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RESEARCH ARTICLE

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Overlap of eastern and western mangroves in the South-western Pacific: hybridization of all three *Rhizophora* (*Rhizophoraceae*) combinations in New Caledonia

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Key words

hybrids
New Caledonia
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taxonomy

Abstract A recent survey of mangroves in New Caledonia located 7 taxa of the genus *Rhizophora* – with 6 co-existing in one estuary. This is arguably the greatest concentration of co-occurring *Rhizophora* taxa anywhere. Two are well-known mangrove species of the Indo West Pacific, *R. stylosa* and *R. apiculata*, and another, *R. samoensis* resembles the widespread Atlantic East Pacific species, *R. mangle*. The other four are hybrid intermediates, *R.* × *lamarckii* (= *R. stylosa* × *R. apiculata*), *R.* × *selala* (= *R. stylosa* × *R. samoensis*), and two previously undescribed combinations, *R.* × *tomlinsonii* (*R. apiculata* × *R. samoensis*) and *R. samoensis* var. *neocaledonica* (= *R. samoensis* × *R.* × *selala)*. The new entities are unknown elsewhere. While *R.* × *tomlinsonii* is considered endemic to New Caledonia, *R. samoensis* var. *neocaledonica* may occur elsewhere based on the co-distribution of putative parental taxa. All seven *Rhizophora* are described with new observations on their morphology and ecology, distribution maps, plus a revised key for the region.

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INTRODUCTION

The genus *Rhizophora* L., with their distinctive stilt roots, commonly characterize intertidal mangrove habitat throughout tropical coastal areas worldwide (Tomlinson 1986). In the Indo-West Pacific, taxa of this genus are distributed (Fig. 1) from the east coast of Africa, through Asia to the north western Pacific through Micronesia to the Marshall Islands, and south to northern Australia extending east in the southern Pacific from New Caledonia to Samoa (Guppy 1906, Salvoza 1936, Hou 1958, Tomlinson 1986, Duke 2006a). Seven taxa have been recognised in the region (Duke 2006a) including four species, *R. apiculata* Blume, *R. mucronata* Lam., *R. samoensis* (Hochr.) Salvoza and *R. stylosa* Griff., plus three putative hybrid intermediates (Tomlinson 1986, Kathiresan 1995), *R.* × *annamalayana* Kathiresan, *R.* × *lamarckii* Montrouz. and *R.* × *selala* (Salvoza) Toml.

While the hybrid status of such intermediates was proposed based on morphological intermediacy and a lack of viable propagules (summarised by Tomlinson 1986), these have been affirmed for two with molecular assessments in relatively recent decades. Assessments include: Parani et al. (1997) for *R.* × *annamalayana* (= *R. apiculata* × *R. mucronata*); and Lo (2003) in Zhou et al. (2008) for *R.* × *lamarckii* (= *R. apiculata* × *R. stylosa*). The determination of hybrid status of *R.* × *selala* (= *R. samoensis* × *R. stylosa*) is based solely on the intermediate morphological and reproductive characters (Tomlinson 1978).

Rhizophora mucronata and *R. stylosa* are further considered closely-related (= sibling) species (some in fact consider *R. stylosa* to be a variety of *R. mucronata* var. *stylosa* (Griff.) Salvoza). While quite similar, they are morphologically distinct, based on style length, supported by other inflorescence characters. In addition, the entities commonly occupy different salinity conditions in the eastern part of their ranges (Duke & Bunt 1979). While their ranges overlap (Duke 2006a, b), they extend with characteristic bias west and east in the Indo West Pacific region (see Fig. 1). The range of *R. mucronata* is widest, extending from eastern Africa where it occurs as the only member of the genus, to the western Pacific where it overlaps with all other Indo West Pacific species. By contrast, *R. stylosa* extends exclusively eastward, notably into the south-western Pacific. While *R. apiculata* dominates mangroves of the Southeast Asian region, it also extends further east in the southern Pacific than *R. mucronata*, but otherwise, its range mostly fits within the ranges of other Indo West Pacific *Rhizophora*.

Hybrid taxa have distributions in keeping with their status. As such, they are usually located wherever the ranges of their putative parents overlap. Records of hybrid distributions confirmed by the author show *R.* × *lamarckii* (the best known of all hybrid intermediates of the genus) to be widespread in the western Pacific extending to New Caledonia, while *R.* × *annamalayana* (Parani et al. 1997) has been found only in India and Sri Lanka along the western limits of *R. apiculata* (Fig. 1). However, past distributional records for these taxa are largely unreliable since such hybrid taxa are poorly described and their diagnostic morphological characters incompletely defined.

The south-western Pacific region is further distinguished by two notable features for the genus. One is the disjunct and outlying occurrence of *R. samoensis*. This entity is difficult to distinguish from the common Atlantic East Pacific taxon, *R. mangle* L. (Tomlinson 1986, Duke & Allen 2006). These taxa are thought to be closely-related species, comparable in this respect to the relationship between *R. mucronata* and *R. stylosa*. The other notable feature of the south western Pacific region is the occurrence of two widely acknowledged hybrid intermediate taxa.

One of these hybrids is the widely occurring *R.* × *lamarckii*, the other is *R.* × *selala*, the intermediate of *R. stylosa* and *R. samoensis* which co-occur also in New Caledonia. Its

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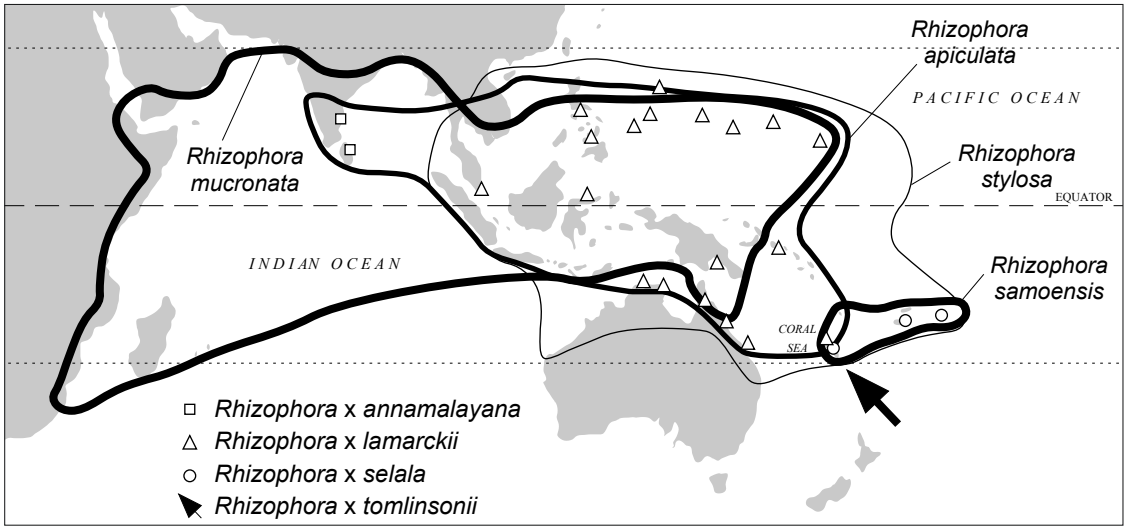

Fig. 1 The Indo West Pacific distribution of *Rhizophora* taxa of four species (lines) and three widespread hybrid intermediates (symbols). *Rhizophora* × *tomlinsonii*, only in New Caledonia, indicated by the arrow.

range is correspondingly recorded only in New Caledonia and Fiji (Tomlinson 1978, Smith 1981), although its distribution is expected in Vanuatu, Tonga and Samoa where both parental ranges extend – albeit that *R. stylosa* is rare in the latter locations (Smith 1981). As with the other two hybrids, this intermediate was also considered a distinct entity based on its consistent morphological and ecological characteristics across its range (Tomlinson 1978).

Within this region of overlap, New Caledonian mangroves were described as having five *Rhizophora* entities (Tomlinson 1986, Ellison 1995, Munzinger & Lebigre 2005). These included three species, *R. apiculata*, *R. samoensis* and *R. stylosa*, and two hybrid intermediates, *R.* × *lamarckii* and *R.* × *selala*. The current treatment adds two further *Rhizophora* taxa: one is a new intermediate combination, *R. apiculata* × *R. samoensis*, named *R.* × *tomlinsonii*, with stands in five separate estuaries; and the other is a single tree, being a likely combination of *R. samoensis* and *R. selala*, named *R. samoensis* var. *neocaledonica*. Since these *Rhizophora* taxa are difficult to distinguish, all seven observed in New Caledonia are described along with distribution maps, ecological notes, a revised diagnostic key, and detailed assessment of morphological characters.

METHODS

Study sites

During November–December 2006, mangrove species occurrences were recorded at 37 locations and 131 sites around Grande Terre, the main island of New Caledonia (Fig. 2, Table 1). Site access was achieved using a combination of road plus small boat transport to gain access to the extensive range of tidal reaches of rivers, estuaries and bays. Aerial photographs and detailed maps permitted accurate navigation and site identification in conjunction with position coordinates using portable GPS.

Plant collections, observations and measurements

Plant collections were made of all *Rhizophora* taxa encountered from the range of sites visited. Field observations were made on 29 specimens, 8 of which were vouchered with a collection deposited in the herbarium of the Botany and Applied Ecology Department (Laboratoire de Botanique et d'Ecologie Appliquées), Centre IRD de Nouméa (Institut de Recherche pour le Développement), Nouméa, New Caledonia (NOU)

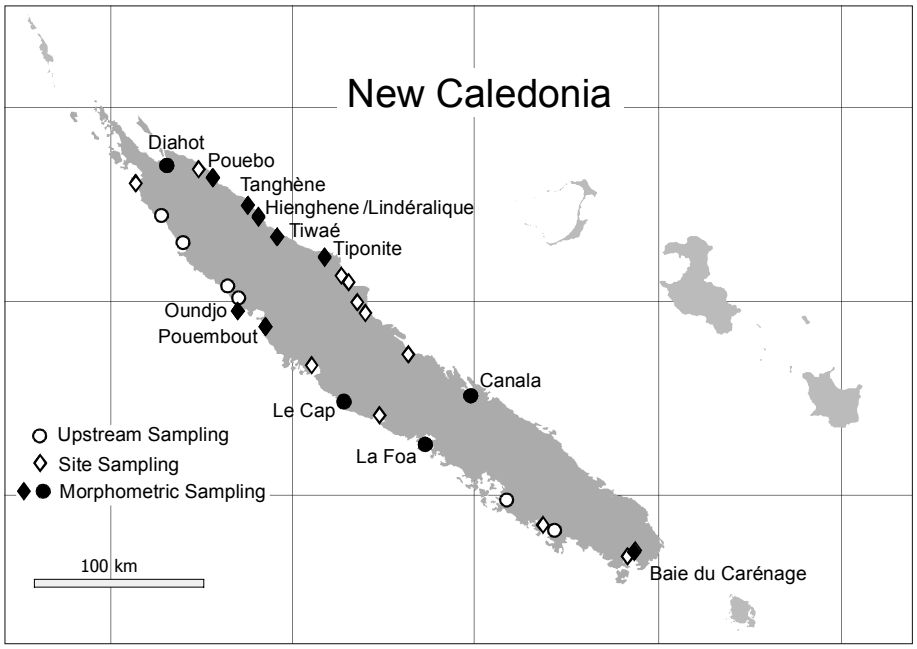

Fig. 2 Locations of field observations and morphometric collections in New Caledonia (also see Table 2).

(see Table 2). Where possible collections for each specimen included all available diagnostic material from individual trees, including: intact leafy shoots with both mature flower buds and attached mature hypocotyls. Based on this range of material, up to 86 attributes were observed, measured and recorded for each specimen, depending on the range of diagnostic material available. For example, only 58 attributes were scored for hybrid intermediates since they lacked mature hypocotyls. All measurements and observations were made from fresh material. The morphological measures and observations (see Table 3) were developed and standardised during prior assessments of this genus (e.g., Duke & Bunt 1979, Duke 2006a, Duke & Allen 2006).

Prior to classificatory analyses 21 characters from leaves, inflorescences, mature flower buds and mature hypocotyls were considered diagnostic (Table 4) and these have been used in the key.

Classificatory analyses

A brief comparative classificatory evaluation was undertaken to reveal likely phylogenetic relationships between the entities encountered. Classificatory analyses used 22 attributes of foliage, leaves and early reproductive parts since these attribute sets were complete (with no missing data) for all seven entities. Specimen data were averaged for each taxonomic entity. The same dataset was analysed using two standard classificatory techniques, including Principal Components Analysis (PCA) and Cluster Analysis using Primer-e software (www.primer-e.com). The Cluster Analysis was derived from the Bray Curtis Similarity Matrix of Untransformed Group Averages. Averaged data were taken and compiled in a data table. These untransformed data were analysed and presented in a PCA plot and cluster dendrogram from the similarity matrix of data.

