malaysia (Mal. Pen., Sumatra, Java, Borneo)	Philippines & Sulawesi	Moluccas	New Guinea & Bismarck Isl.	Solomon Isl. & Bougainville	Vanuatu	New Caledonia	Fiji	Samoa	Cook Isl.	C. Pacific (Society, Marquesas, Austral Isl.)	Australia	New Zealand
<i>Ackama</i>	10						1	1	6	1						2		2
<i>Acrophyllum</i>	1																1•	
<i>Aistopetalum</i>	2								2•									
<i>Anodopetalum</i>	1																1•	
<i>Bauera</i>	3																3•	
<i>Caldeuaria</i>	1	1•															1•	
<i>Callicoma</i>	1																1•	
<i>Ceratopetalum</i>	8–9							1									8	
<i>Codia</i>	15											15•						
<i>Cunonia</i>	25		1									24						
<i>Davidsonia</i>	3																3•	
<i>Euryphia</i>	7	2								1	1	13	4				5	
<i>Geissos</i>	19																	
<i>Gillbeea</i>	3																2	
<i>Hooglandia</i>	1								1									
<i>Karrabina</i>	2																2•	
<i>Lamanonia</i>	6	6•																
<i>Opocunonia</i>	1																	
<i>Pancheria</i>	27																	
<i>Platylophus</i>	1																	
<i>Pseudocavendishia</i>	2																	2•
<i>Pterophylla</i>	68			30	4	4	12	2	4	6	2	4	4	1	1	6		2
<i>Pullea</i>	3							1	2				1					
<i>Schizomeria</i>	10–11							1	7	2								2–3
<i>Spiraeanthemum</i>	19							1	5	2	1	7	4	1				1
<i>Veselauskya</i>	2																	2•
<i>Weinmannia</i>	c. 92	c. 90		2		1 (0)	2 (0)	5 (0)	9 (2)	5 (0)	3 (0)	7 (3)	4 (0)	2 (0)	1 (0)	1 (0)	15 (8)	2 (0)
No. of genera		4 (2)	2 (1)	1 (0)		1 (0)	2 (0)	5 (0)	9 (2)	5 (0)	3 (0)	7 (3)	4 (0)	2 (0)	1 (0)	1 (0)	15 (8)	2 (0)
No. of species	c. 335	c. 100	2	30	2	4	13	6	29	12	4	91	13	2	1	6	36–37	4

Further east, the generic diversity of the Cunoniaceae decreases markedly across the Pacific (Table 3). *Spiraeanthemum* and *Pterophylla* are found in Samoa (Smith 1952) and the latter is the only genus whose distribution extends east of Samoa, to Rarotonga in the Cook Islands, and to the Society, Marquesas and Austral Islands (Hopkins & Florence 1989; Lorence & Wagner 2011) but the genus is always found on “high” islands. Limestone is not generally favoured by members of the family, which are only rarely found on calcareous soils and are absent from coralline islands in the Pacific. Along with *Ackama*, *Pterophylla* also extends southwards to New Zealand (Schönberger *et al.* 2019).

It is remarkable how few genera of Cunoniaceae Australia has in common with the islands of the western Pacific considering the number present (15, of which eight are endemic) and the fact that most members of the family appear to be wind dispersed (exceptions: *Aistopetalum*, *Davidsonia* F.Muell., *Hooglandia*, *Schizomeria*). Australia shares *Ackama* with the Solomon archipelago, as well as eastern Malesia, New Guinea and New Zealand, *Spiraeanthemum* with both Vanuatu and the Solomon archipelago plus New Guinea and New Caledonia, and has two genera in common with Fiji (*Pullea*, *Spiraeanthemum*). It is not surprising that it shares numerous genera with New Guinea (*Ackama*, *Ceratopetalum*, *Gillbeea*, *Pullea*, *Schizomeria*, *Spiraeanthemum*) considering their proximity and the recent terrestrial connection between them.

