Taiwania 60(4):183–193, 2015
DOI: 10.6165/tai.2015.60.183

Taxonomical Identity of *Rhizophora* × *annamalayana* Kathir and *Rhizophora* × *lamarckii* Montrouz (Rhizophoraceae) in the Andaman and Nicobar Islands, India

P. Ragavan[1*], R.S.C. Jayaraj[2], Alok Saxena[4], P.M. Mohan[1] and K. Ravichandran[3]

1.Department of Ocean Studies and Marine Biology, Pondicherry University, Brookshabad Campus, Port Blair, Andaman & Nicobar Islands, India
2.Rain Forest Research Institute, Jorhat-785010, Assam, India
3.Department of Environment and Forests, Andaman and Nicobar Administration, Port Blair, Andaman and Nicobar Islands, India
4.Indira Gandhi National Forest Academy, Dehradun, Uttarakhand, India
**Corresponding author: van.ragavan@gmail.com*

(Manuscript received 28 July 2015; accepted 27 October 2015)

ABSTRACT: In India, *Rhizophora* hybrids have been recorded in Pichavaram (Tamil Nadu) and in the Andaman and Nicobar Islands (ANI). *Rhizophora* hybrids in Pichavaram mangrove forest were identified as *Rhizophora* × *annamalayana*, a cross between *R. apiculata* and *R. mucronata*, whereas *Rhizophora* hybrids in the ANI were identified as *Rhizophora* × *lamarckii*, a cross between *R. apiculata* and *R. stylosa.* However taxonomical distinction between them was not much explored. A recent floristic survey revealed the occurrence both *R.* × *annamalayana* and *R.* × *lamarckii* in the ANI, India. Based on critical analysis of specimens and morphometric analysis, it was found that both *R.* × *lamarckii* and *R.* × *annamalayana* can be distinguished from *R. apiculata* by their smooth green bract and bracteoles and 2-4 flowered inflorescences within the leaf axils. *Rhizophora* × *annamalayana* is distinguished from *R.* × *lamarckii* by its broader leaves (length: width ratio <1.8 *vs* >1.8), and shorter style (<1.5 mm *vs*. > 1.5 mm) and stamens in two whorls *vs*. usually in a single whorl. *Rhizophora* × *annamalayana* is the new record from the ANI. Higher relative density of *R.* × *annamalayana* than *R.* × *lamarckii* in the ANI is attributed to the abundance of its parental species (*R. apiculata* and *R. mucronata*) in the ANI

KEY WORDS: Andaman and Nicobar Islands, India, Mangroves, *Rhizophora*, hybrids, *R.* × *annamalayana*, *R.* × *lamarckii*.

INTRODUCTION

Natural hybridization is a common phenomenon in plants and has a significant role in plant evolution (Arnold, 1997). Among mangroves, interspecific hybrids have been reported in six genera, namely, *Rhizophora* (Duke and Bunt 1979; Kathiresan, 1995; Parani *et al.*, 1997; Duke, 2010; Lo, 2003, 2010; Ng *et al.*, 2013; Ng and Szmidt, 2014), *Bruguiera* (Ge, 2001; Sun and Lo, 2011; Duke and Gu, 2011), *Lumnitzera* (Tomlinson *et al.*, 1978; Tomlinson, 1986; Duke, 2006; Guo *et al.* 2011), *Sonneratia* (Duke *et al.*, 1984; Tomlinson, 1986; Duke 1994; Duke and Jackes, 1987; Zhou *et al.*, 2005) *Avicennia* (Huang *et al.*, 2014) and *Acrostichum* (Zhang *et al.*, 2013; Ragavan *et al.*, 2014). Conventionally, the identification of mangrove hybrids has been based on observation of intermediate morphology between, and co-occurrence with putative parental species (Kathiresan, 1999; Duke, 2010; Tomlinson, 1986).

In India, *Rhizophora* hybrids have been recorded in Pichavaram (Tamil Nadu) and in the Andaman and Nicobar Islands (ANI, Fig. 1) (Ragavan *et al.*, 2011; Kathiresan *et al.*, 2013). *Rhizophora* hybrids in Pichavaram mangrove forest were identified as *R.* × *annamalayana*, a cross between *Rhizophora apiculata* and *Rhizophora mucronata*, as *R. stylosa* is not present in Pichavaram (Kathiresan, 1995). In ANI, the first encounter of a *Rhizophora* hybrid was reported by Singh *et al.* (1987) from Havelock Island of South Andaman. He described this hybrid as *R.* × *lamarckii* and mentioned that the hybrid was found along with *R. apiculata* and *R. mucronata* on a rocky substratum, with style length of 2-3 mm and stamens present in two distinct whorls. But *R.* × *lamarckii* is a putative hybrid between *R. apiculata* and *R. stylosa*. Thus the systemic distinction between *Rhizophora* × *annamalayana* and *Rhizophora* × *lamarckii* remains imprecise, and their parental species are still uncertain (Kathiresan, 1995, 1999; Lo, 2003). *R.* × *lamarckii* is distinguished from *R.* × *annamalayana* by style length <1.7 mm (Duke, 2006). Ragavan *et al.* (2011) reported the possible occurrence both *R.* × *lamarckii* and *R.* × *annamalayana* in Havelock Island, South Andaman based on style length but the coexistence of all possible parents (*R. stylosa*, *R. apiculata* and *R. mucronata*) causes the uncertainty in determination of parentage of hybrids morphologically. Hence, the present study was undertaken to provide the taxonomical identity and distribution of *R.* × *annamalayana* and *R.* × *lamarckii* in the ANI.