Table 1 Locations (with latitude and longitude) of study sites around Grande Terre, New Caledonia, during November – December 2006. Asterisks (*) denote *Rhizophora* specimen collection sites (see Table 2, Fig. 2). Checklists of *Rhizophora* species were made at all sites, including additional upstream estuarine transects (in **bold**) showing respective distributions upstream from the mouth to upstream tidal limit (see Fig. 4).

Coast	Location/Site	Lat.	S	Long.	E	Mangrove Species Nos.
South	Baie du Carénage*	22	19.6	166	49.5	5
South	Corniche Sud	22	18.1	166	51.7	4
South	Boulari	22	18.1	166	51.7	11
West	**Dumbéa**	**22**	**10.5**	**166**	**26.0**	**12**
West	Ondémia	22	9.8	166	21.9	8
West	**South of Tontouta**	**22**	**1.9**	**166**	**9.8**	**14**
West	**La Foa***	**21**	**44.2**	**165**	**43.6**	**13**
West	Néra	21	36.1	165	28.9	11
West	**Le Cap***	**21**	**31.4**	**165**	**28.9**	**11**
West	Poya - Népou	21	20.6	165	6.7	7
West	Népoui	21	8.1	164	51.8	3
West	Pouembout*	21	8.4	164	51.4	10
West	**Témala**	**20**	**55.9**	**164**	**39.2**	**8**
West	**Voh**	**20**	**59.9**	**164**	**41.9**	**7**
West	Oundjo – Pinjane*	21	3.1	164	42.6	2
West	**Iouanga**	**20**	**42.4**	**164**	**22.6**	**10**
West	**Ouanac - Koumac**	**20**	**33.9**	**164**	**15.5**	**10**
West	Sud Néhoué	20	23.6	164	9.3	10
North	**Diahot***	**20**	**16.4**	**164**	**17.9**	**18**
East	Balade	20	18.3	164	30.1	10
East	Pouébo*	20	21.9	164	34.4	8
East	Colnett	20	30.5	164	45.8	6
East	Galarino	20	30.9	164	46.1	5
East	Tao	20	33.8	164	49.2	3
East	Tanghène*	20	40.8	164	55.5	10
East	Hienghene*	20	41.7	164	56.6	
East	Tiouandé - Maina	20	40.5	164	54.3	13
East	Lindéralique*	20	41.3	164	58.9	
East	Tiwaé*	20	46.8	165	10.6	15
East	Tiponite	20	46.7	165	11.2	3
East	Tiwaka	20	52.3	165	15.9	9
East	Amoa	20	55.0	165	18.3	1
East	Pwéeo	20	53.4	165	16.6	8
East	Tchamba	21	0.7	165	23.2	16
East	Houaïlou	21	16.7	165	38.1	7
East	**Canala***	**21**	**30.6**	**165**	**58.7**	**16**
East	Saint Jean Baptiste	21	30.7	165	58.1	8

Table 2 Specimens of *Rhizophora* species collected, photographed and examined for up to 86 morphometric characters each (Table 3). Collections were made in New Caledonia by N.C. Duke, S. Virly and C. Marchand from 21 November to 8 December 2006. Vouchers and type material were lodged with NOU as indicated.

Species	ID#	Herb.	Location/Site	Lat.	S	Long.	E	Collection date
R. apiculata	NC14		Diahot River estuary, downstream	20	17.8	164	18.0	2 Dec. 2006
	NC15		Diahot River estuary, upstream	20	21.1	164	22.2	2 Dec. 2006
	NC29	NOU	Canala River estuary	21	30.7	165	58.8	8 Dec. 2006
R. × *lamarckii*	NC12		Diahot River estuary	20	18.9	164	19.2	2 Dec. 2006
	NC13		Diahot River estuary, midway	20	19.6	164	19.6	2 Dec. 2006
	NC27		Linderalique	20	41.3	164	58.9	5 Dec. 2006
	NC33	NOU	Canala River estuary	21	30.7	165	58.6	8 Dec. 2006
R. stylosa	NC21		Diahot River estuary	20	19.3	164	19.3	4 Dec. 2006
	NC26		Pouébo	20	21.9	164	34.4	5 Dec. 2006
	NC11		Oundjo causeway	20	3.1	164	42.6	28 Nov. 2006
	NC32	NOU	Canala River estuary	21	30.7	165	58.8	8 Dec. 2006
	NC07		Le Cap River estuary	21	31.3	165	16.8	26 Nov. 2006
	NC06		La Foa River estuary	21	43.8	165	46.0	24 Nov. 2006
	NC01		Baie du Carénage	22	19.6	166	49.5	21 Nov. 2006
R. × *selala*	NC17		Diahot River estuary	20	18.9	164	19.2	2 Dec. 2006
	NC31	NOU	Canala River estuary	21	31.2	165	58.6	8 Dec. 2006
	NC08		Le Cap River estuary	21	31.5	165	16.6	26 Nov. 2006
	NC04		La Foa River estuary	21	43.8	165	46.0	24 Nov. 2006
	NC02		Baie du Carénage	22	19.6	166	49.5	21 Nov. 2006
R. samoensis	NC16		Diahot River estuary	20	19.6	164	19.6	2 Dec. 2006
	NC30	NOU	Canala River estuary	21	31.4	165	58.8	8 Dec. 2006
	NC09		Le Cap River estuary	21	31.3	165	16.8	26 Nov. 2006
	NC05		La Foa River estuary	21	43.8	165	46.0	24 Nov. 2006
	NC03		Baie du Carénage	22	19.6	166	49.5	21 Nov. 2006
R. samoensis var. *neocaledonica*	NC10		Pouembout River estuary	21	8.4	164	51.4	28 Nov. 2006
R. × *tomlinsonii*	NC22	NOU	Tanghène River estuary	20	40.8	164	55.0	5 Dec. 2006
	NC23		Hienghene	20	41.7	164	56.6	5 Dec. 2006
	NC24	NOU	Tiwaé River estuary	20	46.9	165	10.6	6 Dec. 2006
	NC28	NOU	Canala River estuary	21	31.2	165	58.6	8 Dec. 2006

Table 3 Listing of 86 measured and multistate characters of foliage, leaves, inflorescences, mature flower buds, mature fruit and mature hypocotyls used in classificatory analyses (modified from Duke & Bunt 1979, Duke 2006a).

Grouping (no.)	Characters
Foliage (4)	number of leaves in rosette; number of leaf scar nodes within leafy rosette; apical shoot length, colour green or red.
Leaves (15)	leaf length, width, ratio of length to width, shape length (length from widest width to petiole juncture), ratio of length to shape length, leaf shape; leaf upper surface colour dark or light green, under surface colour dark or light green, under surface cork warts visible or not; leaf apex acute or rounded; leaf tip mucro folded or spiked, length, width, ratio of length to width; petiole length.
Inflorescence (17)	hierarchical number of branch junctures, first juncture dichotomous or trichotomous; leaf stem node position at attachment beneath apical shoot of bud primordia, mature flower bud, mature fruit, mature hypocotyl; mature bud peduncle length, width, ratio of length to width; mature fruit peduncle length, width, ratio of length to width; mature flower bud bract (beneath calyx) length, width, ratio of length to width, shape bulbous corky or swollen smooth or smooth or slender smooth, colour brown or green or yellowish green.
Mature flower bud (25)	length, width, ratio of length to width, shape ellipsoid or rounded, cross section circular smooth or angular ribbed; calyx lobe number, length from suture to tip, length from corolla to tip, width at base, ratio of length to width, thickness; petal number, length, width, shape linear or lanceolate, margins glabrous or minutely hairy or woolly, hair length; style length from swollen ovary top to tip, length from corolla to tip, tip bilobed deeply to minutely; ratio of calyx lobe length to style length from ovary top to tip, width at base; stamen number, length, width.
Mature fruit (detached from mature hypocotyl) (14)	length, widest width, ratio of length to width, width of distil portion, shape cork-like or pear-shaped or drupe-like; calyx width across opposite lobe junctures, width from tip to tip; calyx lobe length, width, ratio of length to width; collar length, width at fruit juncture, widest width, diameter of abscission aperture.
Mature hypocotyl (11)	length, width at widest point, ratio of length to width, width at plumule end, width at narrowest point, shape length (length from widest width to distal end), ratio of length to shape length; distil tip rounded or blunt, colour green or brown; plumule length, width at base.

Table 4 Diagnostic morphological attributes, including ranges of key measured and multi-state characters, of the 7 *Rhizophora* taxa from New Caledonia, including a rare aberrant individual (*R. samoensis* var. *neocaledonica*). All measurements and observations were taken from fresh material. Missing components were absent in the field. Codes: N = number; L = length; W = width. Measures in mm. Also see Methods.

Component	Attribute	*R. apiculata*	*R.* × *lamarckii*	*R. stylosa*	*R.* × *selala*	*R. samoensis*	*R.* × *tomlinsonii*	*R. samoensis* var. *neocaledonica*
Leaves	Leaf shape	apiculate	apiculate	apic.-spathulate	apic.-spathlate	to spathulate	apiculate	apiculate
	Leaf apex	acute	acute	broadly acute	broad-round	blunt	acute	blunt
	Leaf mucro	spike	narrow spike	narrow spike	folded spike	folded lip	thick small spike	folded lip
Inflorescence	re: Leafy shoot	matures below	matures within	matures within	matures within	matures within	matures within	immature only
	Branching N	2	2	2	2–3	2–3	3	2–3
	Junctures N	1	1–2	1–5	2–4	1–4	1–2	2–4
	Bract condition	bulbous corky	swollen smooth	smooth	slender smooth	slender smooth	smooth	minute
Mature flower buds (closed)	Bud L	12.0–15.2	14.2–16.0	10.1–15.5	9.3–15.5	7.6–12.1	11.0–14.2	
	Bud L/W	1.4–1.5	1.5–2.0	1.9–2.0	1.9–2.2	1.7–2.1	1.7	
	Shape ×-section	rounded	rounded	rounded	slightly 4-sided	4-sided, round	4-sided, sl. ridges	
	Calyx lobe L/W	1.7–1.8	1.7–2.3	2.0–2.2	2.2–2.5	1.7–2.0	1.6–1.7	
	Lobe thickness	1.4–2.2	1.0–1.8	0.9–1.1	0.6–1.0	0.7–1.0	1.2–1.4	
	Petal ×-section	flat	curved	encl. stamen	encl. stamen	encl. stamen	curved	
	Petal margins	glabrous	finely hairy	v. wooly	v. wooly	wooly	minutely hairy	
	Petal hair L	0	1.0–2.0	1.8–3.5	1.2–2.2	0.6–1.2	0.4–0.5	
	Style L	1.1–1.6	3.0–4.5	2.2–3.9	2.1–2.8	1.4–2.2	1.4–2.0	
	Stamen N	10–12	8–19	6–9	8	8	11–18	
Mature hypocotyls	Expended fruit	cork-like L=W		inv. pear-like		drupe-like		
	Hypocotyl L	194–310		188–280		150–260		
	Distal colour	green		green		reddish brown		
	Distal shape	bluntly pointed		narrow pointed		pointed		

RESULTS

Recognition of taxa

Seven *Rhizophora* taxa were identified in New Caledonian mangroves: *R. apiculata*, *R.* × *lamarckii*, *R. stylosa*, *R.* × *selala*, *R. samoensis*, *R.* × *tomlinsonii*, and *R. samoensis* var. *neocaledonica*. The latter two are newly described intermediates. Each entity is described and their diagnostic attributes summarized in Table 4.

Four taxa were determined to be hybrid intermediates based on intermediacy of characters, lack of mature reproductive stages, and proximity in the field of relevant parent entities. Furthermore, individuals thus diagnosed as hybrids were frequently larger in stature and luxuriance compared with neighbouring parent trees. This expression of hybrid vigor was commonly observed as greater tree height, stem diameter, leaf density and leaf size. In each case, the diagnostic morphological characters were reliable determinants and consistent with the other criteria.

A unique, intermediate entity was determined from a single individual as the likely combination, *R. samoensis* × *R. selala*. In this case, the tree was not appreciably different in stature from neighbouring trees of *R. samoensis*, but the most notable and obvious feature was the presence of prolific immature inflorescences with numerous branching primordia rather than small immature flower buds. No more advanced reproductive components could be found. In addition, a lack of larger scars of advanced reproductive components along branch stems indicated that the tree rarely (over recent years) produced more advanced reproductive material.

