

Neuburgia novocaledonica, comb. nov. and the first record of domatia in the family Loganiaceae

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Abstract. The New Caledonian species *Couthovia novocaledonica* Gilg & Benedict (Loganiaceae) is supported as a species distinct from *Neuburgia corynocarpa* (A.Gray) Leenh. *Neuburgia novocaledonica* is different in having domatia on its abaxial leaf surfaces, two rings of hairs within the corolla tube, and generally obovate leaf shape. Therefore, the new combination *Neuburgia novocaledonica* (Gilg & Benedict) J. Molina & Struwe is hereby made. The presence and morphology of domatia on the lower surface of the leaves of *Neuburgia novocaledonica* are discussed. This appears to be the first record of domatium occurrence in Loganiaceae.

Introduction

Neuburgia, described by Blume (1850), is a genus of woody understory trees or shrubs often found in the everwet lowland tropical forests of the Philippines, Celebes, Caroline Islands, Papuasia, New Hebrides, New Caledonia and Fiji. There are approximately 10–12 species in *Neuburgia* according to Leenhouts (1963) and Conn (1995).

Couthovia was described as a new genus by the taxonomist Gray (1858) and placed in the family Loganiaceae. Leenhouts (1963) found *Couthovia* to be identical with Blume's *Neuburgia* (1850), and validly included *Couthovia* in *Neuburgia*. The International Plant Names Index (1999) lists 28 published species for *Couthovia*, nine of which are already moved to and accepted in *Neuburgia*, and 18 species reduced to synonymy (Leenhouts 1963). In the same publication, Leenhouts recognised six species formerly placed in *Couthovia*.

Couthovia novocaledonica was described by Gilg and Benedict (1921) from New Caledonia and has often been misspelled as *C. 'neo-caledonica'*. Leenhouts (1963) speculated that *C. novocaledonica* Gilg & Benedict may be 'possibly combined with *Neuburgia corynocarpa* (A.Gray) Leenhouts' (Leenhouts 1963 p. 366). Leenhouts (1963) reduced 13 names of *Couthovia* to a synonymy of *N. corynocarpa*. Owing to lack of material, Leenhouts was unable to confirm the taxonomic status of *C. novocaledonica*. Our recent discovery of domatia on the lower surface of the leaves of this species strongly supports its distinctiveness from the domatia-less *N. corynocarpa*. Differences in three additional characters between the two species are also presented (Figs 1, 2; Table 1). *Couthovia novocaledonica* is therefore distinct from *N. corynocarpa*, and the new combination, *Neuburgia novocaledonica*, is here proposed.

Although Brouwer and Clifford (1990) published one recorded example of domatia for the family Loganiaceae, namely *Coinochlamys angolana* var. *laurentii* de Wild, this species has been now reduced to the synonym of *Mostuea hirsuta* (T.Anders.ex Benth. & Hook.f.) Baill ex Bak. of the segregate family, Gelsemiaceae (Leeuwenberg 1961; Struwe *et al.* 1994). Our study appears to be the first documentation of domatia in the genus *Neuburgia* and also, the first published record for true Loganiaceae.

Materials and methods

Herbarium specimens for *Neuburgia novocaledonica* and *Neuburgia corynocarpa* (see Appendix) from Arnold Arboretum, Harvard University (A), New York Botanical Garden (NY), United States National Herbarium (USA), Field Museum of Natural History (F), Chicago Academy of Sciences (CACS), and Nationaal Herbarium Nederland, Leiden University branch (L) were examined. Type material of *N. corynocarpa* at NY and *C. novocaledonica* at L were also examined. For detailed studies, samples of pressed flowers, fruit and leaves were rehydrated by boiling in water for 30–60 s in a microwave. Structures were observed with Zeiss Stemi 2000-C (Edmund Optics Inc., Barrington, NJ) or Olympus SZ (Olympus America Inc., Melville, NY) dissecting microscopes. Photographs were taken with Nikon DXM1200 digital camera with ACT-1 version 2.11 software.