Acknowledgements

We thank the following herbaria for access to specimens: BM, G, K, L, MO, NOU and P, plus CANB (especially Brendan Lepschi) and LAE (especially Robert Kiapranis) for supplying images of specimens. Greg Plunkett was very helpful regarding recent collections from Vanuatu. We thank Andrew Brown for the beautiful line drawings and we are grateful to Aleck Yang and the National Museum of Natural Science, Taichung, Taiwan (TNM) for the image of *Geissois pentaphylla*, and also to Tian-Chuan Hsu (TFRI) for his assistance. Photographs of plants in the field were kindly made available to us by Odile Poncy and Michael J. Balick. Some photographs by JCB were previously published (in B&W) in *Flora Malesiana*. HCFH thanks Ian Turner for advice on types and Odile Poncy for hospitality during visits to P. Variation in *G. denhamii* was originally analysed by R. D. Hoogland and his notes are preserved at P. Finally, we thank the reviewers for their helpful comments.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Bachman, S., Moat, J., Hill, A. W., de la Torre, J. & Scott, B. (2011). Supporting Red List threat assessments with GeoCAT: geospatial conservation assessment tool. In: V. Smith & L. Penev (eds), eInfrastructures for data publishing in biodiversity science. *ZooKeys* 150: 117–126. <https://doi.org/10.3897/zookeys.150.2109>
- Bennett, J. A. (2000). The grievous mistakes of the Vanikoro concession: The Vanikoro Kauri Timber Company, Solomon Islands, 1926–1964. *Environm. Hist.* 6: 317–347. <https://doi.org/10.3197/096734000129342325>
- Bernardi, L. (1964). Revisio generis Weinmanniae. Pars III: Sectiones III-IV-V-VI. *Bot. Jahrb. Syst.* 83: 126–184, 185–221.
- Bishop Museum (BISH) 2018 (Database of collections, published on the internet). <http://nsdb.bishopmuseum.org/>. [Accessed Sept. 2018].
- Blume, C. L. (1825 – 1826). *Bijdragen tot de flora Nederlandsch Indië*. Lands Drukkerij, Batavia. (*Cunonia celebica* in part 15: 868, 1826). <https://doi.org/10.5962/bhl.title.395>
- _____. (1855). *Mélange botaniques*. Privately published.
- Bouchet, P., Le Guyader, H. & Pascal, O. (eds) (2011). *The natural history of Santo*. Museum National d'Histoire Naturelle, Paris, IRD, Marseille & Pro-Natura International, Paris.
- Bradford, J. C. (1998). A cladistic analysis of species groups in *Weinmannia* (Cunoniaceae) based on morphology and inflorescence architecture. *Ann. Missouri Bot. Gard.* 85: 565 – 593. <https://doi.org/10.2307/2992017>
- _____, Hopkins, H. C. F. & Barnes, R. W. (2004). Cunoniaceae. In: K. Kubitzki (ed.), *The Families and Genera of Vascular Plants*, Vol. 6. Springer, Berlin, pp. 91–111.
- Brooks, T. M., Pimm, S. L., Akçakaya, H. R., Buchanan, G. M., Butchart, S. H. M., Foden, W., Hilton-Taylor, C., Hoffmann, M., Jenkins, C. N., Joppa, L., Li, B. V., Menon, V., Ocampo-Peñuela, N. & Rondini, C. (2019). Measuring terrestrial area of habitat (AOH) and its utility for the IUCN Red List. *Trends Ecol. Evol.* 34: 977 – 986. <https://doi.org/10.1016/j.tree.2019.06.009>

- Burslem, D. F. R. P. & Whitmore, T. C. (1996). *Silvics and wood properties of the common timber species on Kolombangara*. Tropical Forestry Papers 34, Solomon Islands Forest Record 7. Oxford Forestry Institute, Dept Plant Sciences, Oxford University. <https://herbaria.plants.ox.ac.uk/bol/oxford/ftp>
- _____, _____ & Brown, G. C. (2000). Short-term effects of cyclone impact and long-term recovery of tropical rain forest on Kolombangara, Solomon Islands. *J. Ecol.* 88: 1063–1078. <https://doi.org/10.1046/j.1365-2745.2000.00517.x>
- C. V. Starr Virtual Herbarium (NY). (Database of collections, New York Botanical Garden, published on the internet). <https://sweetgum.nybg.org>. [Accessed Sept. 2018, Aug. 2021].
- Cabalion, P. (2003). Traces ethnobotaniques de Lapérouse à Vanikoro? In: Association Salomon (ed.), *Lapérouse à Vanikoro. Résultats des dernières recherches franco-salomonaises aux îles Santa Cruz*, pp. 67–82. IRD, République Française & Association Salomon, Nouméa.