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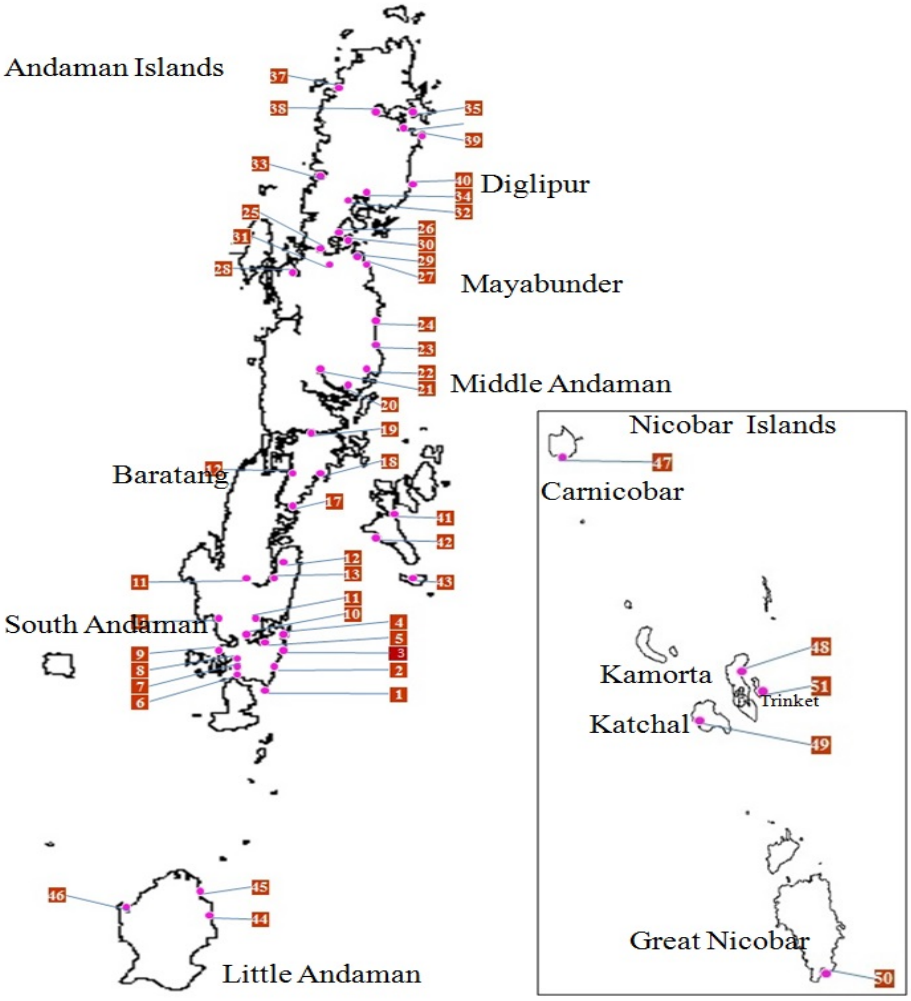


Fig. 1 Map showing the study area details. South Andaman: 1, Chidiyatapu; 2, Burmanallah; 3, Beadonabad; 4, Corbyn's Cove; 5, Sippighat; 6, Manjeri; 7, Guptapara; 8, Manglutan; 9, Wandoor; 10, Ograbraj; 11, Bambooflat Creek; 12, Wright Myo Creek 13, Shoal Bay Creek; 14, Jirkatang; 15, Tirur. Baratang: 16, Middle Strait; 17, Wrafter's Creek; 18, Baludera. Middle Andaman: 19, Kadamtala Creek; 20, Yerrata Creek; 21, Shyamkund Creek; 22, Dhaninallah Creek; 23, Rangat Bay; 24, Panchawati. Mayabunder: 25, Austin Creek; 26, Mohanpur Creek; 27, Karmatang Creek; 28, Chainpur Creek; 29, Rampur; 30, Danapur; 31, Tugapur. Diglipur: 32, Parangara Creek; 33, Kishorinagar Creek; 34, Kalighat Creek; 35, Smith Island; 36, Ariel Bay; 37, Radhanagar; 38, Lakshmipur; 39, Durgapur; 40, Ramnagar. Havelock: 41, Govindnagar; 42, Radhanagar; 43, Neil Island. Little Andaman: 44, V.K. Pur Creek; 45, Dugong Creek; 46, Jackson Creek. Nicobar Islands: 47, Car Nicobar; 48, Kamorta; 49, Katchal; 50, Campbell Bay; 51, Trinket Island.

MATERIALS AND METHODS

During 2009-2013, a qualitative survey was carried out randomly over 51 sites in 8 forest divisions of the ANI to record the occurrence of *Rhizophora* hybrids in the mangroves of the ANI. Plant collections were made of all *Rhizophora* taxa encountered from the range of sites visited. To better assess the taxonomic placement and distinguishing characteristics between *R.* × *lamarckii* and *R.* × *annamalayana*, a morphometric analysis of the *Rhizophora* taxa present in the ANI was performed. Specimens were collected from Shoal Bay Creek, Kadamtala Creek, Yerrata Creek, Austin Creek, Danapur, Havelock and Neil Island (Table 1). In addition *R. stylosa* specimen collected from Corbyn's cove (where hybrids are not present) was also subjected to morphometric analysis. We examined 17 attributes of leaves, inflorescences, and flowers (Table 2) for each taxon. All measurements and observations were made from fresh material. The dataset was used for cluster analysis with Primer-e software (Version 6). Results of the cluster analysis were then used to assess the taxonomical distinction between *Rhizophora* species of the ANI. T-tests were used to determine which attributes differed significantly between the two taxa. For each species 2-5 specimens were sampled with flowers and fruits for herbarium preparation. Herbarium specimen has been prepared and deposited to the National Botanical Collection of Andaman Nicobar

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Table 1. Specimens of *Rhizophora* species collected photographed and examined for morphometric analysis.