Taxonomic treatment

Neuburgia novocaledonica (Gilg & Bened.) J. Molina & Struwe, comb. nov. Basionym: *Couthovia novocaledonica* Gilg & Bened., Bot. Jahrb. 56: 547. 1921. Lectotype: NEW CALEDONIA. Nordbezirk auf den Bergen bei Ou-Hinna, [altitude] 500 m, 1903, *Schlechter 15650* (L) (Fig. 1B)

Selected specimens examined

NEW CALEDONIA: am Kugel om Poindelen ob Kene auf Schiefer, *Däniker 1068*, 1.ii.1925, L. Col d' Amieu, Sarramea, *Webster & Hildreth 14896*, 29.iv.1968, A. Col d' Amieu, *McKee 8065*,



Fig. 1. Predominant leaf shape of mature leaves (A) *N. corynocarpa*, broadly elliptic or oval (type, NY). (B) *N. novocaledonica* (type, L), obovate.



Fig. 1. (continued)

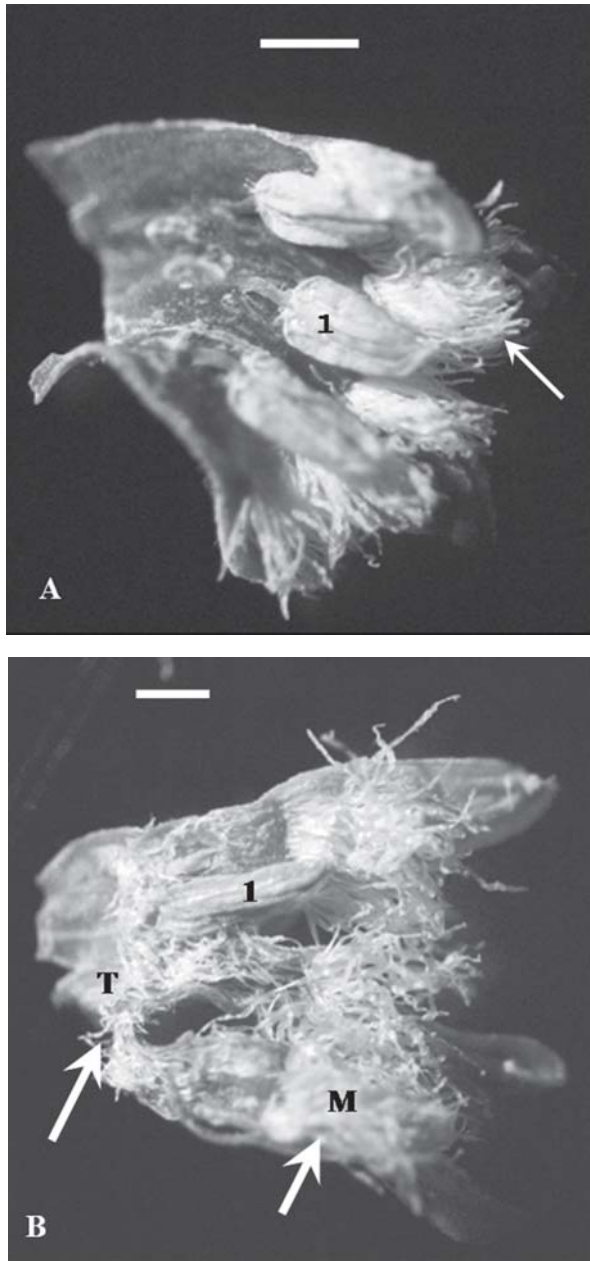


Fig. 2. Position of hairs on inside of corolla (indicated by arrow) (A) *N. corynocarpa* (AC Smith 7133, NY), hairs only in mouth of corolla. (B) *N. novocaledonica* (Guillaumin 10116, NY), hairs both in corolla mouth (M) and base (T) of tube (1, stamen). Bars = 1 mm (A, B).