Numerical analyses

Classificatory and numerical analyses were used to quantify and conceptualise likely phylogenetic relationships proposed

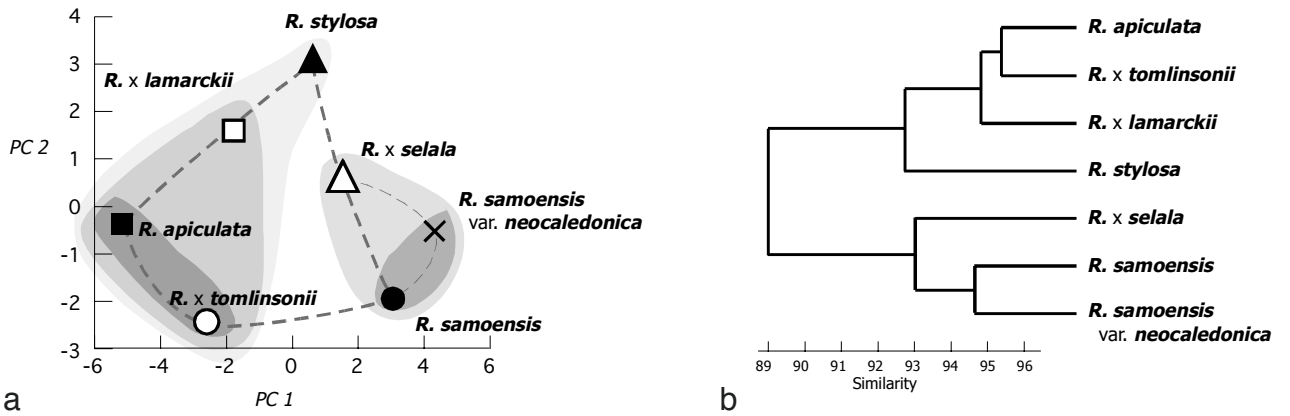

Fig. 3 a. PCA plot with cluster groupings shaded; and b. the cluster dendrogram; of the similarity matrix of averaged measures of foliage, leaves and early reproductive components showing putative phylogenetic affinities of seven New Caledonian *Rhizophora* taxa.

by determinations of hybrid status and putative parents (Fig. 3). The PCA plot accounted for 83.2 % of variation in eigenvalues. The seven entities were distributed roughly in a triangular arrangement – with the three key species, *R. stylosa*, *R. apiculata* and *R. samoensis* (solid symbols), at each triangle point, and the putative hybrids, *R.* × *lamarckii*, *R.* × *selala* and *R.* × *tomlinsonii* (open symbols), positioned between respective species pairs. *Rhizophora samoensis* var. *neocaledonica* was placed in an intermediate position between its putative parents. This finding was supported further in the cluster dendrogram where this combination grouped first with *R. samoensis* and then with *R.* × *selala*.

Distributional patterns and ecological influences

New Caledonian occurrences of the seven *Rhizophora* taxa are shown in Fig. 7, 10 and 14. Although individual species ranges vary, the genus is common and widespread, thriving in most, if not all, tidal wetland systems around the island. In each location visited, *Rhizophora* stands dominated estuarine margins that were also often backed by extensive, low thickets of hybrids in more arid regions. Ranges upstream in estuaries commonly reached the uppermost limit of tidal influence. The association of three taxa, namely *R. stylosa*, *R. samoensis* and *R.* × *selala*, was very common, being present in most estuarine locations visited. The proportional numbers in the field of these respective taxa was roughly 20 : 40 : 40, with each having different upstream ranges (Fig. 4). In this way, *R. stylosa* was common in downstream locations and more exposed marine settings, while *R. samoensis* was common in mid- to upstream locations reaching the upper tidal influence, and *R.* × *selala* occurred mostly in between in mid estuarine positions.

By contrast, *R. apiculata*, *R.* × *lamarckii* and *R.* × *tomlinsonii* were restricted to the wetter north-eastern part of Grande Terre (Fig. 7, 14). While *R. apiculata* was common within these estuaries, this species occurred mostly within midstream reaches (Fig. 4). *Rhizophora* × *lamarckii* and *R.* × *tomlinsonii* were also located in these midstream reaches but *R.* × *tomlinsonii* was relatively uncommon to rare, while *R.* × *lamarckii* was common. For instance, *R.* × *tomlinsonii* was not observed in the Diahot River estuary where both parents were present, although there were extensive stands of *R.* × *lamarckii*.

One riverine estuary, near Canala on the eastern coast (Fig. 2, Table 1), was the only location having six *Rhizophora* taxa present. Such an occurrence is unknown elsewhere in the world. Fig. 4 displays the distribution of each taxon on this location.

Rhizophora samoensis var. *neocaledonica* was recorded as a single individual tree in one site in the Pouembout River estuary (Fig. 2, Table 1). This tree was growing on the waters edge in a midstream reach of the estuary.

The regional and upstream distributional patterns of these taxa imply that salinity and rainfall are dominant ecological factors. While *R. stylosa* had a preference for marine salinities, *R. apiculata* and *R. samoensis* were more commonly associated with estuarine systems with more regular freshwater flows. In addition, the latter was found in areas of appreciably higher rainfall. It is more difficult to draw conclusions from the ranges of hybrid taxa since they are restricted to locations where both parents co-occur. However, their respective midstream distributional preferences suggest they also have individual salinity preferences.

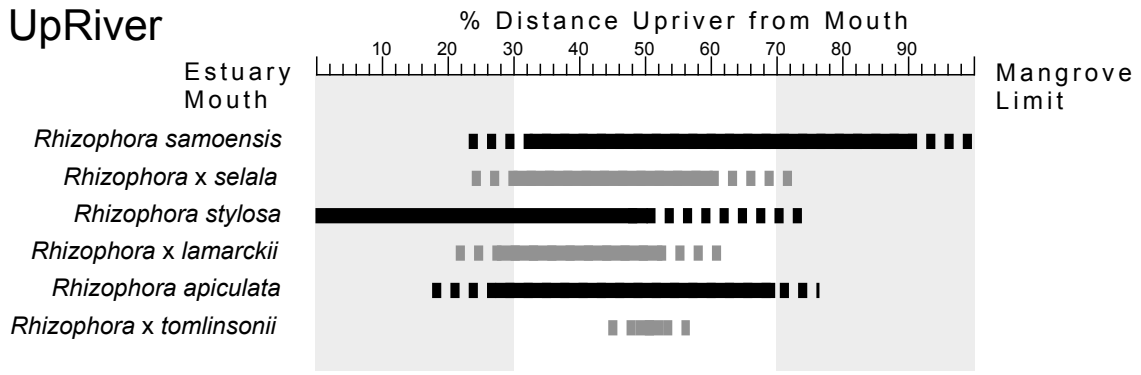

Fig. 4 Upriver distribution of six *Rhizophora* taxa, based on the Canala River (Fig. 2) along with other estuarine sites on Grande Terre, New Caledonia.

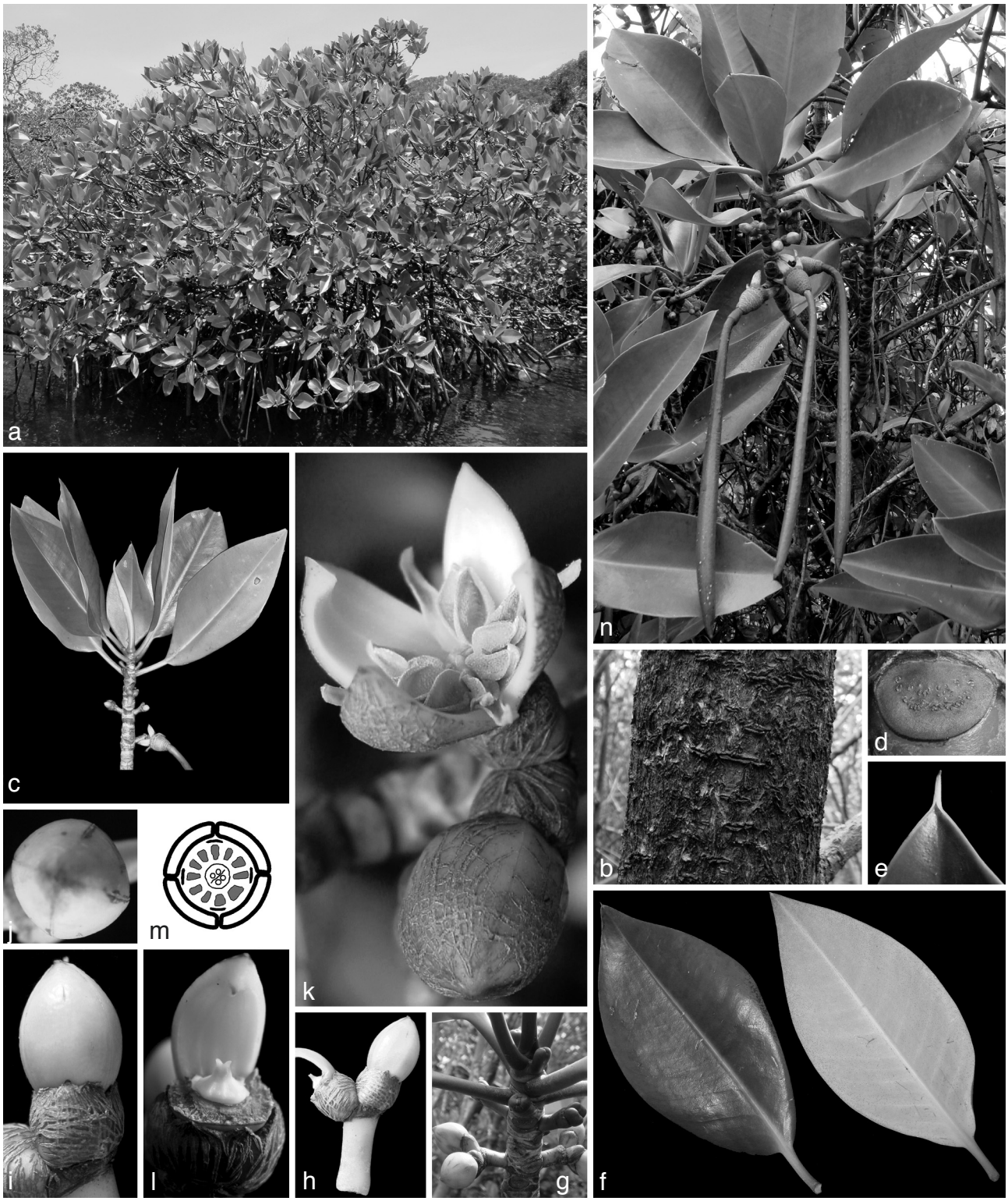

Fig. 5 *Rhizophora apiculata* Blume. a. Habit, Diahot River; b. bark; c. leafy rosette with mature flower buds and hypocotyl; d. leaf scar; e. leaf mucro; f. leaves; g. inflorescence in rosette; h. inflorescence; i. closed mature flower bud, side view; j. closed mature flower bud, end view; k. flower; l. style and single calyx lobe of mature flower bud; m. floral diagram; n. hypocotyls with mature flower buds below leafy rosette (c: *Duke*, *Virly & Marchand nc29*).

KEY TO NEW CALEDONIAN SPECIES AND HYBRIDS

1. Leaf mucronate tip prominent, erect, mature flower buds rounded, inflorescences always bifurcate (2-branching) at first juncture 2
1. Leaf mucronate tip not erect, mature flower buds often 4-angled, inflorescences bi- and trifurcate (3-branching) at first juncture 4
2. Mature flower buds and fruit within leaves in leafy shoot, bracts smooth green, petals with marginal hairs, style > 2 mm long, stamens mostly 8 (rarely 6–9) 3
2. Mature flower buds and fruit below leaves on leafy shoot, bracts corky brown, petals with no marginal hairs, style < 2 mm long, stamens 10–12 . . . . . 1. *R. apiculata*
3. Mature flower buds < 15 mm long, petal margins very hairy, petals fully enclosing stamens, calyx lobes < 1 mm thick, mature fruits and hypocotyls seasonally present . . . . . 3. *R. stylosa*
3. Mature flower buds > 15 mm long, petal margins minutely hairy, petals not enclosing stamens, calyx lobes > 1 mm thick, mature fruits and hypocotyls not present . . . . . 2. *R.* × *lamarckii*

4. Leaf apex acute, leaf mucronate tip folded with length equal to width, mature flower buds usually present, mature fruits and hypocotyls never present 5
4. Leaf apex blunt, leaf mucronate tip a broad fold with length much less than the width, mature flower buds, mature fruits and hypocotyls regularly present 6
5. Leaf apex broadly acute, mature flower buds smooth, stamens 8, style > 2 mm long, minutely bifurcate, petal margins woolly, calyx lobes < 1 mm thick . . . . . 4. *R.* × *selala*
5. Leaf apex sharply acute, mature flower buds with slight ribs at base of lobe sutures, stamens 11–18, style < 2 mm long, deeply bifurcate, petal margins minutely hairy, calyx lobes > 1 mm thick . . . . . 6. *R.* × *tomlinsonii*
6. Inflorescences immature to mature, bi- or trifurcate at first juncture, bifurcate at second, includes mature flower buds, fruits and/or hypocotyls, stamens 8 . . . . . 5. *R. samoensis*
6. Inflorescences always immature, trifurcate at first and second junctures, never with mature flower buds, fruits and hypocotyls, stamens absent 5a. *R. samoensis* var. *neocaledonica*

SPECIES DESCRIPTIONS

1. *Rhizophora apiculata* Blume — Fig. 5, 7, 14

Rhizophora apiculata Blume (1827) 91. — Type: "Crescit in maritimus Javae meridionalis."; Hou (1958) 452.
Rhizophora conjugata Arn. (non L.) (1838) 363.

