

Definition of South Pacific taxa of *Nicotiana* section *Suaveolentes* (Solanaceae)

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Abstract

The taxonomy of South Pacific species of *Nicotiana* requires clarification. Examination of type and other herbarium specimens supports recognition of three species: *N. forsteri* Roem. & Schult., *N. fragrans* Hook., and *N. fatuhivensis* F.Br. *Nicotiana forsteri* is synonymised with *N. debneyi* Domin. In agreement with previous authors, *N. forsteri* is considered to be validly published and the name takes precedence over *N. debneyi*. Plants from the Marquesas Islands are distinct from *N. fragrans* Hook., and thus are recognised at species level as *N. fatuhivensis* F.Br. rather than *N. fragrans* var. *fatuhivensis* (F.Br.) Goodsp. *Nicotiana fatuhivensis* is treated as a member of section *Suaveolentes* Goodsp., not section *Paniculatae* Goodsp., but more data are required to resolve its relationships. Key features for discriminating taxa are the presence of a caudex, ellipsoid-headed glandular hairs and flower size.

Keywords: taxonomy, species, Australia, New Caledonia, Marquesas Islands.

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Introduction

In terms of species, *Nicotiana* section *Suaveolentes* Goodsp. is a somewhat taxonomically difficult group. Although there are some species that are clearly defined, distinctive and present no taxonomic or identification problems, others are difficult to separate and identify. The section *Suaveolentes* is monophyletic (Aoki & Ito 2000; Chase *et al.* 2003; Clarkson *et al.* 2004) and was retained in the recent sectional classification (Knapp *et al.* 2004). Intriery *et al.* (2008) suggest the section is polyphyletic but their analyses are phenetic and not phylogenetic.

The aim of this paper is to address species and subspecies level taxonomic problems and to redefine taxa where appropriate. Many invalid names for Australian *Nicotiana* are still widely used, such as *N. eastii* Kostoff and *N. exigua* H.-M.Wheeler, particularly in molecular studies published outside of Australia (Table 1). This may be caused partly by lack of awareness of publications in Australian journals not widely available overseas; for example Horton's comprehensive 1981 revision was published in the Journal of the Adelaide Botanic Gardens.

Nicotiana plants are not widespread in the South Pacific and have a patchy distribution (Fig. 1). *Nicotiana fatuhivensis* F.Br. is found only on eight of the twelve Marquesas Islands, a group of isolated volcanic islands that form part of French Polynesia, located in the east central Pacific at approximately 8–10° S and 140° W. *Nicotiana fragrans* Hook. has been recorded on the island of Tongatapu, part of the Kingdom of Tonga, at approximately 21° S and 175° W, as well as almost 2000 km further west on several islands of New Caledonia (approximately 21° S and 165° E). The third South Pacific taxon, *N. debneyi* Domin, is found on New Caledonia, Lord Howe Island 600 km from the Australian mainland (31°30' S, 159° E) and in eastern Australia. *Nicotiana cordifolia* Phil., which belongs to section *Paniculatae*, is endemic to the eastern Pacific Juan Fernandez Islands, a group of volcanic islands about 667 km from the coast of Chile. It is clearly associated with South American taxa and is not discussed here.

Outstanding taxonomic issues and poorly known taxa have combined to make the South Pacific *Nicotiana* the most problematic members of section *Suaveolentes*. The two most recent revisions of the Australian taxa (Burbidge 1960; Horton 1981) did not include South