- Chew, W.-L. (1975). The phanerogamic flora of the New Hebrides and its relationships. *Philos. Trans., Ser. B* 272: 315–328. <https://doi.org/10.1098/rstb.1975.0090>
- Chiou, W.-L., Yang, T. Y. A. & Sun, W.-H. (2016). *Suoluomen Qundao zhi wu tu jian (= Field guide to the plants of Solomon Islands)*. National Museum of Natural Science, Taichung.
- Conn, B. J., Lee, L. L. & Kiapranis, R. (2004 onwards, published on the internet). PNGplants database. Plant collections from Papua New Guinea. <http://www.pngplants.org/PNGdatabase> [Accessed Sept. 2021].
- Cunningham, A. (1839). Florae insularum Novae Zelandiae precursor; or a specimen of the botany of the islands of New Zealand. *Ann. Nat. Hist.* 2: 356–360. <https://www.biodiversitylibrary.org/item/72225#page/370/mode/lup>
- Dawen, E. & Cannon, J. C. (2017, published on the internet). *Delicate Solomon Island ecosystem in danger of heavy logging*. <https://news.mongabay.com/2017/05/delicate-solomon-island-ecosystem-in-danger-of-heavy-logging/> [Accessed March 2019].
- de Labillardière, J. J. H. (1824–1826). *Sertum austro-caledonicum*. Dominiae Huzard, Paris.
- Don, D. (1830). A monograph on the family of plants called Cunoniaceae. *Edinburgh New Philos. J.* 9: 84–96. <https://www.biodiversitylibrary.org/item/82199#page/104/mode/lup>
- Engler, A. (published 1928, dated 1930). Cunoniaceae. In: A. Engler & K. Prantl (eds), *Die natürlichen Pflanzenfamilien*, 2nd edn., 18a: 229–262. Engelmann, Leipzig.
- Flora of Solomon Islands (Database of collections from Solomon Islands preserved at TNM, published on the internet). <http://siflora.nmns.edu.tw/> [Accessed July 2021].
- Flora of Vanuatu (PVNH). (Database of collections, published on the internet). <http://pvnh.net/collections/> [Accessed Sept. 2021]
- Foreman, D. B. (1971). *A check list of the vascular plants of Bougainville, with descriptions of some common forest trees*. Botany Bulletin no. 5. Dept Forests, Division of Botany, Papua New Guinea.
- GeoCAT, geospatial conservation assessment tool (published on the internet). <http://geocat.keew.org> [Accessed Aug. 2021].
- Global Witness (2018, published on the internet). *Paradise Lost. How China can help the Solomon Islands protect its forests*. Global Witness, London. www.globalwitness.org/en/campaigns/forests/paradise-lost/ [Accessed Oct. 2019].
- Good, R. (1969). Some phytogeographical relationships of the angiosperm flora of the British Solomon Islands Protectorate. *Philos. Trans., Ser. B*, 255: 603–608. <https://doi.org/10.1098/rstb.1969.0033>
- Gray, A. (May 1854). Characters of some new genera of plants mostly from Polynesia, in the collection of the United States Exploring Expedition under Captain Wilkes (continued). *Proc. Amer. Acad. Arts* 3: 127–129. <https://www.jstor.org/stable/20021167?seq=19>
- _____. (June 1854). *United States Exploring Expedition. Botany, Phanerogamia*, part 1: 666. Philadelphia.
- _____. (1856). *United States Exploring Expedition. Atlas, Botany, Phanerogamia*, vol. 1: t. 83A. Philadelphia.
- Guillaumin, A. (1931). Contribution to the flora of the New Hebrides. Plants collected by S. F. Kajewski in 1928 and 1929. *J. Arnold Arbor.* 12: 221–264. <https://www.jstor.org/stable/43780599>
- _____. (1935). Contribution à la flore des Nouvelles-Hébrides. Plantes recueillies par M. et Mme Aubert de la Rüe en 1934 (Phanérogames). *Bull. Soc. Bot. France* 82: 346–354. <https://doi.org/10.1080/00378941.1935.10832990>
- _____. (1937). Contribution à la flore des Nouvelles-Hébrides. Plantes recueillies par M. et Mme Aubert de la Rüe dans leur deuxième voyage (1935–1936). (Phanérogames). *Bull. Mus. Natl. Hist. Nat. Sér.* 2(9): 283–306. <https://www.biodiversitylibrary.org/item/216867#page/301/mode/lup>
- _____. (1948). Compendium de la flore phanérogamique des Nouvelles Hébrides. *Ann. Mus. Colon. Marseille Sér.* 6 (5–6): 5–56. (Cunoniaceae on p. 24).