13.i.1961, USA. Col d' Amieu, *Guillaumin 8472*, 21.xi.1950, A & NY. *Guillaumin 10116*, 2.ii.1951, NY. Ferme Modelle, *Balansa 360*, NY. L.O. de Canala, *Balansa 2003*, A. Route de Gomen, *Hurlimann 1813*, 24.viii.1951, NY & A. Col d' Petchicara, *McKee 6579*, 11.ix.1958, 2 sheets, A and USA. Ourai, *Lecard 20* Oct. 1879, A. *Viellard 681*, 1861–1867, A. *Pancher s.n.*, 1870, A. *Henecart s.n.*, iv.1879, A. UNITED STATES: HAWAII: (cultivated ex New Caledonia) Kauai, Koloa Distr., Lawai Valley: National Tropical Botanical Garden, Maidenhair Falls section, *Lorence 7370*, 29.iv.1993, F.

Shrub or tree up to 20 m high, glabrous throughout except flowers; branches slightly quadrangular or terete, solid; bark smooth or fissured. Leaves opposite, simple, petiolate, narrow to broadly obovate, 8–19 × 3–11 cm, chartaceous to subcoriaceous, margins entire; venation pinnate, primary and secondary veins raised abaxially and adaxially, tertiary veins obscure and laxly reticulate; pit-type domatia in vein axils on abaxial leaf surface, starting from third to sixth secondary vein from base of midvein and regularly occurring until leaf apex, first order [i.e. in the axils of primary nerves (Jacobs 1966)] and second order; base cuneate; apex rounded to obtuse; petiole 0.8–1.9 cm long; stipules interpetiolar, 0.5–1.2 × 0.3–0.9 cm, deltoid, cupuliform, connate with petioles. Inflorescence a dichasium, dividing three or four times, terminal; fourth order (most distal relative to florets) peduncle 8–11 cm, succeeding orders of peduncles decreasing in length, with the central peduncle always shortest; bracts broadly ovate, ciliated. Flowers white, perfect, actinomorphic, hypogynous, terminal, 5-merous, 5.0–6.5 × 3.0–3.9 mm; pedicels 0.5–2.0 mm long, with punctate glands. Calyx 5-lobed, synsepalous, cupuliform, coriaceous, imbricate; calyx lobes suborbicular to orbicular, 1.5–2.7 × 1.5–2.3 mm, apex rounded, margin entire, ciliolate, lobes densely punctuate, light yellow when dry. Corolla 5-lobed, sympetalous, salverform, subcoriaceous, valvate; corolla tube 2.2–5.0 mm long, point of insertion of stamens barbate; corolla lobes narrowly ovate, 1.2–4.9 mm long, apex acute, margins entire, mouth more densely barbate than basal part of corolla tube; hairs at corolla mouth 0.9–1.8 mm long; hairs at corolla base 0.4–0.9 mm long. Stamens 5, alternating with corolla lobes, adnate to corolla tube, inserted at 1/4 of tube length from corolla base, introrse; filaments 1.0–2.6 mm long; anthers narrowly ovate, 2.0–3.5 × 1 mm, longitudinally dehiscent. Gynoecium obclavate, *c.* 6.6 mm long; ovary ovoid, 2-seeded, one seed aborted, placentation axile; style 2.0–2.6 × 0.5 mm, gradually confluent with ovary; stigma *c.* 0.6–0.7 × 0.6–0.7 mm, ovoid. Fruit a drupe, white, clavate, 2.0–2.2 × 0.9–1.1 cm, indehiscent; exocarp with fine longitudinal ridges; mesocarp very fibrous.

Results

Neoburgia corynocarpa and *N. novocaledonica* primarily differ in three morphological characters, namely leaf shape, position of hairs in corolla and domatium occurrence, all of which were studied and analysed in this paper.