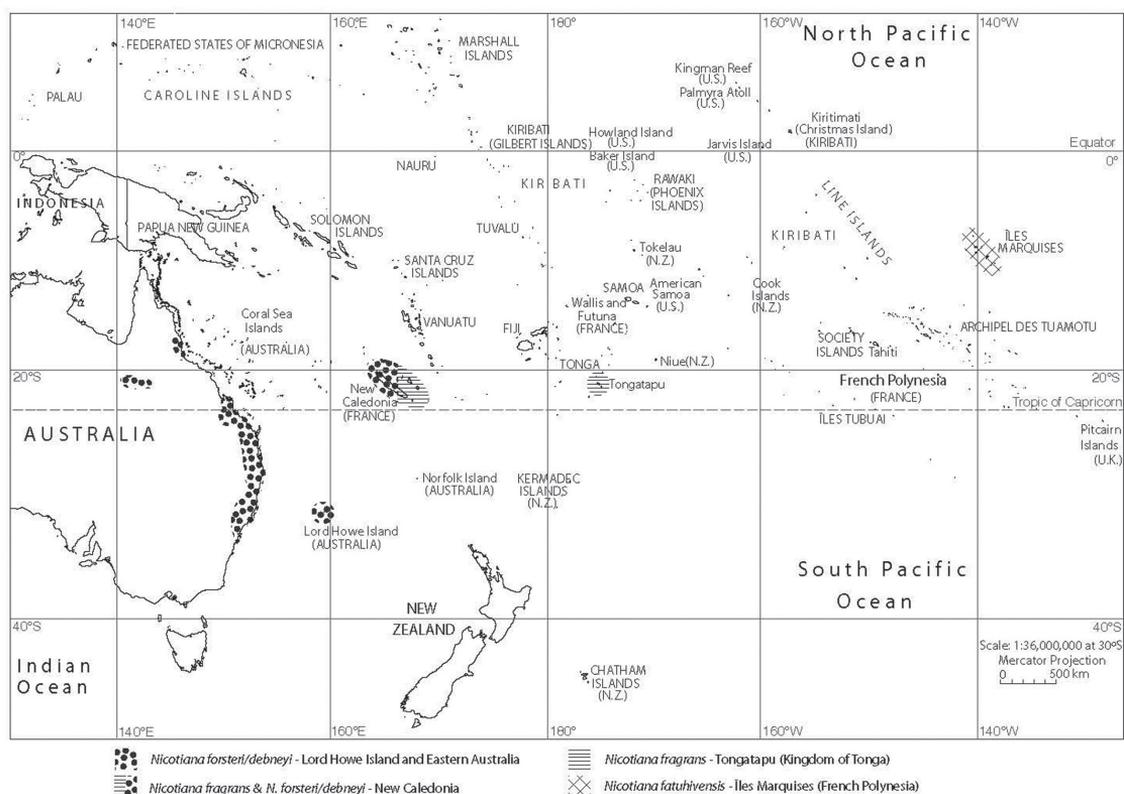


Figure 1. Distribution of *Nicotiana* taxa of the South Pacific.

Pacific taxa, making Goodspeed (1954) the most recent revision that includes all taxa in *Suaveolentes*. These species have been less well collected than those of the rest of the genus, and herbarium sheets that do exist are spread between distant herbaria.

South Pacific taxa are not well represented in molecular studies. *Nicotiana fragrans* (New Caledonia and Tonga) was included in two molecular phylogenies (Aoki & Ito 2000; Chase *et al.* 2003) but was not included in a recent and comprehensive study by Clarkson *et al.* (2004). There are no published sequences of *N. fatuhivensis* (Marquesas Islands) and the provenance of the *N. debneyi* specimen that was sequenced is not listed, and therefore it could be Australian or from New Caledonia.

The published chromosome number for *N. debneyi* (Goodspeed 1933) and *N. fragrans* is $n=24$ (Wheeler 1945), although unfortunately the provenance of the plants used for these counts is not known. These numbers fit within the $n=16, 18, 19, 20, 21, 23, 24$ sequence reported for section *Suaveolentes*. A chromosome number has not been published for *N. fatuhivensis* or *N. forsteri* Roem. & Schult.

In summary, the specific taxonomic questions addressed are:

- 1) Is *N. forsteri* Roem. & Schult. (New Caledonia) a separate species, or is it the same as *N. debneyi* (Australia) or *N. fragrans* (New Caledonia)?
- 2) Was *N. forsteri* validly published and should the name take precedence over *N. debneyi*?
- 3) Is *N. fatuhivensis* different from *N. fragrans*? Should *N. fatuhivensis* be maintained as a species or as a variety of *N. fragrans*?

Materials and methods

Herbarium material, including type specimens, was examined in August 2006 at the New York Botanical Garden (NY), at the Royal Botanic Gardens, Kew (K) and the Natural History Museum, London (BM). Specimens were examined using a light microscope to determine hair types, and vernier callipers were used to make key measurements of flowers, capsules and leaves. Measurements included corolla tube length, width at apex and at calyx; calyx length, width and length



Figure 2. Specimens of *Nicotiana*. a. *N. forsteri*, type, J.R. & G. Forster, 29–30.ix.1774, Botany Isle, New Caledonia (BM) © The Natural History Museum, London. b. *N. fragrans*, type, Milne, x.1853, Isle of Pines, New Caledonia (K). c. *N. fatuivivensis*, P.A. Schaffer 5705, 19.viii.1975, Mohotani Island, Marquesas Islands (K). d. *N. debneyi*, type, J. Dallachy, 1868, Rockingham Bay, Queensland, Australia (K). b, c, & d. © The Board of Trustees of the Royal Botanic Gardens, Kew. Reproduced with the consent of the Royal Botanic Gardens, Kew.