- Hallé, F. (2003). La forêt de Vanikoro et les botanistes de Lapérouse. In: Association Salomon (ed.), *Lapérouse à Vanikoro. Résultats des dernières recherches franco-salomonaises aux îles Santa Cruz*, pp. 57–66. IRD, République Française & Association Salomon, Nouméa.
- Hancock, I. R. & Henderson, C. P. (1988). *Flora of Solomon Islands*. Research Bull. no. 7, Dodo Creek Research Station, Research Dept, Min. Agriculture & Lands, Honiara.
- Harvard University Herbaria (A, GH). (Database of collections, published on the internet). <https://huh.harvard.edu/pages/digital-resources>. [Accessed Sept. 2018].
- Herold, M., Sambale, J., Lindner, M., Urban, M. & Weaver, S. (2007). Satellite based monitoring of the national forest resources in the Pacific island state of Vanuatu. *Proc. Tri-National Conf. 2007 Swiss, Austrian & German Soc. Photogrammetry & Remote Sensing*, 19–21 June 2007, Basel, Switzerland, pp. 319–398. www.carbonpartnership.co.nz/uploads/8/2/1/0/8210062/herold_vanuatu_dgpf07.pdf [Accessed Oct. 2019].
- Hochreutiner, B. P. G. (1904). *Plantae bogorienses exsiccatae*. Instituti botanici bogorienses, Buitenzorg.
- _____. (1907). Rectification touchant les plantae bogorienses exsiccatae. *Annuaire Conserv. Jard. Bot. Genève* 10: 118–119. <https://www.biodiversitylibrary.org/item/113039#page/434/mode/lup>
- Hoogland, R. D. (1979). Studies in the Cunoniaceae II. The genera *Caldcluvia*, *Pullea*, *Acsmithia* and *Spiraeanthemum*.

- Blumea* 25: 481–505. <https://repository.naturalis.nl/pub/526101>
- _____. (1984). *Acsmithia* (216), *Caldcluvia* (262), *Geissois* (263), *Pullea* (264), *Spiraeanthemum* (265). In: M. M. J. van Balgooy (ed.), *Pacific Plant Areas* Vol. 4: 160–169. Rijksherbarium, Leiden.
- Hopkins, H. C. F. (2006). Nomenclature and typification in *Geissois* (Cunoniaceae) in the South-West Pacific. *Adansonia, Sér.* 3, 28: 311–327. <https://sciencepress.mnhn.fr/sites/default/files/articles/pdf/a2006n2a6.pdf>
- _____. (2018). The taxonomy and morphology of *Schizomeria* (Cunoniaceae) in New Guinea, the Moluccas and the Solomon Islands, with notes on seed dispersal and uses throughout the genus. *Kew Bull.* 73: 11. <https://doi.org/10.1007/s12225-017-9726-1>
- _____. & Bradford, J. C. (1998). A revision of *Weinmannia* (Cunoniaceae) in Malaysia and the Pacific 1. Introduction and an account of the species of Western Malasia, the Lesser Sunda Islands and the Moluccas. *Adansonia, Sér.* 3(20): 5–41. <https://sciencepress.mnhn.fr/sites/default/files/articles/pdf/a1998n1a1.pdf>
- _____. & Florence, J. (1989). A revision of *Weinmannia* (Cunoniaceae) in Malasia and the Pacific 4. The Society, Marquesas and Austral Isla. *Adansonia, Sér.* 3(20): 107–130. <https://sciencepress.mnhn.fr/sites/default/files/articles/pdf/a1998n1a4.pdf>
- _____. & Hoogland, R. D. (2002). Cunoniaceae. *Flora Malesiana Ser. I* 16: 53–165. Flora Malesiana Foundation, Leiden.
- _____. & Jennings, L. V. S. (2021). Cunoniaceae. In: T. M. A. Utteridge & L. V. S. Jennings (eds), *Trees of New Guinea*, pp. 219–225. Royal Botanic Gardens, Kew.