Neoburgia corynocarpa leaves are ovate or broadly elliptic (Fig. 1A), whereas *N. novocaledonica* leaves are obovate, with the widest part conspicuously displaced towards the apex (Fig. 1B). Furthermore, the leaves have subacute apices in the type of *N. corynocarpa* (Fig. 1A), whereas leaves of *N. novocaledonica* are obtuse (Fig. 1B).

Table 1. Character differences between *N. corynocarpa* and *N. novocaledonica* based on protologues, personal observations and herbarium sheet notes

Character	Protologue		Personal observations	
	<i>N. corynocarpa</i>	<i>N. novocaledonica</i>	<i>N. corynocarpa</i>	<i>N. novocaledonica</i>
Leaf shape	Suborbicular or broadly elliptic to obovate (Gillespie 1931)	Obovate or broadly obovate (Engler 1921)	Oval to slightly ovate, very rarely obovate; sometimes orbicular	Obovate; sometimes oval
Position of hairs on corolla	Corolla throat (Gillespie 1931)	Corolla mouth (Engler 1921)	Inner surface of corolla lobes only	Inner surface of corolla lobes and base of corolla tube
Domatia	Not mentioned	Not mentioned	Absent	Present
Altitude of occurrence	Not mentioned	500 m (Engler 1921)	30–200 m	300–650 m

In *Neuburgia corynocarpa*, hairs are inserted only at the entrance to the corolla mouth (Fig. 2A), unlike *N. novocaledonica*, where hairs are inserted in the corolla both at the base of the stamens and at the mouth (Fig. 2B).

Domatia are absent in the vein axils of the abaxial surface of the leaves of *Neuburgia corynocarpa* (Fig. 3A), but are persistently present in the first (Fig. 3B) and second (Fig. 3C) order vein axils of *N. novocaledonica*. *N. novocaledonica* has pit-type domatia (Fig. 3B, C).

Discussion

Domatia (Lundstroem 1887) refer to plant structures that may provide shelter to animals. However, Jacobs (1965, 1966) restricted the usage of the term to spatial structures occurring in or near vein axils of the first, second or third order, and were restricted to the abaxial surface of leaves. He further confined the term to features that accommodate only mite symbionts, hence excluding ants and bacteria (Jacobs 1966). Domatia are plant-produced formations and are not induced by their resident symbionts (O'Dowd and Willson 1991). They appear early in plant development (Brouwer and Clifford 1990), but may not be inhabited until maturity (Willson 1991). Interestingly, domatia are also restricted to woody dicotyledons growing in humid habitats (Jacobs 1965).

The ecological significance of domatia has long been the subject of debate, but recent studies demonstrate the beneficial role of domatia in promoting plant–arthropod mutualism (Pemberton and Turner 1989; O'Dowd and Pemberton 1994; Agrawal and Karban 1997). Domatia provide protective domiciles and nurseries for mites, and additionally, these mites keep the leaf lamina healthy by feeding on pathogenic fungi and herbivorous mites (O'Dowd and Pemberton 1994).

Domatia have been recorded in 277 families and in almost 2000 species (Agrawal and Karban 1997) in many geographical regions (O'Dowd and Pemberton 1994). Since domatia are heritable structures, Brouwer and Clifford (1990) considered domatium occurrence as a reliable taxonomic character. Robbrecht (1988) suggested that domatia may only be taxonomically useful in species

discrimination, but also commented that higher taxa (subgenera, genera) may sometimes exhibit a particular domatium type. In Jacobs' comprehensive discussion of domatia, he noted that there are studies supporting the usefulness of domatia in species delineation, in much the same way as hairs and glands do (Jacobs 1966). van Steenis (1967, p. 1568) also affirmed its 'systematical value in specified cases.' Hence, domatium occurrence on the abaxial leaf surfaces of *Neuburgia novocaledonica* is a satisfactory discriminatory character at the species level. Domatia have never been observed by us in *N. corynocarpa*, *N. tubiflora*, *N. rumphiana*, *N. macrocarpa*, *N. kochii*, *N. macroloba*, and *N. moluccana* (see Appendix).