Species	ID	Herbarium	Site	Lat	Lon
R. apiculata	30989 30990	PBL	Shoal Bay Creek Havelock Austin Creek	11°47′58″ 12°02′28″ 12°52′37″	92°43′03″ 92°58′46″ 92°50′40″
R. mucronata	30955 30956	PBL	Shoal Bay Creek Yerrata Creek Austin Creek	11°47′58″ 12°26′53″ 12°52′37″	92°43′03″ 92°53′25″ 92°50′40″
R. stylosa	30953 30954	PBL	Corbyn's cove Havelock Neil	11°38′30″ 12°02′28″ 11°50′14″	92°44′28″ 92°58′46″ 93°15′15″
R. x *annamalayana*	30943 30944 30991 30992	PBL	Yerrata Creek Shoal Bay Creek Danapur Austin Creek	12°26′53″ 11°47′58″ 12°54′10″ 12°52′37″	92°53′25″ 92°43′03″ 92°54′09″ 92°50′40″
R. x *lamarckii*	31007 31008	PBL	Neil Island Havelock Island	11°50′14″ 12°02′28″	93°15′15″ 92°58′46″

Table 2. Characters used for classification analysis of *Rhizophora* species of the ANI; average value (range) in cm for each taxon. Where no range is included, the values for the taxon showed no variation. Values that differ significantly ($p < 0.05$) between the *R.* × *lamarckii* and *R.* × *annamalayana* are marked with an asterisk.

Characters	*R. apiculata*	*R. mucronata*	*R. stylosa*	*R.* × *annamalayana*	*R.* × *lamarckii*
Leaf length	13±2.39 (8.5-16.2)	13.55±2.27 (8.5-18)	11.1±1.50 (8-13)	12.39*±1.12 (10-16)	13.08*±1.80 (8-16)
Leaf width	5.9±1.39 (4-8.5)	8.47±1.51 (5.7-11.3)	5.68±1.39 (4-6.3)	7.4±0.69 (6-12)	6.45±0.94 (4.5-8.5)
Leaf length width ratio	2±0.35 (1.7-3.12)	1.6±0.11 (1.4-1.8)	2.02±0.37 (1.8-2.8)	1.67*±0.08 1.4-1.7	2*±0.11 (1.79-2.2)
Leaf mucro length	0.4±0.06 (0.4-0.5)	0.5±0.03 (0.4-0.6)	0.5±0.07 (0.4-0.6)	0.34±0.02 (0.3-0.5)	0.45±0.03 (0.4-0.5)
Petiole length	1.8±0.44 (1.4-2.5)	2.61±0.49 (1.5-3)	3.35±0.79 (2-3.5)	2.17*±0.27 (1.8-2.5)	2.39*±0.52 (1-3)
Petiole width	0.2±0.05 (0.2-0.3)	0.31±0.07 (0.3-0.5)	0.23± 0.05 (0.3-0.4)	0.3±0.07 (0.3-0.4)	0.3±0.04 (0.3-0.4)
Number of flowers per inflorescences	2	5±1.74 (2-8)	5± (2-8)	2+0.89 (2-4)	2±0.64 (2-4)
Bud length	1.2±0.18 (1-1.6)	1.47±0.11 (1.2-1.6)	1±0.2 (0.7-1.2)	1.5*±0.08 (1.4-1.6)	1.65* ±0.05 (1.5-1.7)
Bud width	1±0.05 (0.9-1)	0.8 ±0.03 (0.8-1)	0.43± 0.1 (0.3-0.6)	1±0.08 (0.8-1.1)	0.8 ±0.03 (0.7-0.8)
Bud length width ratio	1.2±0.21 (0.9-1.4)	1.81±0.13 (1.69-2.23)	2.39± 0.6 (1.81-2.51)	1.68±0.23 (1.2-1.81)	2.06 ±0.26 (1.79-2.32)
Peduncle length	1±0.06 (0.8-1)	3.15±0.36 (1.5-6)	3.9±0.90 (2.5-5.5)	1.3*±0.14 (1.2-1.5)	1.85*±0.50 (1-2.5)
Peduncle width	0.5 ±-.07 (0.4-0.6)	0.3±0.05 (0.3-0.5)	0.2 ±0.05 (0.2-0.3)	0.5±0.06 (0.4-0.5)	0.4±0.03 (0.3-0.4)
Petal length	0.8 ±0.12 (0.7-1)	0.8 ±0.07 (0.8-1)	0.8 ±0.07 (0.7-0.9)	1.2 ±0.06 (1-1.2)	1±0.03 (0.9-1.1)
Petal width	0.2 ±0.04 (0.2-0.3)	0.3±0.02 (0.3-0.4)	0.3 ±0.05 (0.2-0.4)	0.4±0.03 (0.3-0.4)	0.3±0.02 (0.2-0.3)
Stamen number	12±1.64 (9-14)	8	8	12*±1.76 (8-16)	12*±1.65 (8 –16)
Stamen length	0.8±0.11 (0.8-1.1)	0.7±0.04 (0.7-0.9)	0.5± 0.08 (0.4-0.6)	0.8±0.09 (0.4-1)	0.6 ±0.07 (0.4-0.8)
Style length	0.1±0.03 (0.06-0.12)	0.1±0.03 (0.08-0.12)	0.4± 0.06 (0.3-0.5)	0.12*±0.02 (0.08-0.15)	0.3*±0.03 (0.28-0.41)

Regional Centre, Botanical Survey of India, Port Blair. A key for *Rhizophora* species of the ANI has also been provided to facilitate identification.