Tree: multi-stemmed, sprawling to columnar, height to 20 m, stem to 450 mm diam (measured just above the highest established prop root), stem base diminished beneath prop root insertion. *Bark*: often crocodile-skin like, smooth blackish patches separated by pale greyish off-white pustular horizontal and vertical fissures, or grey roughly fissured. *Roots*: above ground props, sturdy at stem base, arching to 2 m, surface lenticels numerous; aerial roots often extend from upper limbs. *Foliage*: comprised of rosettes of paired leaves, c. 7 leaves, clustered at 2–5 leaf scar nodes around spicate apical shoot, terminal, prominent, 51–108 mm long, red-green, enclosed by paired lanceolate stipules. *Leaves*: petiole green, 17–31 mm long; lamina generally flat, elliptic rather than obovate, 99–201 by 47–105 mm, ratio of length to width c. 2.0, shape length (= length from widest width to petiole juncture) 44–94 mm, ratio of length to shape length c. 2.2, apex acute; upper surface shiny, dark green; lower surface dull, pale green with numerous small brown cork wart spots; mucronate tip prominent, spicate, 2.5–4.8 by 0.5–1.3 mm, ratio of length to width c. 4.0. *Inflorescence*: 2-flowered, branching bifurcate at single juncture, stout, maturing beneath leafy rosette; leaf scar nodes beneath apical shoot of mature flower buds 6–10, mature fruit 9–13, mature hypocotyls 11–14; peduncle 11–18 by 5–6 mm, ratio of length to width c. 2.8; bract beneath calyx bulbous, corky, heavily fissured, brown, 6–8 by 7–11 mm, ratio of length to width c. 0.8, margins brown, crenulate. *Mature flower bud*: robustly ellipsoidal, yellow-white, slight brown superficial fissures upon maturity, 12–15 by 8–11 mm, ratio of length to width c. 1.5; calyx lobes 4, 11–15 by 6–9 mm, c. 1.8 mm thick; apex bluntly pointed, cross-section circular smooth. Petals 4, creamy white, oblong, linear, 8–11 by c. 1.6 mm, glabrous, membranous, not hooded or involute, flat. Stamens 10–12, angular, pale brown, 8–9 by c. 2.8 mm. Style centrally placed on domed ovary, length from ovary top to tip 1.1–1.6 mm, length from corolla to tip 2.1–3.3 mm, ratio of calyx lobe length to style length from ovary top to tip c. 9.7, width at base 3.0–3.6 mm, tip bilobed, tinged orange or red. *Mature fruit*: cylindrical, tapered, stout, rough-textured, dimensions when detached from mature hypocotyl, 22–25 mm long, widest width 17–20 mm, ratio of length to width c. 1.3, width of distil portion 12–14 mm; cotyledon collar-like, exposed at hypocotyl maturity, shiny, pale yellow, 9–13 by 8–9 mm; calyx 15–17 mm wide, lobes angular, erect, thick, c. 16 by 9–10 mm, spread c. 38 mm wide. *Mature hypocotyl*: narrowly cylindrical, wider towards distil end, shiny, dark green, 194–310 by 13–14 mm at the widest point, ratio of length to width c. 19, width at plumule end 7–8 mm, shape length (= length from widest width to distal end) 49–55 mm, ratio of length to shape length c. 4.8, surface with raised brown lenticels, distil end rounded to blunt; plumule green, spicate, 17–22 mm long, width at base 4–5 mm. Specimens examined and vouchers are listed in Table 2.

Distribution — India, Sri Lanka across Asia south to northern Australia and the western Pacific to Kosrae in the north, and New Caledonia to Vanuatu in the southwest (Fig. 1). The southern-most occurrence on the Australian east coast is Port Clinton (22°35'S) (Duke 2006b). In New Caledonia, the species occurs in 10 of 35 locations surveyed on Grande Terre (Fig. 2) to Canala River in the south (21°31'S), including: Diahot, Balade, Colnett, Galarino, Tanghene, Tiouandé, Tiwaé, Pwéeo and Tchamba.

Habitat & Ecology — Common in mid intertidal zones of intermediate tidal reaches (Fig. 4) of rivers and streams in areas of higher rainfall. Taller forests noted in the middle tidal reaches and growing on mud substrate. Associated with *R. stylosa* and *Bruguiera gymnorhiza* (L.) Sav. in middle tidal reaches. In upstream locations, the species commonly occurs behind frontal low thickets of *R. samoensis.* Mature flower buds, flowers and some mature hypocotyls present in November and December. At similar latitudes in Australia, flowering peaks in April to June and hypocotyls mature mostly around February and March (Duke 2006b).

Etymology — Named for its apiculate leaf apices.

Note — Distinguished from congeners by: leaves with acute apices having spicate mucronate tips, inflorescences positioned mostly beneath lower leaves in leafy shoots, swollen corky bracts, large flower buds and glabrous flat petals (Duke & Bunt 1979, Tomlinson 1986). In the field, leaf colour, shape, size and erect orientation in foliage make trees distinguishable from other species. Identification has rarely been problematic, especially after early confusion regarding an erroneous alternate name, *R. conjugata*, synonymised in regional treatments like Hou (1958). Characters like the presence of cork warts on leaf undersurfaces, indicate that New Caledonian populations have a greater genetic affinity with Asiatic populations rather than with those across the Coral Sea in northern Australia.

2. *Rhizophora* × *lamarckii* Montrouz. — Fig. 6, 7

Rhizophora × *lamarckii* Montrouz. (1860) 201; Salvoza (1936) 179; Ding Hou (1978) 550 (= *R. stylosa* × *R. apiculata*).
Rhizophora conjugata Arn. (non L.) var. *lamarckii* (Montrouz.) Guillaumin (1914) 56.

Tree: multi-stemmed, sprawling to columnar tree, often emergent to 25 m, stem to 550 mm diam (measured just above the highest established prop root), stem base diminished beneath prop root insertion. *Bark*: light to dark grey, smooth to rough, sometimes crocodile-skin like, sometimes black, very coarse, friable. *Roots*: above ground props, sturdy at stem base, arching to 2.5 m, surface lenticels numerous; aerial roots from upper limbs sometimes prolific. *Foliage*: comprised of rosettes of paired leaves, c. 11 leaves, clustered at 3–9 leaf scar nodes around spicate apical shoot, terminal, prominent, 49–82 mm long, deep red-light green, enclosed by paired lanceolate stipules. *Leaves*: petiole green 16–30 mm long; lamina obovate to apiculate, sides curled down towards apex, 84–153 by 51–87 mm, ratio of length to width c. 1.8, shape length (= length from widest width to petiole juncture) 36–76 mm, ratio of length to shape length c. 2.1, apex acute; upper surfaces smooth, shiny, bright yellowish

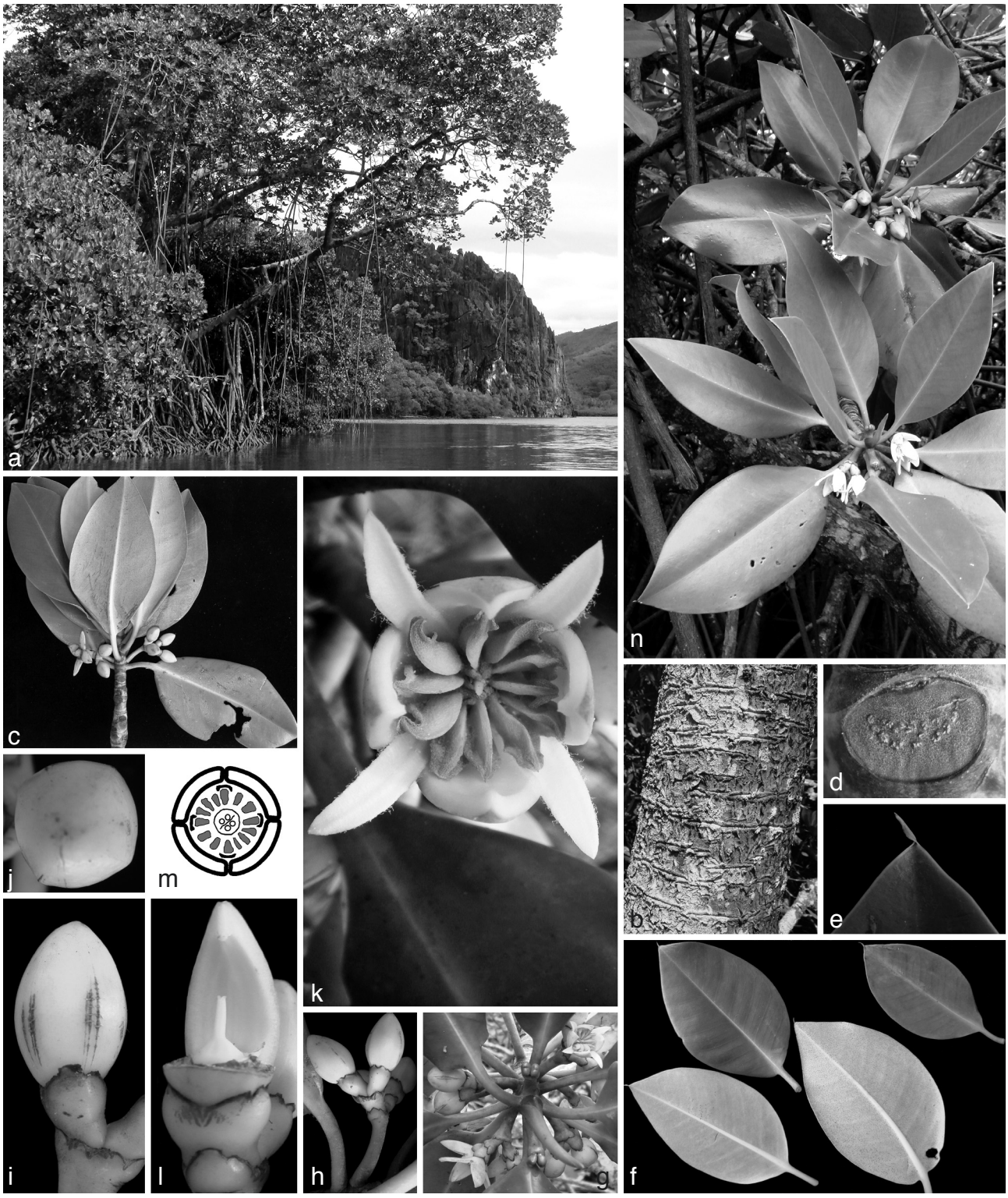

Fig. 6 *Rhizophora* × *lamarckii* Montrouz. a. Habit, Lindéralique; b. bark; c. leafy rosette with mature flower buds and immature fruit; d. leaf scar; e. leaf mucro; f. leaves; g. inflorescence in rosette; h. inflorescence; i. closed mature flower bud, side view; j. closed mature flower bud, end view; k. flower; l. style and single calyx lobe of mature flower bud; m. floral diagram; n. mature flower buds and flowers within leafy rosette (c: *Duke*, *Virly & Marchand nc33*).

green; lower surface dull, with numerous small brown cork wart spots; mucronate tip spicate, 3.2–5.2 by 0.6–0.8 mm, ratio of length to width c. 5.5. *Inflorescence*: 2–4-flowered, branching bifurcate at first juncture, stout, maturing within leafy rosette; leaf scar nodes beneath apical shoot of mature flower buds 3–5, not observed with mature fruits or hypocotyls; peduncle 15–24 by 4–5 mm, ratio of length to width c. 4.9; bract beneath calyx sturdy not bulbous, smooth, green, 6–7 by 7–8 mm, ratio of length to width c. 0.9, margins brown, crenulate. *Mature flower bud*: robustly ellipsoidal, smooth, yellow, 14–16 by 7–11 mm, ratio of length to width c. 1.7; calyx lobes (3 or) 4, 12–14 by 5–8 mm, c. 1.4 mm thick; apex rounded; cross-section circular smooth. Petals (3 or) 4, creamy white, linear to lanceolate, 7–11 by 2–3 mm, slightly tomentose margins, slightly involute, hooded to flat. Stamens 8–19, angular, brownish, c. 9.2 by c. 2.6 mm. Style terete, centrally placed on domed ovary, length from ovary top to tip 3.0–4.5 mm, length from corolla to tip 5.0–6.9 mm, ratio of calyx lobe length to style length from ovary top to tip c. 3.6, width at base 2.3–4.2 mm, tip minutely bilobed, pale orange. *Immature fruit*: pyriform, coriaceous but

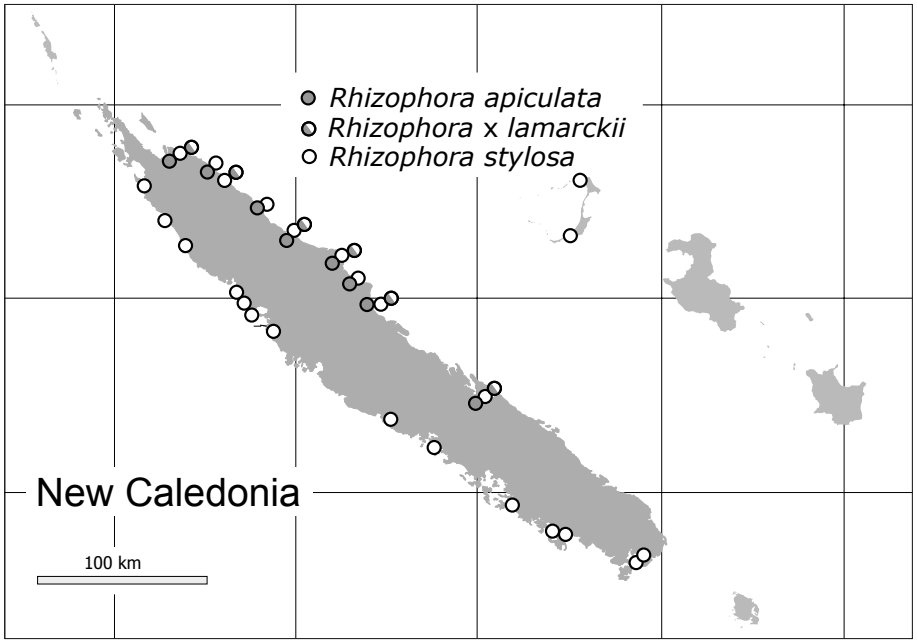

Fig. 7 Distribution of *Rhizophora* species, *R. apiculata*, *R. stylosa* and hybrid *R.* × *lamarckii*, in New Caledonia.

shiny, calyx lobes angular, erect, thick. Reproductive units not observed beyond immature fruit stage. Specimens examined and vouchers are listed in Table 2.