Table 1. *Nicotiana* taxa in section *Suaveolentes*. Those marked Y have been included in published molecular studies. A = Aoki and Ito (2000), B = Chase *et al.* (2003), C = Clarkson *et al.* (2004). Nine taxa have not been included in any molecular studies: *N. burbidgeae*, *N. fatuhivensis*, *N. heterantha*, *N. megalosiphon* ssp. *sessifolia*, *N. monoschizocarpa*, *N. occidentalis* ssp. *obliqua*, *N. truncata*, *N. wuttkei*, and *N. sp. Corunna* (D.E.Symon 17088). Other molecular phylogenies with only minimal sampling of the *Suaveolentes* include: Olmstead *et al.* 2008, three taxa; Komarnitsky *et al.* 1998, eight taxa but minimal

Taxa	Name history	A	B	C
<i>N. africana</i> Merxm.	current		Y	Y
<i>N. amplexicaulis</i> N.T.Burb.	current	Y	Y	Y
<i>N. benthamiana</i> Domin	current	Y	Y	
<i>N. burbidgeae</i> Symon	current			
<i>N. cavicola</i> N.T. Burb	current	Y	Y	Y
<i>N. debneyi</i> Domin	current - syn. <i>N. forsteri</i> Roem. & Schult.	Y	Y	Y
<i>N. excelsior</i> (J.M.Black) J.M.Black	current		Y	
<i>N. fatuhivensis</i> F.Br.	current			
<i>N. fragrans</i> Hook.	current	Y	Y	
<i>N. goodspeedii</i> H.-M.Wheeler	current		Y	Y
<i>N. gossei</i> Domin	current	Y	Y	Y
<i>N. heterantha</i> Symon & Kenneally	current			
<i>N. maritima</i> H.-M.Wheeler	current		Y	Y
<i>N. megalosiphon</i> Van Heurck & Mull.Arg. subsp. <i>megalosiphon</i>	current	Y	Y	Y
<i>N. megalosiphon</i> Van Heurck & Mull.Arg. subsp. <i>sessifolia</i> P.Horton	current			
<i>N. monoschizocarpa</i> (P.Horton) Symon & Lepschi	current			
<i>N. occidentalis</i> H.-M.Wheeler subsp. <i>hesperis</i> (N.T.Burb.) P.Horton	current		Y	
<i>N. occidentalis</i> H.-M.Wheeler subsp. <i>obliqua</i> N.T.Burb.	current			
<i>N. occidentalis</i> H.-M.Wheeler subsp. <i>occidentalis</i>	current		Y	Y
<i>N. rosulata</i> (S.Moore) Domin subsp. <i>ingulba</i> (J.M.Black) P.Horton	current		Y	
<i>N. rosulata</i> (S.Moore) Domin subsp. <i>rosulata</i>	current		Y	
<i>N. rotundifolia</i> Lindl.	current		Y	Y
<i>N. simulans</i> N.T.Burb	current	Y	Y	
<i>N. suaveolens</i> Lehm.	current		Y	Y
<i>N. truncata</i> Symon	current			
<i>N. umbratica</i> N.T.Burb.	current	Y	Y	
<i>N. velutina</i> H.-M.Wheeler	current		Y	Y
<i>N. wuttkei</i> J.R.Clarkson & Symon	current			
<i>N. sp. Corunna</i> (D.E.Symon 17088)	unpublished possible new species			
<i>N. eastii</i> Kostoff	invalid		Y	
<i>N. exigua</i> H.-M.Wheeler	not current – syn. <i>N. suaveolens</i>	Y	Y	Y
Totals	29 current taxa, one possible new species	10	22	13

of calyx tube; corolla limb width; capsule length and width; leaf length and width; petiole length and width of winged petiole and basal auricles. Note was also made of leaf tip and base shape, corolla lobe shape, and seed shape and ornamentation.

Is *N. forsteri* (New Caledonia) the same as *N. debneyi* (in Australia) or *N. fragrans* (New Caledonia)?

Several authors have argued that *N. forsteri* and *N. debneyi* are synonymous (Wheeler 1935; Goodspeed 1954; Green 1994), however, Heine (1976) synonymised *N. forsteri* with *N. fragrans*. The specimens of these three species have been examined and are summarised in Table 2. Photographs of the specimens are shown in Figure 2.