RESULTS

The present mangrove floristic survey over 51 selected sites in the ANI revealed the occurrence of *Rhizophora* hybrids in 10 sites of the ANI. Among them, in sites such as Shoal Bay Creek, Kadamtala Creek, Yerrata Creek, Austin Creek and Danapur *Rhizophora* hybrids were coexisting with *R. apiculata* and *R. mucronata*; *R. stylosa* was not present, whereas in Neil Island *Rhizophora* hybrids coexist with *R. apiculata* and *R. stylosa*; only a few *R. mucronata* individuals were observed. In other sites such as Havelock Island, Chidiyatapu, Manjery and Kimous Bay *Rhizophora* hybrids were observed with all possible parents. Specimens of hybrids collected from Neil Island did not match morphologically with hybrids collected from other sites. Hybrids collected from Neil Island have narrowly elliptic leaves, 3-4 mm long style and occurrence of stamens in single whorls; whereas hybrids collected from sites, where only *R. apiculata*

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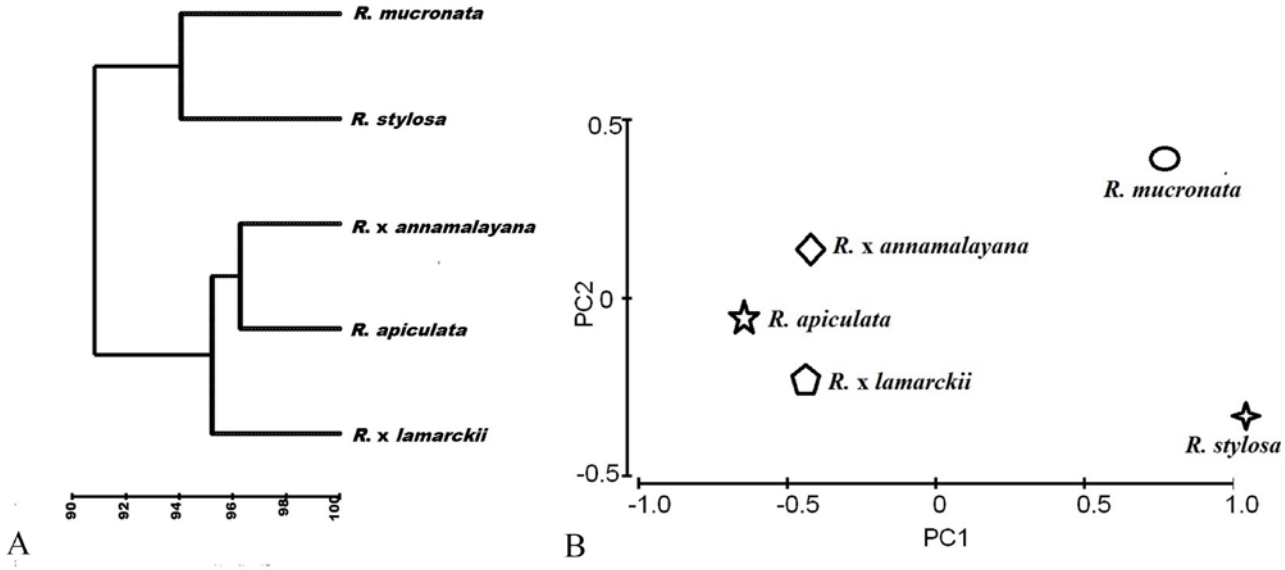


Fig. 2 Affinities of *Rhizophora* species of the ANI. A: The cluster dendrogram. B: Principal Component Analysis (PCA) plot.

and *R. mucronata* present, have broadly elliptic leaves, small style and occurrence of stamens in two whorls. Hence it is proposed that the observed putative hybrids in Shoal Bay Creek, Kadamthala Creek, Yerrata Creek, Austin Creek and Danapur are product of *R. apiculata* and *R. mucronata* i.e. *R.* × *annamalayana* and in Neil Island it is *R.* × *lamarckii*.

The morphometric analysis shows that both *Rhizophora* × *lamarckii* and *R.* × *annamalayana* are morphologically closer to *R. apiculata*. In the dendrogram two major clusters are formed and each cluster is further subdivided into two clades (Fig. 2A), where *R. mucronata* and *R. stylosa* are clustered separately; *R.* × *annamalayana* and *R. apiculata* are clustered together in the same clade and *R.* × *lamarckii* is in a different clade. This proves that *R.* × *annamalayana* and *R.* × *lamarckii* are two morphologically different hybrids. In Principal Component Analysis (PCA) plot (Fig. 2B) also *R. apiculata*, *R.* × *annamalayana* and *R.* × *lamarckii* are grouped in one axis whereas *R. mucronata* and *R. stylosa* are grouped in another axis. Further, putative hybrids *viz*., *R.* × *annamalayana* and *R. lamarckii* are positioned between respective species pairs. Results of t-test show that attributes such as leaf length, leaf length/width ratio, petiole length, peduncle length, bud length, stamen number and style length are significantly different ($p < 0.05$) between the *R.* × *lamarckii* and *R.* × *annamalayana* (Table 2).