- _____. Bradford, J. C. & Hoogland, R. D. (1998). A revision of *Weinmannia* (Cunoniaceae) in Malasia and the Pacific 3. New Guinea, Solomon Islands, Vanuatu and Fiji, with notes on the species of Samoa, Rarotonga, New Caledonia and New Zealand. *Adansonia, Sér.* 3(20): 67–106. <https://sciencepress.mnhn.fr/sites/default/files/articles/pdf/a1998n1a3.pdf>
- _____. Pillon, Y. & Hoogland, R. D. (2014). Cunoniaceae. *Flora de la Nouvelle-Calédonie* Vol. 26: 1–455. MNHN, Paris & IRD, Marseille.
- _____. Rozeffelds, A. C. & Pillon, Y. (2013). *Karrabina* gen. nov. (Cunoniaceae), for the Australian species previously placed in *Geissois*, and a synopsis of genera in the tribe Geissoieae. *Austral. Syst. Bot.* 26: 167–185. <https://doi.org/10.1071/SB12037>
- IUCN (2019, published on the internet). *Guidelines for using the IUCN Red List Categories and Criteria*. Version 14 (August 2019). Prepared by the Standards and Petitions Subcommittee. <http://www.iucnredlist.org/documents/RedListGuidelines.pdf> [Accessed July 2021].
- Jstor Global Plants (published on the internet). <http://plants.jstor.org/> [Accessed August 2018, March 2019].
- Kajewski, S. F. (1930). A plant collector's notes on the New Hebrides and Santa Cruz Islands. *J. Arnold Arbor.* 11: 172–180. <https://www.jstor.org/stable/43780559>
- Katovai, E., Burley, A. L. & Mayfield, M. M. (2012). Understorey plant species and functional diversity in the degraded wet tropical forests of Kolombangara Island Solomon Islands. *Biol. Conservation* 145: 214–224. <https://doi.org/10.1016/j.biocon.2011.11.008>
- _____. Edwards, W. & Laurance, W. F. (2015). Dynamics of logging in Solomon Islands: The need for restoration and conservation alternatives. *Trop. Conservation Sci.* 8: 718–731. <https://doi.org/10.1177/194008291500800309>
- King, P. (2007). *Country environmental analysis: Vanuatu*. Asian Development Bank, Technical Assistance Consultant's Report. Project no. 38031. <https://www.sprep.org/att/IRC/eCOPIES/Countries/Vanuatu/71.pdf> [Accessed March 2019].
- Koorders, S. H. (1918). *Supplement op het Eerste Overzicht der Flora van N. O. Celebes*. Part 1. Visser & Co., van Ruygrok & Co., Batavia [Jakarta].
- Lavery, T. H. & Judge, H. (2017). A new species of giant rat (Muridae, *Uromys*) from Vangunu, Solomon Islands. *J. Mammal.* 98: 1518–1530. <https://doi.org/10.1093/jmammal/gyx116>
- Linnean Collections, Smith Herbarium (LINN-SH). (Database of collections, published on the internet). <http://www.linnean.org> [Accessed Aug. 2018].
- Lorence, D. H. & Wagner, W. L. (2011). *Weinmannia marquesana* var. *angustifolia* (Cunoniaceae), a new variety from the Marquesas Islands. *PhytoKeys* 4: 61–66. <https://doi.org/10.3897/phytokeys.4.1605>
- Mallick, D. I. J. (1975). Development of the New Hebrides archipelago. *Philos. Trans. Ser. B* 272: 277–285. <https://doi.org/10.1098/rstb.1975.0087>
- Marsh, S. T., Brummitt, N. A., de Kok, R. P. J. & Utteridge, T. M. A. (2009). Large-scale patterns of plant diversity and conservation priorities in South East Asia. *Blumea* 54: 103–108. <https://doi.org/10.3767/000651909X474159>
- Miquel, F. A. W. (1855–1859). *Flora van Nederlandsch Indië*. C. G. van der Post, Amsterdam, 3 vols. (*Spiraeopsis celebica* in Vol. 1(1): 719, 1856). <https://www.biodiversitylibrary.org/item/1862#page/743/mode/1up>
- Muséum National d'Histoire Naturelle, Paris (P). (Database of collections, published on the internet). <https://science.mnhn.fr/all/search> [Accessed August 2018, July 2021].
- National Museum of Nature and Science, Japan (TNS). (Database of collections, published on the internet). www.type.kahaku.go.jp/TypeDB/vascular/458 [Accessed Sept. 2021].