From examination of these type specimens it appears most likely that *N. forsteri* and *N. debneyi* are synonymous and *N. fragrans* is a distinct entity. There are four key characters:

1) *N. fragrans* has a distinct caudex, or woody perennial base. The base of the stem and roots of *N. forsteri* and *N. debneyi* are not shown, but from the stems that are present it seems unlikely that they are woody at the base. Other authoritatively determined specimens and plants of *N. debneyi* that I have seen do not form a caudex.

The woody caudex is an adaptation to a specialised ecological niche: for *N. fragrans*, this niche is fissures in seaside rocks. A photograph of *Nicotiana fragrans* growing in a littoral volcanic rockfield in New Caledonia is shown in Figure 3. From *Flore de la Nouvelle-Calédonie et Dépendances* (Heine 1976) it is clear that *N. fragrans* is only found on seaside rocks and cliffs, often of limestone composition, sometimes in the spray zone alongside other halophyte vegetation. In New Caledonia *N. debneyi* is found growing on sandy beaches, sedimentary sands, and in sandy ground just above the beach (Heine 1976).

2) Both the specimens of *N. forsteri* and *N. debneyi* have ovate to elliptic, subpetiolate, auriculate cauline leaves. This auriculate, stem-clasping character was a key part of both type descriptions and is clearly lacking in *N. fragrans*. The type specimen of *N. fragrans* has distinctly spatulate leaves with narrowly winged petioles as per Hooker's description.

3) *N. debneyi* and *N. forsteri* have smaller flowers than *N. fragrans*. The measurements taken from the *N. fragrans* specimen fit within Goodspeed's (1954) description of the corolla tube as 40–100 mm long, and the types of both *N. forsteri* and *N. debneyi* fit

within Goodspeed's description of *N. debneyi* as having a corolla tube 15–21 mm long.

4) The presence of ellipsoid-headed glandular hairs is an important character for defining taxa within *Suaveolentes*. *Nicotiana debneyi*, *N. forsteri*, *N. occidentalis* H.-M.Wheeler, *N. umbratica* N.T.Burb. and *N. cavicola* N.T.Burb. all have these distinctive hairs with dark, ellipsoid, multicellular glands. The fact that *N. forsteri* and *N. debneyi* have these hairs and the type of *N. fragrans* does not, is compelling evidence for the *N. forsteri* type to be associated with *N. debneyi*.

A survey of the taxonomic literature reveals marked similarities between descriptions of *N. debneyi* based predominantly on Australian specimens (Wheeler 1935; Goodspeed 1954; Horton 1981; Purdie *et al.* 1982), with the *N. forsteri* description (Green 1994) based on Lord Howe Island specimens, and the *N. debneyi* description (Heine 1976) based on New Caledonian specimens (Table 3). There is also concordance of key traits such as corolla tube length between the descriptions of *N. fragrans* by Wheeler (1935), Goodspeed (1954) and Heine (1976) based on New Caledonian only or New Caledonian and Tongan collections (Table 4). All descriptions of *N. debneyi/forsteri* note the auriculate bases of the cauline leaves, a feature which is not found in any descriptions of *N. fragrans*. Heine (1976), Green (1994) and Goodspeed (1954) also note the unusual (for the section) pink or purple flushing of the corolla tube in *N. debneyi/forsteri*, which has been observed by the author for Australian plants, and which has never been documented for *N. fragrans*. The corolla limb lobes are held diagonally in *N. debneyi/forsteri*, with upper lobes flaring back towards the tube and the lower larger lobes projected forwards. In *N. fragrans* the corolla lobes are equal and actinomorphically spreading. This character is impossible to judge from herbarium specimens but various authors have described or illustrated this feature (Tables 3 and 4). *N. fragrans* has leaves clustered at the apex of the caudex and at the base of each scape, whereas *N. debneyi/forsteri* has some radical and some cauline leaves. These descriptions add further weight to the argument for synonymy of *N. debneyi* and *N. forsteri* and the separation of *N. fragrans*.

Was *N. forsteri* validly published and should the name take precedence over *N. debneyi*?