Key to *Rhizophora* spp. of ANI

1a. Peduncle shorter than petiole.....2
1b. Peduncle as long as or longer than petiole…….....4
2a. Mature flower bud and fruits below the leaves; inflorescences two-flowered; bract corky, brown; hypocotyl present.....***R. apiculata***
2b. Mature flower buds within the leaves; inflorescences 2-4-flowered; bract smooth and green; hypocotyls not present…....3
3a. Leaves broadly elliptical; styles 0.8-1.2 mm long; stamens in two whorls, inner shorter; mature flower bud four-sided in cross-section.....***R.* × *annamalayana***
3b. Leaves narrowly elliptical; styles 2-3 mm long; stamens in one whorl; mature flower bud rounded in cross-section....***R.* × *lamarckii***
4a. Bract and bracteoles minute; style 1 mm long, seated on elongate, tapering ovary; hypocotyls 50-80 cm long…….....***R. mucronata***
4b. Bract and bracteoles prominent, forming two-lobed, cup-like structure; style 3-4 mm, seated on short ovary; hypocotyls 20-40 cm long…….....***R. stylosa***

Rhizophora* × *annamalayana Kathiresan, Environ Ecol 17 (2): 500, 1999. (Fig. 3)

Tree: spreading, multi-stemmed, height to 25 m, evergreen (Fig. 3A). *Bark*: light grey, rough, slightly fissured both horizontally and vertically, resembles *R. apiculata* (Fig. 3L). *Roots*: extensively developed stilt roots and aerial roots growing from lower branches, stilt roots are highly conspicuous arching above ground to 3 m. *Leaves*: simple, opposite, margin entire, broadly elliptic, yellowish green to dark green (Fig. 3B & 3C) , 12-16 by 6-10 cm, ratio of length to width c. 1.67 (not greater than 1.8), base cuneate, apex acute with pointed mucronate to 0.5 cm long (Fig. 3O) ; petiole thick, green, 1.8-2.5 by 0.3-0.4 cm. *Inflorescence* axillary, 2-4 flowered; peduncle green, 1-1.5 by 0.4-0.5 cm; pedicel stout; bract swollen, smooth, light green (Fig. 3G). *Mature flower bud*: yellowish green, ovate (Fig. 3D & 3E), 1.4-1.6 by 0.8-1.1 cm, ratio of length to width c. 1.68 (not greater than 1.8), cross section four sided (Fig. 3F); calyx lobes 4, thick, apex acute; petals 4, creamy white, thin, slightly hairy in the margin (Fig. 3J), linear, 1-1.2 by 0.3-0.4 cm; stamens 12-16, pale brown, occur in two distinct whorls (Fig. 3K), outer 8 long stamen, 1cm long, inner smaller stamens varied from 2-8, 0.4-0.6 cm long (Fig. 3G); style bilobed, 0.1-0.15 cm

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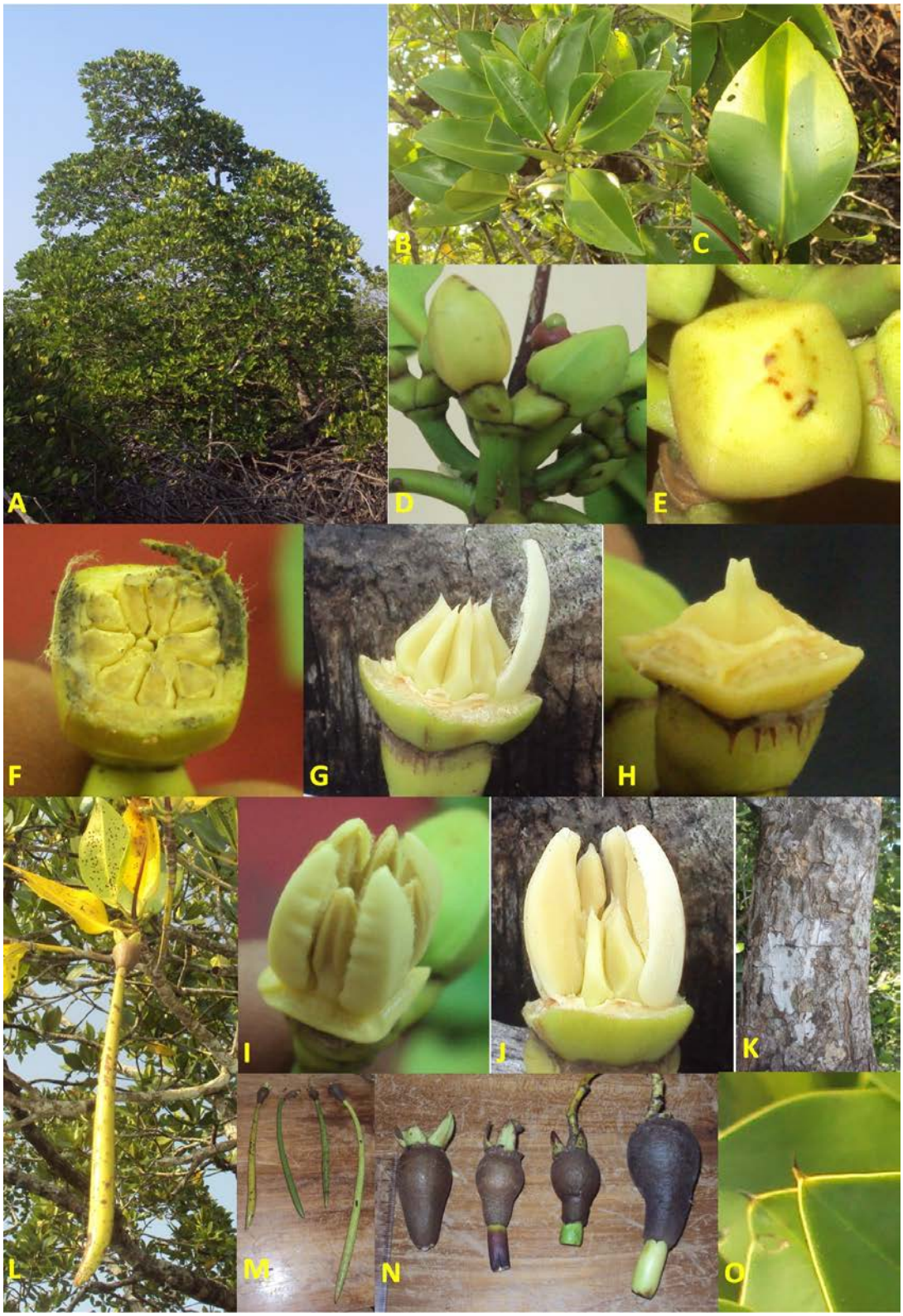