Distribution — Southeast Asia, China to northern Australia and the western Pacific (Fig. 1). Extends south on the Australian east coast (Duke 2006b) to Port Clinton (22°35'S). In New Caledonia, the hybrid occurs in 7 of 35 locations surveyed (Fig. 2), to Canala River in the south (21°31'S), including: Diahot, Pouébo, Lindéralique, Tiouandé, Tiwaé and Tchamba.

Habitat & Ecology — Common in mid intertidal zones of intermediate-downstream tidal reaches (Fig. 4) of river estuaries in areas of higher rainfall. Occurs only in estuaries where *R. apiculata* and *R. stylosa* occur. It forms large trees commonly projecting above the canopy of stands dominated by other *Rhizophora* species and *Bruguiera gymnorhiza.* Stunted, multi-stemmed forms common at higher tidal levels as gnarled thickets up to 3 m in height. Mature flower buds and flowers were plentiful in early December. No hypocotyls were observed in New Caledonia. In Australia, at comparable latitudes, peak flowering occurs during September to January, and rare maturation of propagules between February and May (Duke 2006b).

Etymology — Named in honour of French biologist, Jean Baptiste Antoine Pierre de Monnet de Lamarck (1744–1829).

Note — This entity is distinguished from congeners by inflorescences positioned mostly within leafy shoots, sturdy smooth bracts, large flower buds and slightly tomentose petal margins (Duke & Bunt 1979, Tomlinson 1986). These characters are supported by distinctive leaf colour, shape, size and relatively loose orientation in foliage. Diagnostic characters are consistent across its range.

3. *Rhizophora stylosa* Griff. — Fig. 7, 8, 10

Rhizophora stylosa Griff. (1854) 665. — Type: "Hab. Malacca. In littoribus limosus, Pulo Bissar."; Salvoza (1936) 179; Ding Hou (1958) 456.
Rhizophora mucronata Lam. var. *stylosa* A.Schimp. (1891) 92.

Tree: multi-stemmed, sprawling to columnar tree to 15 m in height, stem to 350 mm diam (measured just above the highest established prop root), stem base diminished beneath prop root insertion. *Bark*: varies from smooth, red-brown in seaward and exposed rocky locations, to grey fissured rough in sheltered muddy locations. *Roots*: above ground props, sturdy at stem base, arching to 2 m, surface lenticels numerous; aerial roots sometimes extend from upper limbs. *Foliage*: comprised of rosettes of paired leaves, c. 9 leaves, clustered at 3–7 leaf scar nodes around spicate apical shoot, terminal, prominent, 17–65 mm long, red-green in colour, enclosed by paired lanceolate stipules. *Leaves*: petiole 5–31 mm long; lamina margins revolute, obovate, 31–116 by 14–68 mm, ratio of length to width c. 1.8, shape length (= length from widest width to petiole juncture) 16–60 mm; ratio of length to shape length (= length from widest width to petiole juncture) c. 2.0, apex broadly acute; upper surface smooth, shiny, bright yellow-green; lower surface dull, pale green, with numerous small cork wart spots; mucronate tip narrow, spicate, 3.5–6.2 by 0.5–1.3 mm, ratio of length to width c. 5.7. *Inflorescence*: 2–20-flowered, branching bifurcate at first juncture, slender, maturing within leafy rosette; leaf scar nodes beneath apical shoot of mature flower buds 2–5, mature fruit 4 or 5, mature hypocotyls 4–8; peduncle 18–34 by 2–4 mm, ratio of length to width c. 8.5; bract beneath calyx regular, smooth, green, 4–8 by 5–7 mm, ratio of length to width c. 1.2, margins brown, crenulate. *Mature flower bud*: ellipsoid, widest near base, smooth, green to pale yellow at maturity, 10–16 by 5–8 mm, ratio of length to width c. 1.8; calyx lobes (3 or) 4, 9–12 by 4–5 mm, c. 1.0 mm thick; apex rounded, cross-section circular smooth. Petals (3 or) 4, pale yellow-green, lanceolate, 8–11 by c. 2.7 mm, very woolly margins, involute, hooded, completely enclosing stamens at sepal juncture. Stamens (6–)8(–9), angular, pale golden brown, 6–9 by c. 1.8 mm. Style terete, filiform, centrally placed on ovary, length from ovary top to tip 2.2–3.9 mm long, length from corolla to tip 2.8–5.3 mm, ratio of calyx lobe length to style length from ovary top to tip c. 3.3, width at base 2.2–3.3 mm, tip bilobed, minute, creamy white. *Mature fruit*: pyriform, bulbous, slightly rough-surfaced, dimensions when detached from mature hypocotyl 29–33 mm long, widest width 22–25 mm, ratio of length to width c. 1.3, width of distil portion 14–16 mm; cotyledon collar-like, exposed at hypocotyl maturity, shiny, pale yellow, 1.5–5.4 by 7.3–8.6 mm; calyx 14–16 mm wide, lobes rounded, often reflexed, thin, blunt, 11–16 by 9–10 mm, spread c. 25 mm wide. *Mature hypocotyl*: narrowly cylindrical, wider towards distil end, green, smooth, 188–280 mm long, 13–15 mm at the widest point, ratio of length to width c. 17, width at plumule end 7.6–8.4 mm, shape length (= length from widest width to distal end) 74–94 mm, ratio of length to shape length c. 2.8, surface with small brown lenticels, distil end narrowly pointed; plumule green, spicate, 12–21 mm long, width at base 4–6 mm. Specimens examined and vouchers are listed in Table 2.

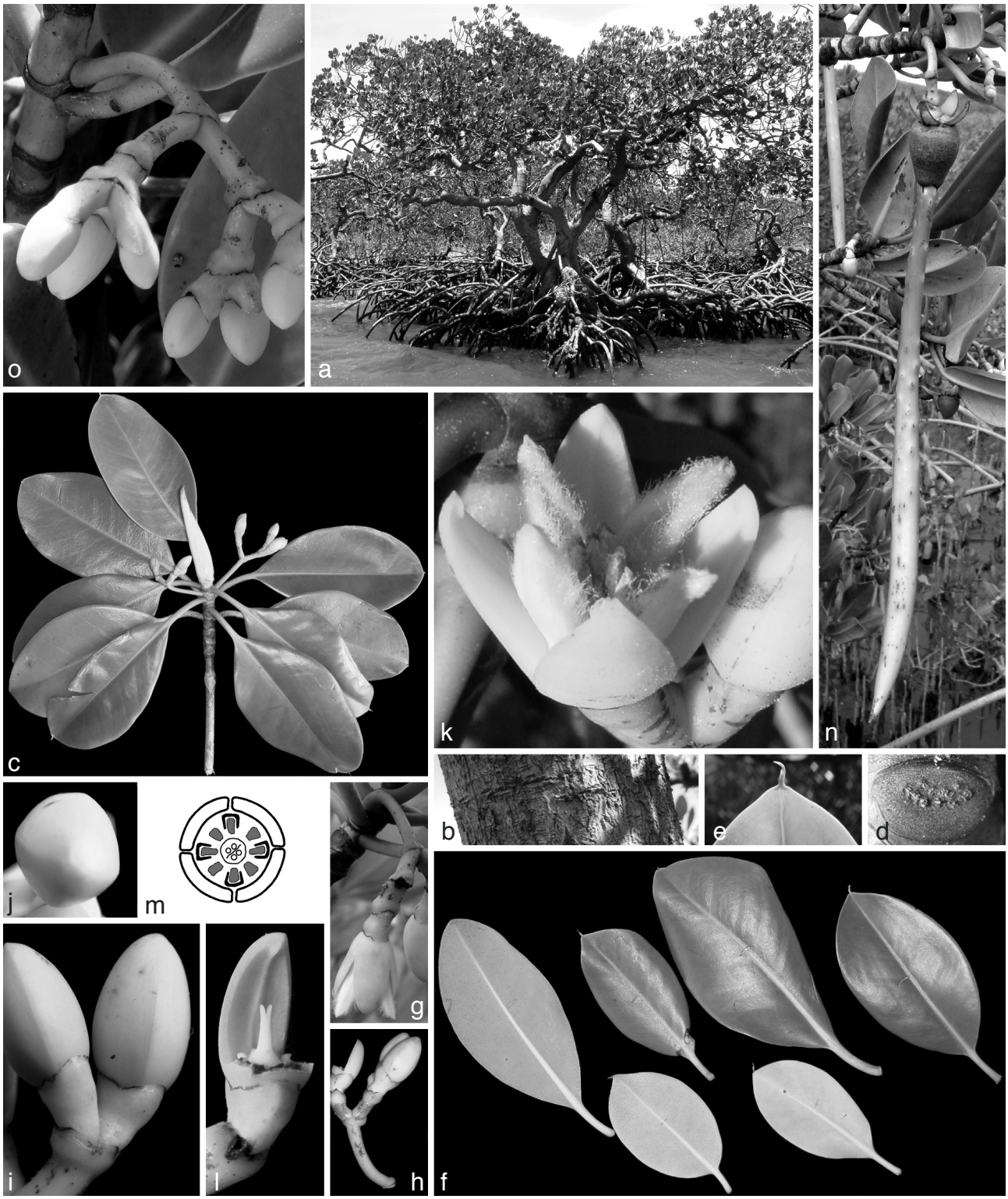

Fig. 8 *Rhizophora stylosa* Griff. a. Habit, Diahot River; b. bark; c. leafy rosette with mature flower buds; d. leaf scar; e. leaf mucro; f. leaves; g. inflorescence in rosette; h. inflorescence; i. closed mature flower bud, side view; j. closed mature flower bud, end view; k. flower; l. style and single calyx lobe of mature flower bud; m. floral diagram; n. hypocotyl just below leafy rosette; o. inflorescence, 2-branching first juncture (c: *Duke*, *Virly & Marchand nc29*).

Distribution — Malay Peninsula, Southeast Asia, China to northern Australia and the western Pacific to Samoa (Fig. 1). Southern-most occurrence on the Australian east coast is South West Rocks (30°53'S) (Duke 2006b). In New Caledonia, the species is present in 26 of 35 locations surveyed on Grand Terre (Fig. 2) to Baie du Carénage in the south (22°20'S), including: Boulari, Dumbéa, Ondémia, Tontouta, La Foa, Néra, Le Cap, Pouembout, Témala, Voh, Oundjo, Iouanga, Ouanac, Sud Néhoué, Diahot, Balade, Pouébo, Tao, Tanghene, Tiouandé, Tiwaé, Pwéeo, Tchamba, Canala and Comboui (St Jean Baptiste). Recorded also on the larger island of Ouvea at Ngimeck (20°41.81'S, 166°30.10'E) and Lekine (20°25.15'S, 166°34.48'E).