The name *N. debneyi* has until recently been

Table 2. Observations and measurements of three *Nicotiana* specimens. The specimens are: *Nicotiana debneyi* Domin (J. Dallachy, Rockingham Bay, Queensland, K), *N. forsteri* Roem. & Schult. (J.R. & G. Forster, Botany Isle (Île Améré), New Caledonia, BM) and *N. fragrans* Hook. (J. McGillivray, Isle of Pines, New Caledonia, K). The type of *N. fragrans* (Milne, x.1853, Isle of Pines, New Caledonia, K) has damaged flowers so another specimen from the same voyage and locality was

Character	<i>N. debneyi</i> type	<i>N. forsteri</i> type	<i>N. fragrans</i>
Caudex present	Not shown, unlikely	Not shown, unlikely	Yes
Ellipsoid headed hairs	Yes	Yes	No
Hair density	Stems moderately hairy at top, sparse at base.	Stems pubescent to base, leaves medium-dense covering of short eglandular or glandular hairs.	Very dense pubescence of long, tangled, white eglandular hairs
Inflorescence	Leafless, many branched.	Leafless, many-branched, stems long and wiry, erect.	Leafless, many branched.
Petioles	Wide wings	Wide wings	Narrow wings
Leaf bases	Broadly auriculate and stem-clasping	Broadly auriculate and stem-clasping	Simple (not auriculate)
Mature leaf length (mm)	220–224	85–150	68–80
Mature leaf width (mm)	69–98	35–70	33–39
Petiole length (mm)	Could not separate	20–50	52–90
Petiole width (mm)	Could not separate	6–10	2.5–3.7
Corolla lobes	unclear	Probably obtuse	Obtuse, slightly emarginate
Floral tube length (mm)	17–19	19–20	72–80
Floral tube width at throat (mm)	3.0	2.2–3.0	5.5–7.0
Floral tube width at calyx (mm)	1.2–1.5	2.0–2.2	2.0–3.0
Calyx length (mm)	5.5–7.0	6.0–7.0	13.0–19.0
Calyx width (mm)	3.0–6.0	2.5–4.5	4.5–6.0

commonly used for all Australian collections, based on Goodspeed (1954), Burbidge (1960) and Horton (1981). However, Green (1993) argued that the name *N. forsteri* had been validly published. He considered the two taxa to be synonymous and because *N. forsteri* was the earlier publication, it had priority (Green 1993, 1994). This position to sink *N. debneyi* was supported by Nicolson and Fosberg (2004) but has not been widely accepted. *Nicotiana debneyi*, not *N. forsteri*, was used in the most recent sectional classification (Knapp *et al.* 2004) and in the *Flora of Australia* account (Purdie *et al.* 1982). The Australian Plant Census (Orchard 2006) retains *N. debneyi* based mainly on the strength of recommendation of Dr Sandra Knapp (BM) who 'doubts that the two taxa are indeed the same, and has reservations about the publication of *N. forsteri*'.

So was *N. forsteri* validly published? Roemer and Schultes (1819) list 22 species in the genus *Nicotiana* in Section a. — 'caule arborescente vel fruticoso' or b.

—'caule herbaceo'; under the heading 'Dubiae' they list four more species including *N. forsteri*. Neville Walsh (MEL, pers. comm.) advises that this 'doubtful' heading more likely refers to doubt about placement in Sections a or b, rather than it being a doubtful species. The short description is as follows:

23. *N. forsteri*; foliis lanceolatis subpetiolatis amplexicaulibus, floribus acutis, caule frutescente. *N. fruticosa* Forst. *Floral. Insul. Austr. Prodr. p.17. Lehm. Hist. Nicot. p. 51. Ipse Forster dubitat utrum sua eadem cum fruticosa Linn. Brown et Labillard. Silent. Videant possessores Herbarii Forsteriani.*

(English translation by N. Walsh) *N. forsteri*. with leaves lanceolate, subpetiolate (petiole not fully differentiated from lamina), stem-clasping, flowers acute (probably refers to corolla limb lobes), stem shrubby. Forster himself doubts if it is the same as *fruticosa* L. Brown and Labillardière make no comment. They may have seen the Forster herbarium specimens.

Table 3. Comparison of various authors treatments of *Nicotiana debneyi* and *N. forsteri* based on specimens from mainland Australia, Lord Howe Island and New Caledonia. Attributes important for distinguishing *N. forsteri* and *N. fragrans* (Table 4) are shown.