- Naturalis (L, U) (Database of collections, published on the internet.) <https://biportal.naturalis.nl> [Accessed Sept. 2018, July 2021].
- Papua New Guinea Mine Watch (2018, published on the internet). *Bougainvilleans want Filipino miner out of their ancestral land*. <https://ramumine.wordpress.com/tag/logging/> [Accessed Oct. 2019].
- Perry, L. M. (1949). *Plantae Papuanae Archboldianae*, XIX. *J. Arnold. Arbor.* 30: 139–165. <https://www.jstor.org/stable/43781328>
- Pierce, R. (2014). *Surveys of threatened birds and flying foxes in the Santa Cruz Islands, Solomon Islands, Sept. – Oct. 2014*. EcoOceania report. https://www.cepf.net/sites/default/files/oceanswatch_stacruzreportdec2014.pdf [Accessed March 2019].
- Pillon, Y. (2011). Focus on *Geissois* (Cunoniaceae): another example of the Melanesian connection. In: P. Bouchet, H. le Guyader & O. Pascal (eds), *The natural history of Santo*, pp. 93–94. MNHN, Paris, IRD, Marseille & PNI, Paris.
- _____. Hopkins, H. C. F., Maurin, O., Epitawalage, N., Bradford, J. C., Rogers, Z. S., Baker, W. J. & Forest,

- F. (2021a). Phylogenomics and biogeography of Cunoniaceae (Oxalidales) with complete generic sampling and taxonomic realignments. *Amer. J. Bot.* 108: 1181–1200. <https://doi.org/10.1002/ajb2.1688>
- _____, _____, Munzinger, J. & Chase, M. W. (2009). A molecular and morphological survey of generic limits of *Acsmithia* and *Spiraeanthemum* (Cunoniaceae). *Syst. Bot.* 34: 141–148. <https://doi.org/10.1600/036364409787602410>
- _____, Rigault, F., Jaffré, T. & Stacy, E. A. (2014). Cryptic adaptive radiation in tropical forest trees in New Caledonia. *New Phytol.* 202: 521–530. <https://doi.org/10.1111/nph.12677>
- _____, Jaffré, T., Birnbaum, P., Bruy, D., Cluzel, D., Ducousso, M., Fogliani, B., Ibanez, T., Jourdan, H., Lagarde, L., Léopold, A., Munzinger, J., Pouteau, R., Read, J. & Isnard, S. (2021b). Infertile landscapes on an old oceanic island: the biodiversity hotspot of New Caledonia. *Biol. J. Linn. Soc.* 133: 317–341. <https://doi.org/10.1093/biolinnean/blaa146>
- Pineda, R. (2011). Deforestation on Santo and logging operations. In: P. Bouchet, H. le Guyader & O. Pascal (eds), *The natural history of Santo*, pp. 67–68. MNHN, Paris, IRD, Marseille & PNI, Paris.
- Plunkett, G. M., Ranker, T. A., Sam, C. & Balick, M. J. (2022). Towards a checklist of the vascular flora of Vanuatu. *Candollea* 77: 105–118. <https://doi.org/10.15553/c2022v771a8>
- PNGexposed Blog (2014, published on the internet). *Malaysian company to log forests on Bougainville*. <https://pngexposed.wordpress.com/2014/11/17/malaysian-company-to-log-forests-on-bougainville/> [Accessed Oct. 2019].
- Porter, D. & Allen, M. (2015). *The political economy of the transition from logging to mining in Solomon Islands*. State, Society & Governance in Melanesia, Discussion Paper 2015/12, Coral Bell School of Asia Pacific Affairs, ANU. https://openresearch-repository.anu.edu.au/bitstream/1885/98441/2/01_Porter_The_Political_Economy_of_the_2015.pdf [Accessed Nov. 2019].
- Ramon, L. & Sam, C. (2015). *Plantes remarquables du Vanuatu, Mélanésie Océanie*. Biotope & New York Botanical Garden.
- REDD in Solomon Islands (2014, published on the internet). <https://theredddesk.org/countries/solomon-islands/> [Accessed March 2019].
- REDD in Vanuatu (2013, published on the internet). <https://www.theredddesk.org/countries/Vanuatu> [Accessed March 2019].