Without careful inspection, it is difficult to distinguish between *Neuburgia corynocarpa* and *Neuburgia novocaledonica*, and the latter was treated as a synonym of the former by Leenhouts (1963). However, the presence of domatia shows the distinctiveness of *N. novocaledonica* (Table 1). Two additional traits are presented here, which may be supplementary features that can aid in species delimitation and determination of *N. novocaledonica* (Figs 1–3). *Neuburgia corynocarpa* has broadly elliptic or oval leaves and occurs at an altitudinal range of 30–200 m. Smith (1942) claimed that occurrence above 500 m is unusual. *Neuburgia novocaledonica* has obovate leaves and occurs at a higher elevation of 300–650 m. Leaf morphology and altitude of occurrence are possibly highly variable characters in *N. corynocarpa*. Further investigations of more herbarium material, as well as field studies, are required to see if these are consistent throughout the broad distributional range of *N. corynocarpa*. In *N. novocaledonica*, the development of hairs in both corolla base and mouth (Fig. 2B) also differentiates it from most individuals of *N. corynocarpa*, which has only hairs at the corolla mouth. Documented exceptions (Conn 1979) in *N. corynocarpa* warrant further examination. In addition, Conn (1981) had described the lectotype of *N. corynocarpa* var. *sarcantha* as being 'laxly woolly in tube, at and above point of insertion of stamens'. We have only seen three specimens of *N. corynocarpa* (White 10299, Streismann 44393, Streismann & Lelean 18332) that are sparsely pubescent at the base of the inner corolla tube