Author	Wheeler 1935	Goodspeed 1954	Heine 1976	Horton 1981	Purdie et al. 1982	Green 1994
Taxon name	<i>N. debneyi</i>	<i>N. debneyi</i>	<i>N. debneyi</i>	<i>N. debneyi</i> ssp. <i>debneyi</i>	<i>N. debneyi</i> ssp. <i>debneyi</i>	<i>N. forsteri</i>
Plant height	to more than 1m	0.5–1.2m	0.5–2.0m	to 0.9(–1.5)m	to 1.5m	to 1(–1.5)m
Caudex present?	—	no (annual)	no (illustration)	no (herb)	no (herb)	no (herb)
Corolla tube length (mm)	15–21	15–21	up to 20	(10–)14–20(–23)	10–25	10–25
Corolla tube width (mm)	2–2.5	2.5 at throat	approx 2.5	1.5–3.0 at top of calyx	1.5–3.0 at top of calyx	—
Corolla tube colour	frequently pink or purple tinged on outside	frequently pink or purple tinged on outer surface	white washed with pink or crimson on outside	—	—	dull purplish red to white
Corolla limb lobe shape	—	short, obtuse subentire or emarginate	broad	broad (often broader than long), obtuse (rarely slightly emarginate)	broad, obtuse	rounded to slightly emarginate
Corolla limb lobes held diagonally?	yes	yes	yes	—	—	—
Leaf length (cm)	23–35	15–35	15–35	(1.5–)3–17(–25)	up to 25	5–20
Some leaves auriculate & +/- stem clasping?	yes	yes	yes	yes	yes	yes
Total specimens cited	11	12	18	18 (total seen 126)	5	5
Mainland Australia	7	9	0	16	5	0
Lord Howe Island	1	1	0	1	0	5
New Caledonia	3	2	18	1	0	0

The type specimen of *N. forsteri* was collected by Forster on Île Améré, or Botany Isle, a tiny islet lying between Grande Terre and the Isle of Pines. Forster referred this type collection, with doubt, to *N. fruticosa* L. (syn. *N. tabacum* L.) in *Florulae insularum Australium prodromus*. (1797, p. 17). Goodspeed (1954) reads Roemer and Schultes as renaming the plant *N. forsteri* 'but again gave the description of *N. fruticosa*, which Forster had taken from Linnaeus'. However, Green (1993) argues that was an intentional description and Neville Walsh (pers. comm.) also supports this view.

From the examination of type specimens (Fig. 2) and the measurements and comparisons made (Table

2) it is reasonable to assert that *N. debneyi* and *N. forsteri* are the same taxon. Given that *N. forsteri* seems to be validly published, and that *N. debneyi* and *N. forsteri* are synonymous, the logical conclusion is that *N. forsteri* is the current, valid name for Australian and New Caledonian plants.

Is *N. fatuhivensis* different from *N. fragrans*? Should *N. fatuhivensis* be a species or a variety of *N. fragrans*?

Nicotiana fatuhivensis is one of the least known, least collected species of *Nicotiana*. It has never been included in molecular analyses (Table 1). The main herbaria with specimens of *N. fatuhivensis* are the National Tropical Botanical Gardens, Kalaheo, Hawaii

Table 4. Comparison of various authors' treatments of *Nicotiana fragrans* based on specimens from New Caledonia and the Kingdom of Tonga. Attributes important for distinguishing *N. forsteri* (Table 3) and *N.*

Author	Wheeler 1935	Goodspeed 1954	Heine 1976
Taxon name	<i>N. fragrans</i>	<i>N. fragrans</i> var. <i>fragrans</i>	<i>N. fragrans</i> var. <i>fragrans</i>
Plant height	to over 1m	0.2–1m	0.2–2.0
Caudex present?	no, but notes 'stout base' of Tongan specimen.	yes	yes
Corolla tube length (mm)	55–90	40–100	40–100
Corolla tube width (mm)	3–4	2–3	2–3
Corolla tube colour	—	greenish white	pure white
Corolla limb lobe shape	—	obtuse, slightly emarginate	rounded, slightly emarginate
Corolla limb lobes held diagonally?	—	no (as shown in illustration)	no (as shown in illustration)
Leaf length (cm)	to 15	7–20	up to 20
Some leaves auriculate & +/-stem clasping?	no	no	no
Total specimens cited	7	3	17
New Caledonia	6	2	17
Tonga	1	1	0

(PTBG), the Bishop Museum, Honolulu, Hawaii (BISH) and the Smithsonian Institution, Washington (US). There are no collections of this taxon at BM or in any Australian herbaria. The species was first described by Forest Buffen Harkness Brown (1873–1954) in 1935 and a specimen of *N. fatuhivensis* is shown in Figure 2.