- Ridley, H. N. (1916). Report on the botany of the Wollaston expedition to Dutch New Guinea 1912–13. *Trans. Linn. Soc. London, Bot.* 9: 1–269. <https://www.biodiversitylibrary.org/item/13690#page/2/mode/1up>
- Schlechter, F. R. (1918). Bemerkung zu den Cunoniaceae papuanen. *Bot. Jahrb. Syst.* 55: 194. <https://www.biodiversitylibrary.org/item/27454#page/212/mode/1up>
- Schönberger, I., Wilton, A., Boardman, K. F., Breitwieser, I., Cochrane, M., Dawson, M. I., de Lange, P. J., de Pauw, B., Fife, A. J., Ford, K. A., Gibb, E. S. & Glenny, D. S. (2019). *Checklist of the New Zealand Flora – Seed Plants*. Lincoln, Manaaki Whenua-Landcare Research. <https://doi.org/10.26065/s3gg-v336>.
- Seemann, B. (1865–1873). *Flora vitiensis*. L. Reeve & Co., London. [Saxifragaceae pp. 108–111].
- Shorthouse, D. P. (2010, published on the internet). SimpleMappr, an online tool to produce publication-quality point maps. <http://www.simplemappr.net> [Accessed Aug. 2021].
- Smith, A. C. (1952). Studies of Pacific Island plants, XII. The Cunoniaceae of Fiji and Samoa. *J. Arnold Arbor.* 33: 119–149. <https://www.jstor.org/stable/43786474>
- _____. (1985). *Flora Vitiensis Nova*, Vol. 3. Pacific Tropical Botanical Garden, Lawai, Kauai, Hawaii.
- Solomon Islands Government (2014, published on the internet). *National REDD+ Readiness Roadmap 2014–2020*. https://solomonislands-data.sprep.org/system/files/2014_Solomon%20Islands_REDD%20Roadmap_p.pdf [Accessed March 2019].
- Taiwan Forestry Research Institute (TAIF) (Database of collections, published on the internet). <https://taif.tfri.gov.tw/en/> [Accessed Aug. 2021].
- Thorne, R. F. (1969). Floristic relationships between New Caledonia and the Solomon Islands. *Philos. Trans., Ser. B* 255: 595–602. <https://doi.org/10.1098/rstb.1969.0032>
- Tropicos (MO) (Database of collections, Missouri Botanical Garden, published on the internet). www.tropicos.org [Accessed Sept. 2018].
- UNEP-WCMC (2019, published on the internet). *Protected Area Profile from the World Database of Protected Areas*. (Searches for Papua New Guinea, Solomon Islands and Vanuatu.) www.protectedplanet.net [Accessed Oct. 2019].
- Vanuafloora — Vanuatu Herbarium (PVNH). (Database of collections, published on the internet). https://publish.plantnet-project.org/project/vanuafloora_en [Accessed March 2019, July 2021].
- Walker, F. S. (1948). *The forests of the British Solomon Islands Protectorate: a report*. Crown Agents for the Colonies on behalf of the Government of the British Solomon Islands Protectorate, London.
- Wheatley, J. I. (1992). *A guide to the common trees of Vanuatu*. Dept. of Forestry, Republic of Vanuatu.
- White, C. T. (1950). Ligneous plants from the Solomon Islands (and New Guinea). *J. Arnold Arbor.* 31: 81–116. <https://www.jstor.org/stable/43781354>
- Whitmore, T. C. (1966a). *Guide to the forests of the British Solomon Islands*. Oxford University Press, London.
- _____. (1966b). The social status of *Agathis* in a rainforest in Melanesia. *J. Ecol.* 54: 285–301. <https://doi.org/10.2307/2257950>
- _____. (1967). Notes on the systematics of Solomon Islands' plants and some of their New Guinea relatives I–VII. *Gard. Bull. Singapore* 22: 1–21. <https://www.biodiversitylibrary.org/item/148283#page/8/mode/1up>
- _____. (1969). The vegetation of the Solomon Islands. *Philos. Trans., Ser. B* 255: 259–270. <https://doi.org/10.1098/rstb.1969.0010>
- _____. (1989). Changes over twenty-one years in the Kolombangara rain forests. *J. Ecol.* 77: 469–483. <https://doi.org/10.2307/2260763>
- World Bank (published on the internet). <https://data.worldbank.org/indicator/AG.LND.TOTL.K2?locations=VU> [Accessed July 2022].

Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.