Habitat & Ecology — Common in mid to low intertidal zones of downstream tidal reaches (Fig. 4). Throughout its range, *R. stylosa* is located commonly in frontal thickets of downstream coastal estuaries and off shore in small island stands. Often associated with *Sonneratia alba* Sm. or *Avicennia marina* (Forssk.) Vierh. In areas of very low rainfall the species may extend upstream to upper tidal reaches. The species may also extend to the terrestrial fringe of inner tidal saltpan areas in association with *Avicennia marina*. Tallest columnar trees noted in mud

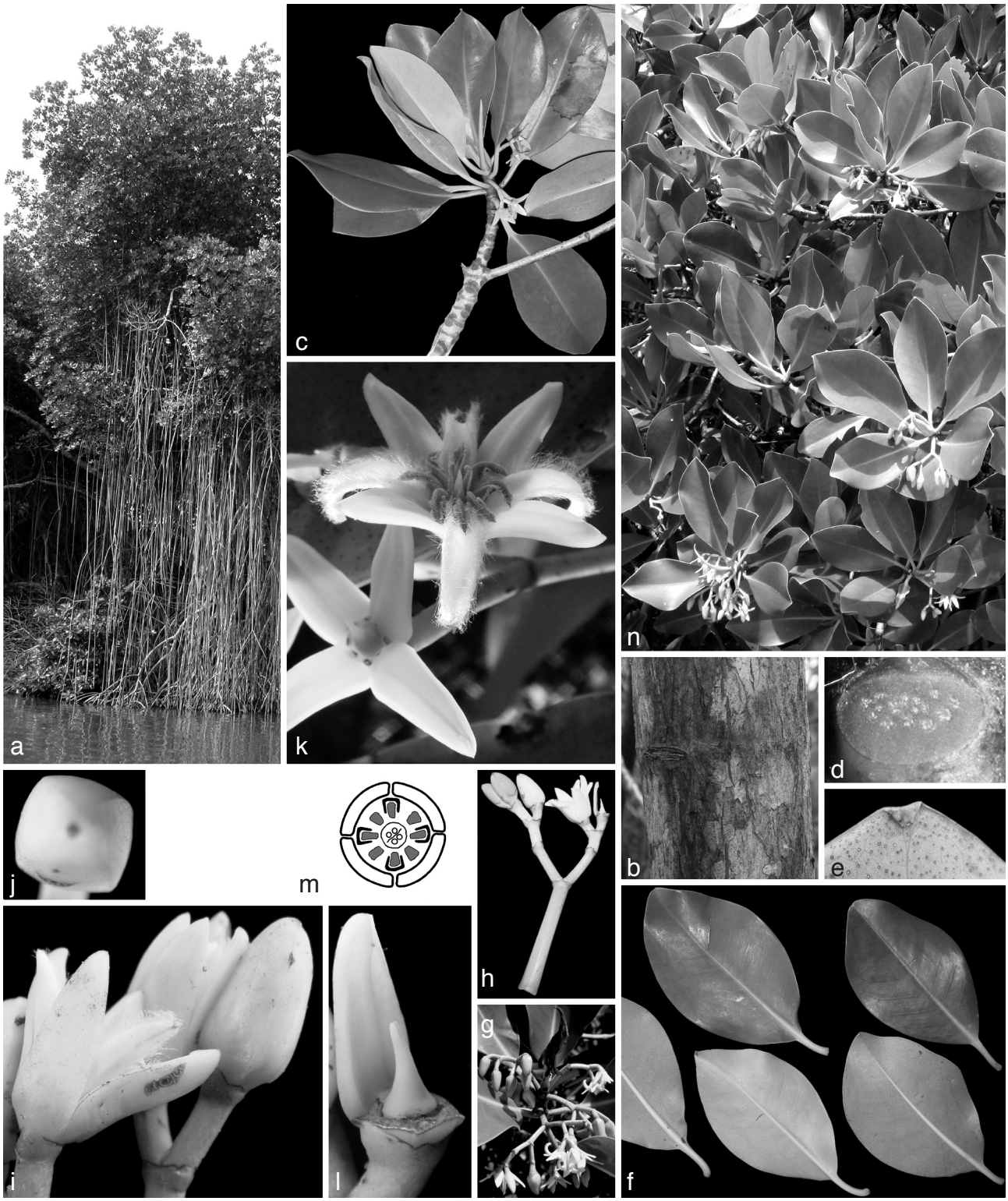

Fig. 9 *Rhizophora* × *selala* (Salvoza) Toml. a. Habit, Diahot River; b. bark; c. leafy rosette with open flowers; d. leaf scar; e. leaf mucro; f. leaves; g. inflorescence in rosette; h. inflorescence; i. closed mature flower bud and flowers, side view; j. closed mature flower bud, end view; k. flower; l. style and single calyx lobe of mature flower bud; m. floral diagram; n. leafy rosettes with mature flower buds and flowers (c: *Duke*, *Virly & Marchand nc32*).

substrate, but found also in sand, coral and rock. Multi-stemmed trees occur in frontal areas, but are more common in the upper intertidal regions. In sheltered bays, enclaves and islands, the species is found almost to the exclusion of other *Rhizophora*. In these situations canopy height is often less than 8 m. Mature flower buds and flowers were plentiful in early December, plus occasional mature hypocotyls. In Australia, at comparable latitudes, peak flowering occurs during March and April, and propagule maturation peaks around February (Duke 2006b).

Etymology — Named for its characteristic long style.

Note — All material from New Caledonia comply with this entities' chief diagnostic character of style length greater than 2 mm (Duke et al. 2002). Leaf colour, shape and size further make this species distinguishable from others. The specific status has been the subject of debate with some authors supporting its sub-specific status under *R. mucronata*. Few characters distinguish these species. Determinations for this treatment follow Hou (1958) and Tomlinson (1986).

4. *Rhizophora* × *selala* (Salvoza) Toml. — Fig. 9, 10

Rhizophora × *selala* (Salvoza) Toml. (1978) 159 (= *R. stylosa* × *R. samoensis*). — Type : *'Selala'* H.B.Guppy (1906) 443, 445, frontisp., non L.
Rhizophora mucronata Lam. var. *selala* Salvoza (1936) 219.
Rhizophora 'selala' Toml. & J.S.Womersley (1976) 9, nom. sine basionymo.

Tree: multi-stemmed, sprawling to columnar tree, often emergent to 20 m, stem to 450 mm diam, stem base diminished beneath prop root insertion. *Bark* black, very coarse and friable to smooth, grey fissured. *Roots* above ground props, sturdy at stem base, arching to 2.5 m, surface lenticels numerous; aerial roots from upper limbs sometimes prolific. *Foliage* comprised of rosettes of paired leaves, c. 9 leaves, clustered at 3–7 leaf scar nodes around spicate apical shoot, terminal, prominent, 33–71 mm long, green, enclosed by paired lanceolate stipules. *Leaves* petiole 9–24 mm long; lamina usually obovate, sides curled, 56–138 by 34–85 mm, ratio of length to width c. 1.6, shape length (= length from widest width to petiole juncture) 30–74 mm, ratio of length to shape length c. 1.9, apex broad to rounded; upper surfaces smooth, shiny, bright green; lower surfaces dull green, with small brown cork wart spots; mucronate tip curled under, gnarled, 1.0–2.4 by 1.2–3.4 mm, ratio of length to width c. 0.8. *Inflorescence*: 4–16-flowered, branching bi- or trifurcate at first juncture, slender, maturing within leafy rosette; leaf scar nodes beneath apical shoot of mature flower buds 1–4, not observed with mature fruits or hypocotyls; peduncle 9–42 by 3–4 mm, ratio of length to width c. 8.3; bract beneath calyx regular, smooth, green, 3–8 by 4–5 mm, ratio of length to width c. 1.2, margins slightly crenulate. *Mature flower bud*: ellipsoid, smooth, yellow, 9–16 by 5–7 mm, ratio of length to width c. 2.1; calyx lobes 4, 9–13 by 4–5 by c. 0.7 mm; apex pointed; cross-section slightly 4-sided. Petals 4, pale green, lanceolate, 8–11 by 2–3 mm, woolly tomentose margins, involute enclosing stamens. Stamens 8, angular, golden brown, 6–10 by 1.0–1.8 mm. Style terete, centrally placed on ovary, length from ovary top to tip 2.2–2.8 mm, length from corolla to tip 4.2–5.6 mm, ratio of calyx lobe length to style length from ovary top to tip c. 4.0, width at base 1.8–3.0 mm, tip bilobed, creamy yellow. *Immature fruit*: pyriform, surface finely coriaceous, calyx lobes erect, thin. Reproductive units not observed beyond immature fruit stage. Specimens examined and vouchers are listed in Table 2.

Distribution — Southwest Pacific, on New Caledonia, Fiji, Tonga and Samoa (Fig. 1). In New Caledonia, this hybrid intermediate is present in 21 of 35 locations surveyed on Grande Terre (Fig. 2) south to Corniche Sud (Mont Dore) in the south (22°18'S), including: Boulari, Dumbea, Ondémia, Tontouta, La Foa, Néra, Le Cap, Poya – Népou, Pouembout, Témala, Voh, Iouanga, Ouanac, Sud Néhoué, Diahot, Pouébo, Tiouandé, Tiwaé, Tchamba and Canala.

Habitat & Ecology — Common in mid-high intertidal zones of downstream-intermediate tidal reaches (Fig. 4) of most rivers and streams. Occurs only in estuaries where *R. stylosa* and *R. samoensis* are found. Larger trees often emergent above the canopy of stands dominated by other *Rhizophora* species and *Bruguiera gymnorhiza*. Thickets of multi-stemmed individuals common at higher tidal contours as gnarled and stunted stands achieving heights around 2–5 m. Mature flower buds and flowers were plentiful in early December. No hypocotyls were observed.

Etymology — Named after its indigenous name in the Fiji islands.

Note — Distinguished from congeners by: leaves having broadly acute apices with reflexed mucronate tips of roughly equal length and width, inflorescences positioned within leafy shoots, inflorescence branching bi- and trifurcate, smooth bracts, and a lack of mature fruit or hypocotyls. First identified in mangroves of Fiji by Guppy (1906) and affirmed by Salvoza (1936) who raised the idea of it being the putative hybrid intermediate of *R. stylosa* and *R. samoensis*. Today there appears little debate or doubt about its hybrid status, affirmed in this current assessment (Fig. 3) with intermediate diagnostic characters consistent across its range.

5. *Rhizophora samoensis* (Hochr.) Salvoza — Fig. 10, 11, 14

Rhizophora samoensis (Hochr.) Salvoza (1936) 220, pl. 6.
Rhizophora mangle sensu H.B.Guppy (1906) 445, f. 11–20, non L.
Rhizophora mangle L. var. *samoensis* Hochr. (1925) 447.

Tree: multi-stemmed, sprawling to columnar tree to 10 m, stem to 200 mm diam (measured just above the highest established prop root), stem base diminished beneath prop root insertion. *Bark*: grey to dark grey and heavily fissured. *Roots*: above ground props, sturdy at stem base, arching to 1.5 m, surface lenticels numerous; aerial roots often extend from upper limbs. *Foliage*: comprised of rosettes of paired leaves, c. 11, clustered at 3–9 leaf scar nodes around spicate apical shoot, terminal, prominent, 19–74 mm long, light green, enclosed by paired

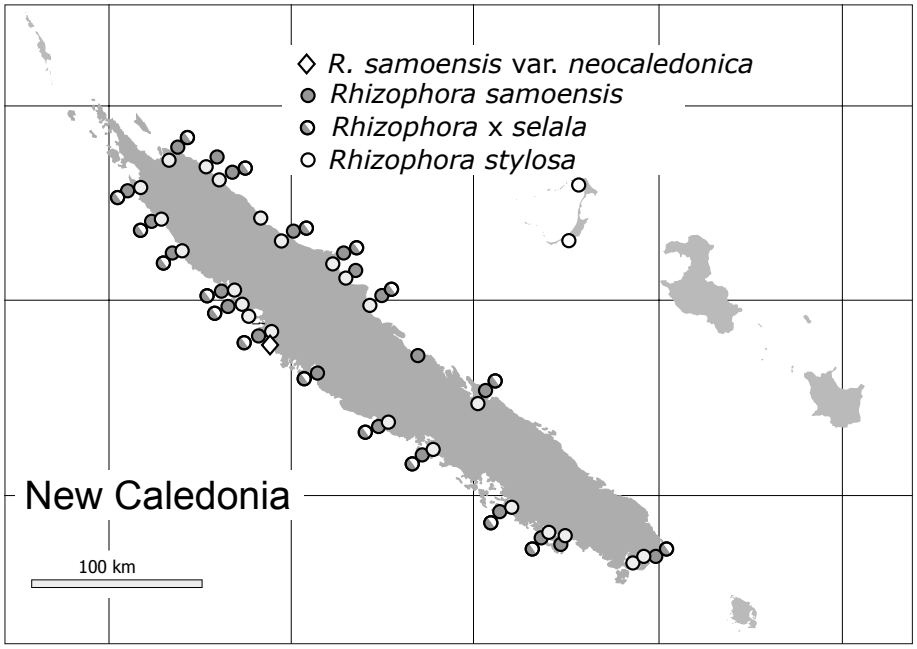

Fig. 10 Distribution of *Rhizophora* species, *R. samoensis*, *R. stylosa* and hybrids, *R.* × *selala* and *R. samoensis* var. *neocaledonica*, in New Caledonia.