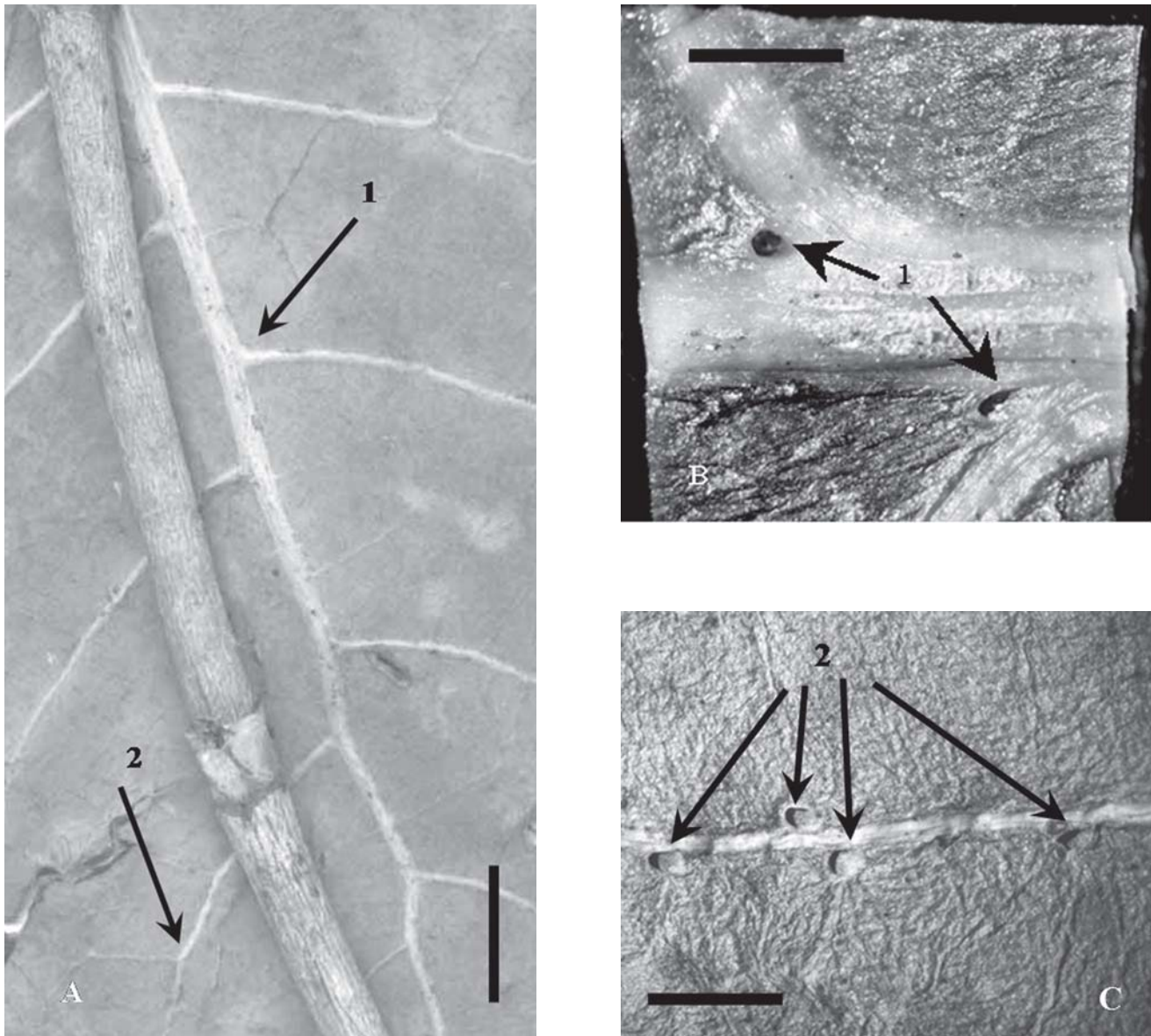


Fig. 3. Presence of domatia in vein axils (indicated by arrow) (A) *N. corynocarpa* (AC Smith 6646, HUH), none in first (1) and second (2) order axils. (B, C) *N. novocaledonica* (Guillaumin 8472, NY), pit-type domatia present in both first (1) and second (2) order axils. Bars = 7 mm (A), 2 mm (B), 3 mm (C).

relative to the corolla mouth. These three were all collected in Papua New Guinea. Hairs at the corolla base are also distinctly shorter (0.15–0.21 mm) than those in the corolla mouth (0.33–0.76 mm). This observation may suggest that position of pubescence within the corolla tube is not a good species-delimiting feature. However, we also suspect that *N. corynocarpa*, in its current circumscription, is a composite of several species. For example, Conn (1979) observed variants of *N. corynocarpa* that possessed only four calyx lobes, which we have not seen so far in *N. novocaledonica*. The taxonomic significance of the occurrence of domatia in *Neuburgia novocaledonica* should not be ignored (Fig. 3).

The pit is the predominant domatium type in all examined specimens of *N. novocaledonica* (Fig. 3B, C). Intermediates between the types are likely, hence it is not the type, but it is the presence or lack of domatia, which must be considered (Jacobs 1965). These axillary structures or domatia in *N. novocaledonica* could not be mistaken for galls, as they are very regular in their position (Jacobs 1966), being regularly present in the first and second order vein axils of the leaf's abaxial surface. Moreover, of 15 herbarium sheets of *N. novocaledonica* examined, all exhibited domatia, except for one specimen (*Balansa 360*, NY), which was difficult to ascertain since a significant portion of the abaxial surface of

the leaves were glued to the sheet. The occurrence of domatia in *N. novocaledonica* is indisputably a taxonomic character that delineates it from *N. corynocarpa*. Therefore, *N. novocaledonica* is here recognised a distinct species, and the transfer from *Couthovia* to *Neuburgia* is proposed here.