Brown (1935) commented that *N. fatuhivensis* was allied to *N. cordifolia* Phil. of the Juan Fernandez Islands, off the coast of Chile. In 1954 Goodspeed transferred *N. fatuhivensis* to a variety of *N. fragrans* – *Nicotiana fragrans* var. *fatuhivensis* (F.Br.) Goodsp., and placed it within section *Suaveolentes*. It is clear from recent molecular evidence (Chase *et al.* 2003; Clarkson *et al.* 2004) that

N. cordifolia is closely related to the other six diploid ($n=12$) South American members of section *Paniculatae* Goodsp. as currently circumscribed (Knapp *et al.* 2004). *Nicotiana fatuhivensis* has never been sequenced, has no published chromosome number and was not included in the recent sectional classification of *Nicotiana* (Knapp *et al.* 2004). No seeds of *N. fatuhivensis* are currently stored at the Millenium Seed Bank, United Kingdom, in the United States Department of Agriculture's National Plant Germplasm System or the Australian Plant Genetic Resources Information System. Based on the limited morphological evidence available *N. fatuhivensis* is treated here as a member of section *Suaveolentes*. Further cytological, molecular and morphological investigation would be highly desirable.

Table 5 summarises a *N. fatuhivensis* specimen at Kew Botanic Gardens (*P.A. Schäfer 5705* 19.viii.1975) in comparison with *N. fragrans*. Unfortunately the type specimen at the Bishop Museum, Hawaii (BISH) has not been seen. A photograph, habitat and an additional herbarium specimen of *N. fragrans* are shown in Figure 3.

The main differences between the specimens are:

1) Location of the leaves. *Nicotiana fragrans* rarely branches and leaves are clustered around the caudex, whereas *N. fatuhivensis* often branches and leaves are clustered at the ends of branches.

2) Leaf shape. *Nicotiana fragrans* has distinctly spatulate or occasionally oblanceolate leaves whereas *N. fatuhivensis* has broadly elliptic leaves.

3) Corolla. The corolla lobes of *N. fragrans* are rounded and obtuse or slightly emarginate, whereas the corolla lobes of *N. fatuhivensis* are mostly acuminate or sometimes acute. The corolla tube of *N. fatuhivensis* is also more slender than *N. fragrans*, especially at the calyx end.

4) Indumentum. *N. fatuhivensis* has ellipsoid glandular hairs whereas *N. fragrans* does not. Leaves and stems of *N. fragrans* are densely covered in long, white, tangled eglandular hairs, whereas leaves and stems of *N. fatuhivensis* are sparsely pubescent to glabrous.

The main similarities between these two taxa are their perennial habit and woody caudex, long corolla tube (compared to other *Suaveolentes*) and occurrence in the South Pacific region. In New Caledonia, *N. fragrans* Hook. is reported to grow on calcareous cliffs (Morat *et al.* 2001), and in a seaside halophytic environment (Jaffré *et al.* 2001) (illustrated in

Table 5. Observations and measurements of *Nicotiana fragrans* and *N. fatuhivensis*. Specimens used: *N. fragrans* Hook. (J. McGillivray, x.1853, Isle of Pines, New Caledonia, K), and *N. fatuhivensis* F.Br. (P.A. Schäfer 5705, 19.viii.1975, Mohotani Island, K).

Character	<i>N. fragrans</i>	<i>N. fatuhivensis</i>
Caudex present	Yes	Yes
Leaf arrangement	Clustered at apex of caudex	Clustered at ends of branches
Ellipsoid headed hairs	No	Yes
Hairs	Flowers, stems and leaves - very dense pubescence of long, tangled, white eglandular hairs.	Corolla and calyx – dense covering of ellipsoid headed glandular hairs. Stems and leaves very sparsely pubescent to glabrous.
Petioles	Narrow wings	No wings
Leaf bases	Simple (not auriculate)	Simple (not auriculate)
Mature leaf length (mm)	68–80	76–95
Mature leaf width (mm)	33–39	40–51
Petiole length (mm)	52–90	20–29
Petiole width (mm)	2.5–3.7	
Corolla lobes	Obtuse, slightly emarginate	Acute, acuminate
Floral tube length (mm)	72–80	62–81
Corolla limb length (mm)	13–17	14
Floral tube width at throat (mm)	5.5–7.0	3.0–6.0
Floral tube width at calyx (mm)	2.0–3.0	1.5–2.0
Calyx length (mm)	13–19	14–16
Calyx width (mm)	4.5–6.0	5.0–7.5

Fig. 3). *Nicotiana fatuhivensis* has been mostly collected from sea cliffs, but also from inland cliff environments (Wagner & Lorence 2008).