Fig. 3 Morphological features of *Rhizophora* × *annamalayana*. A: Habit. B: Leafy rosette with flowers. C: Broadly elliptic leaf. D: Mature bud. E: Closed mature flower bud. F: Mature bud cross section four sided. G: Inner smaller stamens. H: Style. I: Mature propagule. J: Glabrous petal. K: Stamens in two whorls. L: Bark. M: Comparison of propagules *R.* × *annamalayana, R. apiculata, R. stylosa, R. mucronata* (left to right). N: Comparison of fruits R. × *annamalayana, R. apiculata, R. stylosa, R. mucronata* (left to right). O: Acute leaf tip with pointed mucronate.

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Fig. 4 Morphological features of *Rhizophora* × *lamarckii*. A: Habit. B: Apiculate leaf tips with mucronate. C: Inflorescences. D: Mature bud cross section four sided. E: Narrowly ovate mature bud. F: Leaf rosette with flowers. G: Style and slightly hairy petal. H: Inner smaller stamens. I: Flower. J. Bark.

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Table 3. Diagnostic characters of *Rhizophora* species of the ANI. The hybrids do not produce seeds so hypocotyl characters are not present in them and therefore not included in the table.

Component	Attributes	*R. apiculata*	*R. mucronata*	*R. stylosa*	*R. × annamalayana*	*R. × lamarckii*
Leaves	Leaf shape	narrowly elliptic	ovate, broader at base	narrowly obovate broader at apex	broadly elliptic	narrowly elliptic
	Leaf apex	acute	acute	obtuse	acute	acute
	Leaf base	cuneate	broadly acute to rounded	cuneate	cuneate	attenuate to cuneate
Inflorescences	Position relative to leaves	matures below	matures within	matures within	matures within	mature within
	Flower number	2	2-8	2-8	2-4	2-4
	Juncture number	1	1 to 3	1 to 3	1 to 2	1 to 2
	Bract condition	corky	smooth, minute	smooth, conspicuous	smooth, swollen	smooth swollen
Mature flower bud (closed)	Bud length	1-1.6 cm	1.2-1.6 cm	0.7-1.2 cm	1.4-1.6 cm	1.5-1.7 cm
	Bud width	0.9-1 cm	0.8-1 cm	0.3-0.6 cm	0.8-1.1 cm	0.7-0.8 cm
	Shape x-section	rounded	rounded	rounded	four-sided	rounded
	Bud length /width ratio	1.2	1.81	2.39	1.68	2.06
	Petal x-section	flat	enclose stamens	enclose stamens	curved	curved
	Petal margin	glabrous	hairy	hairy	slightly hairy	slightly hairy
	Style length	0.08-0.12 cm	0.08-0.12 cm	0.3-0.4 cm	0.08-0.12 cm	0.2-0.4 cm
	Stamen number	9 to 14	8	8	8- 16 in two whorls	8 -16 in one whorls
Mature hypocotyls	Expanded fruit	cork -like	pear- like	pear-like		
	Hypocotyl length	20-40 cm	50-80 cm	21-35 cm		
	Distal shape	bluntly pointed	narrowly pointed	narrowly pointed		

long, seated on domed ovary (Fig. 3H); *Mature fruits*: rarely produced, only one was collected, 4 cm long, 2.3 cm wide, dark brown (Fig. 3N) ; *Mature hypocotyls*: 29 cm long, green smooth, tip bluntly pointed, 1.5 cm wide at widest point (Fig. 3I & 3M); plumule green, 1.5 cm long. Specimens examined and vouchers are listed in **Table 1.**

Distribution: Sri Lanka, India (Pichavaram and the ANI), Malaysia (Merbok, Kedah), Indonesia (Lombok, West Nusa Tenggara). In Malaysia, it was reported by Ong (2003) and in Indonesia by Baba (1994) but no further collections are available from both the countries (Wan Juliana *et al.*, 2014; Setyawan *et al.*, 2014).

Habitat and Ecology: It is commonly found at mid intertidal areas and intermediate and downstream estuarine position. Often coexists with *R. apiculata* and *R. mucronata*.

Phenology: Flowering occurs throughout the year. Fruits are rarely present.

Rhizophora* × *lamarckii Montrouz. Mém. Acad. Roy. Sci. Lyon, Sect. Sci. sér. 2, 10:201, 1860. (Fig. 4)

Rhizophora conjugata Arn. (*non* L.) var. *lamarckii* (Montrouz.) Guillaumin (1914).