This may be the first record of the occurrence of domatia for the genus *Neuburgia*, and perhaps for the family Loganiaceae. How this species uniquely evolved domatia within an angiosperm family that is not known to produce domatia has interesting implications. Loganiaceae is closely related with Rubiaceae (Backlund *et al.* 2000), and both belong to the order Gentianales, along with three other families, Gelsemiaceae, Gentianaceae, and Apocynaceae (APG 1998). Robbrecht (1988) suggested that Rubiaceae has the highest ratio of occurrence of domatia among all plant families. The close relationship between Loganiaceae and Rubiaceae may explain domatium occurrence in the former. Further studies must be undertaken with respect to the evolution and ecology of these enigmatic leaf formations.

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Appendix

Specimens examined for *Neuburgia corynocarpa* (A.Gray) Leenh.

ISOTYPE: FIJI. Wilkes Expedition (NY).

FIJI: (1) Namosi: Veivatuloa, *Rova & Gutavsson 2433*, 11.ii.1999, NY. (2) Vanua Levu: Mathuata, *Smith 6646*, 25.xi.–8.xii.1947, NY. (3) Vanua Levu: Mathuata: Southern slopes of Mt Numbuiloa, east of Lambasa, *Smith 6330*, 27.x.–10.ii.1947, A. (4) Viti Levu: Namosi: Hills between Navua R. and Suva, *Greenwood 1056*, v.1943, A. (5) Viti Levu: Namosi, 28.ix.1953, *Smith 8750*, NY. (6) Viti Levu: Namosi: Hills bordering Wainavindrau Creek, in vicinity of Wainimakutu, *Smith 8520*, 17.ix.–8 Oct. 1953, USA. (7) Wailoku, 8 km NW of Suva, *Regalado and Vodonaivalu 535*, 12.iv.1993, CACS. (8) Serua, *Smith 8991*, 20.x.1953, NY. (9) Serua, *Smith 9308*, 23.xi.–7.xii.1953, NY. (10) Tailevu, *Smith 7133*, 15–27.iv.1953, NY.

HAWAII: (11) Oahu Island, HSPA Forest Nursery, Manoa Valley, *Yuncker 3598*, 10 Apr. 1933, CACS.

INDONESIA: (12) Bogor: Island Buru, West Buru, Bara, Wae Duna, base camp 9, *Mogea 5431*, 30 Nov. 1984, A.

PAPUA NEW GUINEA: (13) East New Britain District: Kokopo Subdistrict: Trans Vudal, *Streimann 44393*, 18.viii.1969, A. (14) Madang District: Josephstaal, *White 10299*, ix.1958, A. (15) Morobe Province: logging road near Markham Village, 6°43' S, 146°53' E, *Takeuchi 7144*, 10.vii.1991, NY. (16) Western District: Kiunga Subdistrict: Tuidemasuk Road, Kiunga, *Streimann & Lelean 18332*, 17.ix.1972, A.

Specimens examined for other species of *Neuburgia*

(1) *Neuburgia macroloba* (A.C. Sm.) A.C. Sm.

ISOTYPE: FIJI: Borders of lake east of Somosomo, *Smith 917*, 29.xii.1933, L.

(2) *Neuburgia moluccana* (Boerl.) Leenh.

ISOLECTOTYPE: Unknown. Cult. In Hort. Bot. Bog. Java, *Rusdy 3*, 3.iv.1960, L.

ISOLECTOTYPE: INDONESIA: Moluccas, *Unknown IVE.92*, 4.vi.1912, L.

SYNTYPE: INDONESIA: Moluccas, *Unknown s.n.*, N.A., L.

(3) *Neuburgia rumphiana* Leenh.

HOLOTYPE: INDONESIA: New Guinea: Holtekang, E. of Hollandia, *Lam 7787*, 12.x.1954, L.

(4) *Neuburgia sarcantha* (Gilg & Benedek) Leenh.

HOLOTYPE: PAPUA NEW GUINEA: New Guinea Western Highlands District Terr. of New Guinea W. of Togoba, *Hoogland & Pullen 6207*, 9.xii.1956, L.

(5) *Neuburgia tubiflora* Blume

ISOLECTOTYPE: INDONESIA: New Guinea, *Markgraf s.n.*, 1926, L.