These two taxa are morphologically distinctly different. The Smithsonian Institution's *Flora of the Marquesas* project lists *N. fatuhivensis* as a Marquesan endemic species (Wagner & Lorence 2008). It is concluded from

these data that *N. fatuhivensis* should be treated as a separate species and not as a variety of *N. fragrans*.

Conclusions

There are three distinct taxa of *Nicotiana* in the South Pacific:

N. forsteri Roem. & Schult.

Synonym: *N. debneyi* Domin

Distribution: Eastern Australia (New South Wales, Queensland), Lord Howe Island (Australian territory), New Caledonia (Grande Terre, Loyalty Islands also recorded on Île Améré (Botany Isle)).

Note: Nicolson and Fosberg (2004) list Norfolk Island but there is no other evidence that it has ever been found there. Orchard (2006) in the *Australian Plant Census* lists *N. debneyi* as naturalised on Lord Howe Island, however this is an error. It is listed as a native species by Green (1993, 1994) and Rodd and Pickard (1983).

N. fragrans Hook.

Distribution: New Caledonia (recorded on the Isle of Pines, Loyalty Islands and Grande Terre) and the Kingdom of Tonga (Island of Tongatapu).

N. fatuhivensis F.Br.

Distribution: Marquesas Islands (recorded on eight of the twelve islands including Fatu Hiva, Moho Tani, and Tahuata).

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Figure 3. *Nicotiana fragrans* Hook. a. *N. fragrans* growing wild in fissures in a beachside rock, Grande Terre, New Caledonia (photo P.Y. Ladiges). b. Beachside habitat of (a) (photo P.Y. Ladiges). c. *N. fragrans*, Y. Pillon 441, 15.vii.2006, Dranin, Maré, Nouvelle-Calédonie, calcareous cliff (NOU) —the woody caudex is clearly shown. d. close view of flowers

Specimens examined

Nicotiana fatuhivensis: MARQUESAS ISLANDS. Mohotani Island, Partie méridionale, près du sommet de l'île. P.A. Schäfer 5705, 19.viii.1975 (K); Mohotani Island, Versant oriental dans la partie centrale, P.A. Schäfer 5340, 18.iii.1975 (K); Fatu Iva Island, Ouia, lieu-dit Ahoana, P.A. Schäfer 5828, 22.ix.1975 (K); Tahuata Island, Sentier de Hanateio à Hapatoni, lieu-dat Fae Namou au S du col., P.A. Schäfer 5994, 26.xi.1975 (K).

Nicotiana forsteri: **AUSTRALIA**. Rockingham Bay, Queensland, *Dallachy*, 1868 (K). **LORD HOWE ISLAND**. Lord Howe Island, *Capt. J.D. McCornish* 55, 1936 (K); South-east lower slopes of Malabar, *P.S.Green* 1545, 11.xi.1963 (K); West foot of Mt Lidgebird, *I.R. Telford* 7089, 23.x.1978 (CBG 7809873). **NEW CALEDONIA**. Plant cultivée à Nouméa, *M.G. Baumann-Bodenheim* 16051, 10.i.1952 (NY); New Caledonia, *I. Franc* 806, (NY); Nouvelle Calédonie, *M. Pancher*, 1870 (K); Botany Isle, New Caledonia, *J.R. & G. Forster*, 29–30.ix.1774 (BM).

Nicotiana fragrans: **NEW CALEDONIA**. Isle of Pines; seaside forest near Kuto, *Gordon McPherson* 5998, 17.xi. 1983 (MO); Atoll von Ouvéa, *A.U. Däniker* 2210, 27.ix.1925 (K); Isle of Pines, rocks by seashore, *John Mc Gillivray* 859, x.1853 (K); Isle Of Pines, New Caledonia, *Milne*, x.1953 (K). **TONGA**. Tongatapu, Fangaveha on the southern coast of the island, *T.G. Yuncker* 16252, 7.vi.1953 (NY, BM); Tus. Tongatabu. Au von der Brandung benetzten Felsen der Südküste, selsen. *Luerssen* 3/80 *Graeffe leg.* 1360 (K); Tongatapu, Keleti beach on the west coast of the island, *Art Whistler* 6540, 28.vii.1988 (BM).

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