Tree: spreading, multi-stemmed, height to 25 m, evergreen (Fig. 4A). *Bark*: dark grey rough friable, horizontally fissured, chequered (Fig. 4J). *Roots:* both stilt roots and aerial roots growing from lower branches, stilt roots are highly conspicuous arching above ground to 3 m. *Leaves* simple, opposite, green-dark green (Fig. 4F), elliptic to narrowly elliptic, 8-16 by 4.5-8.5 cm, ratio of length to width c. 2 (not less than 1.8), apex acute with pointed mucronate tip 0.4-0.5 cm long (Fig. 4B), base cuneate to attenuate, margin entire; petiole green occasionally red, 1-3 by 0.3-0.4 cm; *Inflorescences*: axillary, 2-4 flowered (Fig. 4C); peduncle 1-2.5 by 0.3-0.4 cm ; pedicel stout; bract swollen, smooth, green; *Mature flower bud:* narrowly ovate-ellipsoidal (Fig. 4E), yellowish green, 1.5-1.7 by 0.7-0.8 cm, ratio of length to width c. 2.06 (not less than 1.8), cross section slightly four sided (Fig. 4D); calyx 4 lobed, yellowish white, thick, apex acute; petals 4, creamy white (Fig. 4I & 4G), thin, slightly hairy in the margin, linear, 0.9-1.1 by 0.2-0.3 cm; stamens 8-14, occur in two distinct whorls, pale brown (Fig. 4H); style bilobed, 0.25-0.3 cm long, seated on domed ovary (Fig. 4G). *Mature fruits*: not observed. Specimens examined and vouchers are listed in **Table 1.**

Distribution**:** *Rhizophora* × *lamarckii* is distributed from South East Asia and Indonesia to the western Pacific and northern Australia (Duke, 2006). In India it is known only from the ANI.

Habitat and Ecology**:** It is commonly found at mid intertidal areas and intermediate and downstream estuarine position. Often coexists with *R. apiculata* and *R. stylosa*.

Phenology**:** Flowering occurs throughout the year. Fruits are rarely present.

DISCUSSION

Rhizophora species are very similar and can be difficult to distinguish (Lo, 2003). The key distinguishing characters of *Rhizophora* spp. in the ANI are given in Table 3. Both *R.* × *lamarckii* and *R.* × *annamalayana* display more luxuriant growth than their putative parents (Kathiresan, 2010; Duke, 2010). In the

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Table 4. Distribution of *Rhizophora* species in the ANI (RA: *R. apiculata*; RM: *R. mucronata*; RS: *R. stylosa*; RXA: *R.* × *annamalayana*; RXL: *R.* × *lamarckii*)

Site name	Latitude	Longitude	*RA*	*RM*	*RS*	*RXA*	*RXL*	Site name	Latitude	Longitude	*RA*	*RM*	*RS*	*RXA*	*RXL*
South Andaman								**Mayabunder**							
Chidiyatapu	11°29′31″	92°42′34″	+	+	+	+	-	Austin Creek	12°52′37″	92°50′40″	+	+	-	+	-
Burmanallah	11°33′36″	92°43′38″	+	+	+	-	-	Mohanpur Creek	12°56′11″	92°51′14″	+	+	-	-	-
Beadonabad	11°34′53″	92°44′12″	+	+	+	-	-	Karmatang Creek	12°50′27″	92°56′02″	+	+	-	-	-
Corbyn's Cove	11°38′29″	92°44′ 28″	+	+	+	-	-	Chainpur Creek	12°56′11″	92°47′23″	+	+	-	-	-
Sippighat	11°36′50″	92°41′ 22″	+	+	-	-	-	Rampur	12°52′ 54″	92°54′31″	+	+	-	-	-
Manjeri	11°32′43″	92°39′ 00″	+	+	+	+	-	Danapur	12°54′10″	92°54′09″	+	+	-	+	-
Guptapara	11°33′23″	92°39′19″	+	+	-	-	-	Tugapur Creek	12°50′48″	92°51′07″	+	+	-	-	-
Manglutan	11°34′32″	92°38′29″	+	+	+	-		**Diglipur**							
Wandoor	11°35′13″	92°36′59″	+	+	+	-	-	Parangara Creek	13°08′19″	92°52′43″	+	+	-	-	-
Ograbraj	11°39′16″	92°40′05″	+	+	-	-	-	Kishorinagar Creek	13°11′44″	92°51′49″	+	+	-	-	-
Bambooflat Creek	11°42′44″	92°42′05″	+	+	-	-	-	Kalighat Creek	13°07′40″	92°56′45″	+	+	-	-	-
Wright My°Creek	11°49′57″	92°43′12″	+	+	-	-	-	Smith Island	13°21′12″	93°00′44″	+	+	-	-	-
Shoal Bay Creek	11°47′58″	92°43′03″	+	+	-	+	-	Ariel Bay	13°16′41″	93°01′01″	+	+	-	-	-
Jirkatang	11°49′43″	92°39′34″	+	+	-	-	-	Radhanagar	13°24′33″	92°54′19″	+	+	-	-	-
.Tirur	11°42′54″	92°36′44″	+	+	-	-	-	Lakshmipur	13°19′51″	92°56′45″	+	+	-	-	-
Baratang								Durgapur	13°16′24″	93°02′08″	+	+	-	-	-
Middle Strait	12°09′24″	92°45′27″	+	+	-	-	-	Ramnagar	13°11′16″	93°02′05″	+	+	-	-	-
Wrafter's Creek	12°05′53″	92°45′51″	+	+	-	-	-	**Havelock**							
Baludera	12°09′32″	92°48′58″	+	+	-	-	-	Govindnagar	12°02′28″	92°58′46″	+	+	+	+	+
Middle Andaman					-	-	-	Radhanagar	12°0′56″	92°57′90″	+	+	-	-	-
Kadamtala Creek	12°19′21”	92°47′28″	+	+	-	+	-	Neil Island	11°50′14″	93°15′15″	+	+	+	-	+
Yerrata Creek	12°26′53”	92°53′25″	+	+	-	+	-	**Little Andaman**						-	
Shyamkund Creek	12°28′34”	92°50′38″	+	+	-	-	-	V.K. Pur Creek	10°44′59″	92°34′36″	+	+	-	-	-
Dhaninallah Creek	12°36′55”	92°57′80″	+	+	-	-	-	Dugong Creek	10°48′00″	92°33′36″	+	+	-	-	-
Rangat Bay	12°30′12”	92°57′02″	+	+	-	-	-	Jackson Creek	10°45′36”	92°23′57″	+	+	-	-	-
Panchawati	12°34′30”	92°57′47″	+	+	-	-	-	**Nicobar**							
Mayabunder								Car Nicobar	9°7′59″	92°46′19″	+	+	+	+	-
Austin Creek	12°52′37”	92°50′40″	+	+	-	+	-	Kamorta	8°10′38″	93°30′47″	+	+	-	-	-
Mohanpur Creek	12°56′11”	92°51′14″	+	+	-	-	-	Katchal	7°57′13″	93°21′25″	+	+	-	-	-
Karmatang Creek	12°50′27”	92°56′02″	+	+	-	-	-	Campbell Bay	6°49′14″	93°51′57″	+	+	-	-	-
Chainpur Creek	12°56′11”	92°47′23″	+	+	-	-	-	Trinket Island	8°6′29″	93°34′43″	+	+	-	-	-
Rampur	12°52′54”	92°54′31″	+	+	-	-	-								
Danapur	12°54′10”	92°54′09″	+	+	-	+	-								
Tugapur Creek	12°50′49”	92°51′07″	+	+	-	-	-								