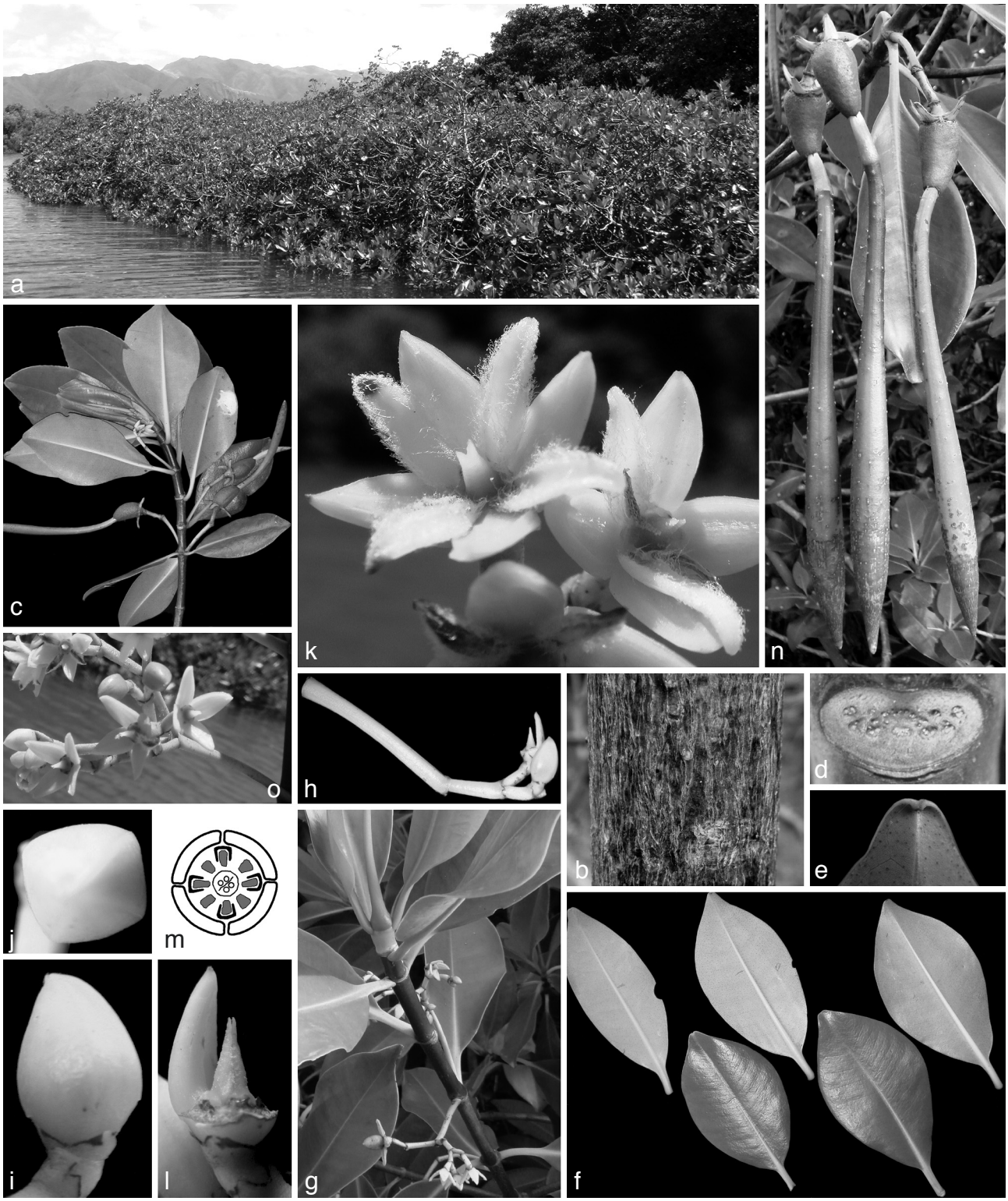

Fig. 11 *Rhizophora samoensis* (Hochr.) Salvoza. a. Habit, near Aéroport Tontouta; b. bark; c. leafy rosette with mature flower buds and hypocotyl; d. leaf scar; e. leaf mucro; f. leaves; g. inflorescence in rosette; h. inflorescence; i. closed mature flower bud, side view; j. closed mature flower bud, end view; k. flowers; l. style and single calyx lobe of mature flower bud; m. floral diagram; n. hypocotyls with mature flower buds within leafy rosette; o. inflorescence, 3-branching first juncture (c: *Duke*, *Virly & Marchand nc30*).

lanceolate stipules. *Leaves*: petiole green, 7–25 mm long; lamina apiculate, 55–136 by 24–73 mm, ratio of length to width c. 2.0, shape length (= length from widest width to petiole juncture) 32–71 mm, ratio of length to shape length c. 1.9, apex distinctly blunt; upper surface smooth, shiny, dark green; lower surface, satiny, green, with numerous small cork wart spots, reddish brown, evenly scattered; mucronate lip distinct, broad, folded under, 0.6–1.4 by 1.9–5.9 mm, ratio of length to width c. 0.2. *Inflorescence*: 2–16-flowered, branching bi- or trifurcate at first juncture, slender, maturing within leafy rosette; leaf scar nodes beneath apical shoot of mature flower buds 1–4, mature fruit 4 or 5, mature hypocotyls 4–8; peduncle 13–58 by 3–4 mm, ratio of length to width c. 12.0; bract beneath calyx minute, smooth, 3–8 by 2–4 mm, ratio of length to width c. 2.0, margins indistinct. *Mature flower bud*: obovate, 4-sided, widest at base, pale yellowish green, smooth, 8–12 by 4–6 mm, ratio of length to width c. 2.0; calyx lobes 4, 7–9 by 4–5 by c. 0.9 mm; apex pointed, cross-section roundly 4-sided, smooth. Petals 4, creamy white, lanceolate, 5–7 by 2–3 mm, woolly, involute, encloses stamens. Stamens 8, angular, golden brown, 4–6 by

Fig. 12 *Rhizophora samoensis* (Hochr.) Salvoza var. *neocaledonica* N.C.Duke. a. Habit, near Pouembout; b. bark; c. leafy rosette with immature inflorescence; d. foliage habit; e. leaf mucro; f. leaf; g. inflorescence in rosette; h. inflorescences, primordial and immature flower buds, 3-branching at first and second junctures (c: *Duke*, *Virly & Marchand nc10*).

0.8–2.0 mm. Style terete, centrally placed on domed ovary, length from ovary top to tip 1.4–2.2 mm, length from corolla to tip 3.6–4.8 mm, ratio of calyx lobe length to style length from ovary top to tip c. 8.1, width at base 1.7–2.3 mm, tip minutely bilobed, pale yellow. *Mature fruit*: pyriform, elongate, drupe-like, slightly coriaceous, dark brown, dimensions when detached from mature hypocotyl, 24–32 mm long, widest width 13–16 mm, ratio of length to width c. 2.0, width of distil portion 8–12 mm; cotyledon collar-like, exposed at hypocotyl maturity, shiny, green, 6–21 by 5–7 mm; calyx 11–13 mm wide, lobes angular, erect, thin, 10–14 by 6–9 mm, spread c. 32 mm wide. *Mature hypocotyl*: narrowly cylindrical, elongate, wider towards distil end, smooth, upper parts green, distil portion brown, 150–260 mm long, 11–17 mm at the widest point, ratio of length to width c. 14, width at plumule end 5–7 mm, shape length (= length from widest width to distal end) 39–70 mm, ratio of length to shape length c. 3.8, surface with brown lenticels, distil end pointed; plumule green, spicate, 11–16 mm long, width at base 3–5 mm. Specimens examined and vouchers are listed in Table 2.

Distribution — Global extent unresolved (see Note). Indo West Pacific range includes New Caledonia, Vanuatu, Fiji, Tonga and Samoa (Fig. 1). In New Caledonia, present in 28 of 37 locations

surveyed on Grande Terre (Fig. 2) to Corniche Sud (Mont Dore) in the south (22°18'S), including: Boulari, Dumbéa, Ondémia, Tontouta, La Foa, Néra, Le Cap, Poya – Népou, Népoui, Pouembout, Témala, Voh, Iouanga, Ouanac, Sud Néhoué, Diahot, Balade, Pouébo, Tanghene, Tiouandé, Tiwaé, Tiwaka, Pwéeo, Tchamba, Houaïlou, Canala and Comboui (St Jean Baptiste).

Habitat & Ecology — Common in lower-mid intertidal zones of intermediate-upstream tidal reaches (Fig. 4) of most rivers and estuaries. There is clear separation of this species from congenerics along key tidal and estuarine gradients. Often observed in low frontal stands as relatively uniform canopies of dense hedge-like thickets, especially along accreting banks in upstream reaches. Good development in both firm mud and sand. Multi-stemmed trees common. Mature flower buds and flowers were plentiful in early December. Mature hypocotyls were also observed in December.

Etymology — Named for its type locality in the southern Pacific.

Note — Distinguished from congeners by: leaves having blunt apices with broadly reflexed mucronate lip, inflorescences positioned mostly within leafy shoots, bi- and trifurcate branching, minute bracts, tomentose petals, presence of mature fruits or hypocotyls. Tomlinson (1986) described this species as 'scarcely distinguishable in morphology' from *R. mangle*, the dominant congeneric from the Atlantic East Pacific. But, while Guppy (1906) first recorded the south-western Pacific entity as *R. mangle*, Salvoza (1936) took a different view. He described its range as including the American west coast, and considered *R. mangle* to be restricted to the Atlantic (Duke & Allen 2006). Perhaps erroneously, this point of view, for the most part, has not prevailed. Entities from the American Pacific coast are usually identified as *R. mangle*, leaving unresolved the possible distinction of these from the populations in New Caledonia and elsewhere in the south-western Pacific (Ellison 1991). The question is whether this latter entity is a different species. If not, the name '*samoensis*' could be preserved with varietial status, as proposed by Hochreutiner (1925).

5a. *Rhizophora samoensis* (Hochr.) Salvoza var. ***neocaledonica*** N.C.Duke, *var. nov.* — Fig. 10, 12

Folia late mucronata, inflorescentiae intra foliorum rosulam rami primarii secundariique trifurcati, alabastrae primordium adest sine gradibus reproductivis ulterioribus. — Typus: *Duke et al. nc10* (Fig. 12), New Caledonia, Grande Terre, Pouembout River estuary upstream estuary (21°8.40'S, 164°51.35'E), 27.xi.2006.

Tree: multi-stemmed, sprawling tree, 5–6 m, stem to 100 mm diam (measured just above the highest established prop root). *Bark*: grey to dark grey and heavily fissured. *Roots*: above ground props, sturdy at stem base, arching to 1.5 m, surface lenticels numerous; aerial roots extend from upper limbs. *Foliage* comprised of rosettes of paired leaves, c. 16 leaves, clustered at 7–10 leaf scar nodes around spicate apical shoot, terminal, prominent, 37–60 mm long, green, enclosed by paired lanceolate stipules. *Leaves*: petiole green, 11–18 mm long; lamina mucronate, 73–113 by 30–58 mm, ratio of length to width c. 1.9, shape length (= length from widest width to petiole juncture) 39–63 mm, ratio of length to shape length c. 1.8, apex blunt; upper surface smooth, shiny, dark green; lower surface, waxy, green, with numerous small cork wart spots, reddish brown, evenly scattered; mucronate tip broad, folded, 0.8–2 by 3.2–5.5 mm, ratio of length to width c. 0.2. *Inflorescence* 4–24-bud flower primordia, branching bi- or trifurcate at first and second junctures, slender, present within leafy rosette; leaf scar nodes beneath apical shoot bud of flower primordia and immature flower buds 1 or 2, not observed with mature flower buds, fruits or hypocotyls; peduncle 13–39 by 2–3 mm, ratio of length to width c. 10.3; bract beneath calyx smooth, green, 4–10 by 4–6 mm, ratio of length to width c. 1.5, margins minute, indistinct. Reproductive units not observed beyond immature flower bud stage. Specimens examined are listed in Table 2.

Distribution — Present in one out of 35 locations surveyed on Grande Terre (Fig. 2), namely Pouembout River estuary (21°8.40'S, 164°51.35'E).

Habitat & Ecology — A single tree was observed in the lower intertidal zone of the intermediate tidal reach of one estuarine location. Flower primordia and immature flower buds only were plentiful in early December. No other reproductive material was observed.

Etymology — Named for its unique occurrence in New Caledonia.

Note — Distinguished from congeners by an abundance of immature and slender inflorescences, with foliage similar to *R. samoensis*. I suspect this to be a back-cross hybrid combination based on its unique occurrence; its close morphological and ecological affinities with *R. samoensis* (Fig. 3); the presence of excessive immature aberrant inflorescences and the absence of mature stages. *Rhizophora stylosa* and *R.* × *selala* are the only other *Rhizophora* entities in the estuarine system and vicinity and may have been involved in its origin.

6. *Rhizophora* × *tomlinsonii* N.C.Duke, *hybrid sp. nov.* — Fig. 13, 14
(= *R. samoensis* × *R. apiculata*).

Folia breviter mucronata, inflorescentiae semper intra foliorum rosulam rami primarii bi- vel trifurcati, alabastra matura sepalorum articulo minuto costiformi elevato, bracteae basales non incrassatae, stamina 11–18, petali margo breviter tomentosus, gradus reproductivi ulteriores desunt. — Typus: *Duke et al. nc28* (holotype NOU), New Caledonia, Grande Terre, Canala River estuary upstream estuary (21°31.2'S, 165°58.6'E), 8.xii.2006.

Tree: multi-stemmed, sprawling tree to 8 m, stem to 250 mm diam (measured just above the highest established prop root), stem base diminished beneath prop root insertion. *Bark*: black, very coarse, friable to smooth, grey fissured. *Roots*: above ground props, sturdy at stem base, arching to 2 m, surface lenticels numerous; aerial roots from upper limbs sometimes numerous. *Foliage*: comprised of rosettes of paired leaves, c. 8 leaves, clustered at 3–6 leaf scar nodes around spicate apical shoot, terminal, prominent, 46–124 mm long, green with some red at base, enclosed by paired lanceolate stipules. *Leaves*: petiole green, 19–35 mm long; lamina flattish, mucronate, 121–207 by 62–104 mm, ratio of length to width c. 2.1, shape length (= length from widest width to petiole juncture) 62–105 mm, ratio of length to shape length c. 2.1, apex acute; upper surfaces smooth, shiny, dark green; lower surface satiny, green, with small brown cork wart spots; mucronate tip short, sometimes curled under, 1.4–2.5 by 1.1–2.5 mm, ratio of length to width c. 1.1. *Inflorescence*: 2–4-flowered, branching bi- or trifurcate at first juncture, slender, maturing within leafy rosette; leaf scar nodes beneath apical shoot of mature flower buds 2–4, not observed with mature fruits or hypocotyls; peduncle 16–35 by 3–4 mm, ratio of length to width c. 6.4; bract beneath calyx smooth, green, 4–10 by 4–6 mm, ratio of length to width c. 1.5, margins minute. *Mature flower bud*: ellipsoid, 4-sided, slightly ribbed at calyx lobe suture base, green, smooth, 11–14 by 6–8 mm, ratio of length to width c. 1.6; calyx lobes 4, 9–12 by 5–7 by c. 1.4 mm; apex sharply pointed; cross-section circular rounded with slight fins. Petals 4, pale green, linear to lanceolate, 7–9 by 2–3 mm, short tomentose margins, slightly involute, hooded to flat. Stamens 11–18, angular, pale golden, 6–8 by 0.9–2.1 mm. Style terete, centrally placed on domed ovary, length from ovary top to tip 1.4–2.0 mm, length from corolla to tip 2.8–3.6 mm, ratio of calyx lobe length to style length from ovary top to tip c. 5.7, width at base 2.0–4.1 mm, tip deeply bilobed, pale

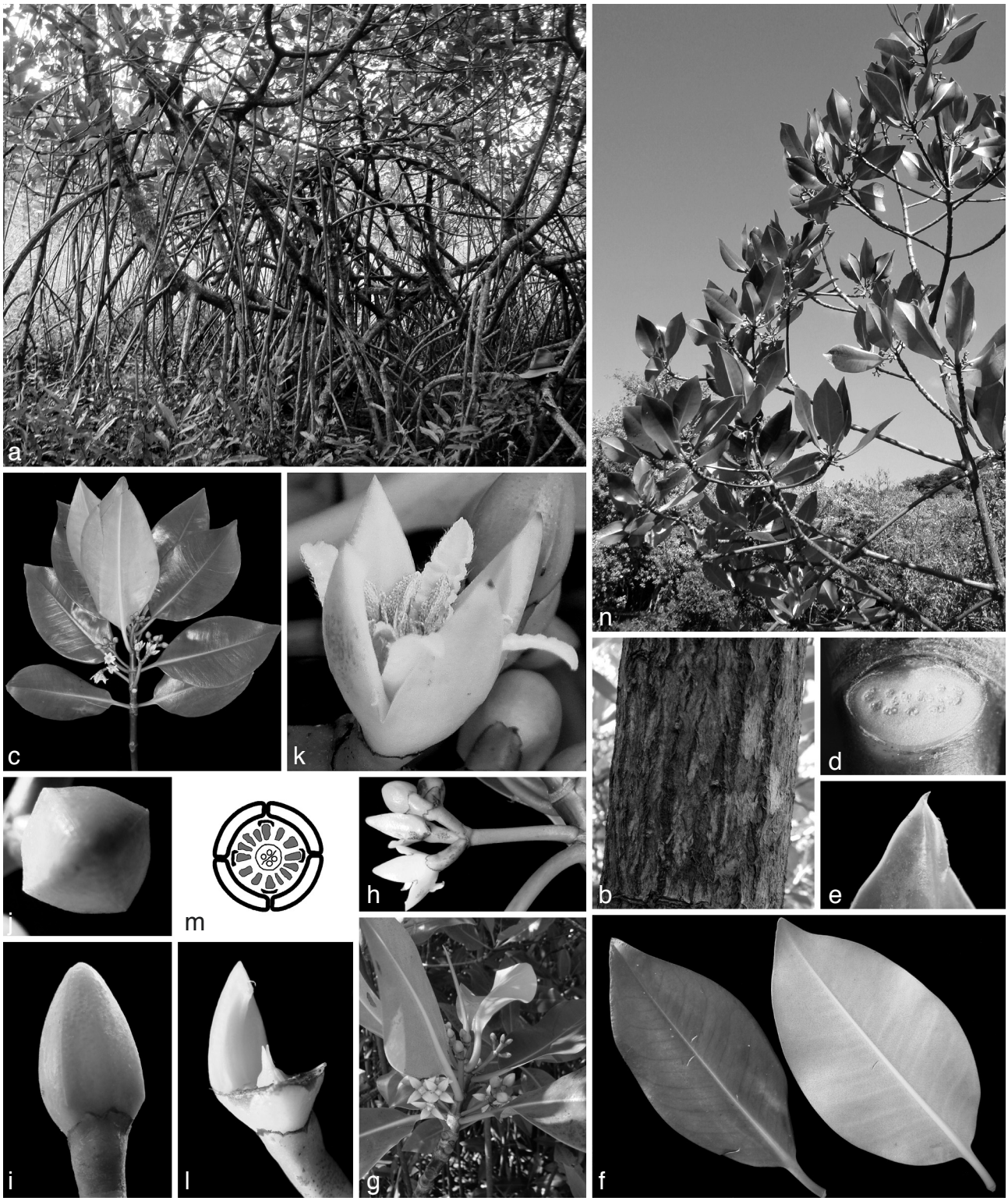

Fig. 13 *Rhizophora* × *tomlinsonii* N.C.Duke. a. Habit, Tiponite; b. bark; c. leafy rosette with mature flower buds and flowers; d. leaf scar; e. leaf mucro; f. leaves; g. inflorescence in rosette; h. inflorescence; i. closed mature flower bud, side view; j. closed mature flower bud, end view; k. flower; l. style and single calyx lobe of mature flower bud; m. floral diagram; n. leafy rosettes with mature flower buds and flowers (c: *Duke*, *Virly & Marchand nc28*).

green. *Immature fruit*: pyriform, shiny, calyx lobes erect, thick. Reproductive units not observed beyond immature fruit stage. Specimens examined and vouchers are listed in Table 2.

Distribution — Endemic to New Caledonia. Present in 5 of 35 locations surveyed on Grande Terre (Fig. 2) to Canala River in the south (21°31'S), including: Tanghène, Hienghene, Tiwaé and Tiponite.

Habitat & Ecology — Low presence in mid intertidal zones of intermediate tidal reaches (Fig. 4) of river estuaries with freshwater influence. Populations appear quite restricted and less common than other *Rhizophora* taxa, and not observed in monotypic stands. The taxon occurs only in estuaries where *R. apiculata* and *R. samoensis* co-occur. Multi-stemmed forms are present within higher tidal contours. Mature flower buds and flowers were plentiful in early December. No mature fruits or hypocotyls have been observed.

Etymology — Named in honour of Prof. P. Barry Tomlinson (Harvard Forest, Harvard University, Massachusetts, and National Tropical Botanical Garden, Hawaii, USA) for inspiration, and for his outstanding contribution to the systematics, bio-

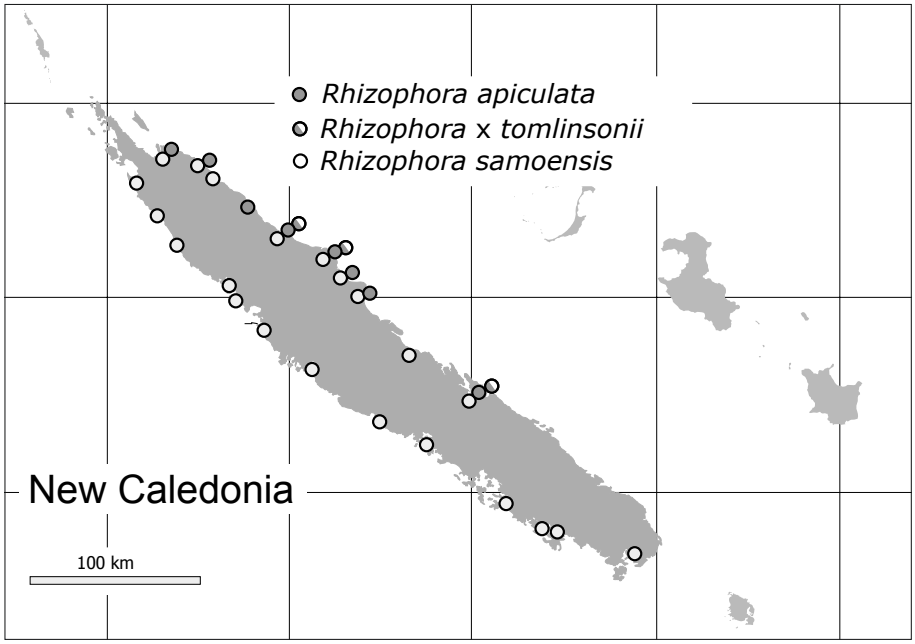

Fig. 14 Distribution of *Rhizophora* species, *R. apiculata*, *R. samoensis* and hybrid *R.* × *tomlinsonii*, in New Caledonia.

geography and ecology of mangrove plants, plus his clarification and description of the two original hybrid *Rhizophora* entities recognised in the south western Pacific.

Note — This taxon is distinguished by minutely spiked leaf mucronate tip, first inflorescence branch bi- or trifurcate always within leafy rosette, mature flower buds with minute, rib-like raised sepal juncture, basal bracts smooth not swollen, stamens 11–18, petal margins thinly hairy, and plants lacking advanced reproductive stages. These characters are supported by leaf colour, shape and size. The discovery of this intermediate in five distinct locations with consistent and intermediate diagnostic characters, demonstrates a relatively close genetic affinity between species of the Atlantic East Pacific and Indo West Pacific. One putative parent, *R. apiculata*, is arguably the most genetically isolated and morphologically distinct member of the genus (Duke & Bunt 1979, Duke et al. 1984, Tomlinson 1986).

DISCUSSION

New Caledonia has uniquely diverse and unusual combinations of *Rhizophora* taxa. While there is no direct evidence of human influences on past dispersal and establishment in New Caledonia, there are inferences to be made concerning the origin and dispersal of ancestral forms.

Observations of species presence and abundance made during this survey provide new insights into local establishment success and probable date of first arrival (Duke et al. 2002). For instance, *R. samoensis* was suggested to be recently introduced to the south-western Pacific in the last few centuries (e.g., Saenger 1998). The distribution of *R. samoensis* here reported suggests that its occurrence now is limited more by the availability of suitable habitats than by geography and distance separating populations around the island. *Rhizophora samoensis* stands are notably present in relatively isolated upper estuarine 'pockets' of respective river systems, and mostly absent in coastal and marine settings. They are often accompanied by hybrid offspring consisting of individuals over 20 m high. While it is not known at what rate hybrids are produced, dispersed and become established, given the life span of individuals, this may be expected to take centuries rather than years. All this implies a much longer period of establishment, as an invading new species would need to gain a foothold in each estuary, where the niche was possibly already occupied by locally-established, reproducing, abundant congeners. This latter view is also in accord with paleontological evidence (Ellison 1991) showing presence over thousands of years.

For these reasons, the unusual overlap of *Rhizophora* species in New Caledonia presents a rare natural experiment in biogeography, where current distributions may be studied to reveal long-term processes of establishment success and dispersal of invading species. The current abundance of hybrid individuals also raises questions about the success rate of natural cross fertilization, and rates of production of viable hybrid propagules from parent species. Perhaps of equal importance, the situation where two hybrid combinations have occurred between taxa from the Indo West Pacific and Atlantic East Pacific bioregions, provides tangible evidence and a natural example of the close genetic similarities between the two divergent extremes of today's global gene pool for this genus.

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