field, *Rhizophora* hybrids are easily identified by their height, a large number of flowers with smooth bract, swollen bracteoles and rare occurrence of propagule. Both *R.* × *lamarckii* and *R.* × *annamalayana* are distinguished from *R. apiculata* by their smooth green bract and bracteoles and 2-4 flowered inflorescences within the leaf axils. *Rhizophora* × *annamalayana* is distinguished from *R.* × *lamarckii* by its broader leaves (length: width ratio <1.8 *vs* >1.8), and shorter style (<1.5 mm *vs*. > 1.5 mm) and stamens in two whorls *vs*. usually in one single whorl. Extracts from various parts of *R.* × *lamarckii* and *R.* × *annamalayana* have been used to treat various human diseases. For instance Prabhakaran and Kavitha (2012) reported the use of *R.* × *lamarckii* against hepatitis and Singh *et al.* (2013) reported the wide range of bioactive substances and antibacterial activities of extracts from various parts of *R.* × *annamalayana*.

Rhizophora × *lamarckii* was first described in the monograph of Salvoza (1936) as an endemic species in New Caledonia. Hybrid status of *R.* × *lamarckii* was described by Duke and Bunt (1979) and Tomlinson (1986) based on its low fertility, intermediate morphological characters and co-occurrence with its putative parents. Hybrid between *R. apiculata* and *R. mucronata* was first recognized by Baba (1994) under nomenclature of *R. lombokensis* Baba & Hayashi from Lombok Island, Indonesia and no further collections are available. Similarly, in Malaysia Ong (2003) reported the occurrence of *R.* × *annamalayana* from Merbok Mangroves and thereafter it has not been recorded. Further, both *R.* × *lamarckii* and *R.* × *annamalayana* are rare and endangered in Malaysia (Wan Juliana *et al.*, 2014). In Pichavaram mangrove forest, the *Rhizophora* hybrids were initially identified as *R.* × *lamarckii* based on morphological features and occurrence of putative parents (Lakshmanan and Rajeswari, 1983; Muniyandi and Natarajan, 1985). However, its parentage was disputed in that *Rhizophora stylosa* does not occur in Pichavaram and the morphological features of *R.* × *lamarckii* described by Duke and Bunt (1979) differed from those of the hybrid. Later, the hybrid was identified

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as *R.* × *annamalayana*, a cross between *Rhizophora apiculata* and *Rhizophora mucronata* (Kathiresan, 1995; Lakshmi *et al.*, 2002). Both reports aimed to name the apparently new species without providing much detail about the plant itself (Jayatissa *et al.*, 2002).

Hybridization in *Rhizophora* species is studied more elaborately by molecular methods than morphometric observation. Molecular evidence for hybrid nature of *R.* × *annamalayana* was given by Parani *et al.* (1997), Lakshmi *et al.* (2002) and Kumar *et al.* (2011). Lo (2003) provided the molecular evidence for *R.* × *lamarckii*. Parani *et al.* (1997) and Sahu *et al.* (2015) stated the maternal role of *R. apiculata* whereas Lakshmi *et al.*, (2002) stated the maternal role *R. mucronata* in *R.* × *annamalayana*. Lo (2003) stated that hybridization in *Rhizophora* species are bidirectional and both the parents can play a maternal role. Recent molecular studies on *Rhizophora* spp. of IWP regions also reveal the same (Ng *et al.*, 2013; Ng and Szmidt, 2014)

Recently Sahu *et al.* (2015) reported that *R.* × *lamarckii* and *R.* × *annamalayana* are two morphologically different hybrids but Lo (2003) reported that remarkable nuclear and chloroplast affinities were found between *R.* × *lamarckii* and *R.* × *annamalayana* and that *R.* × *annamalayana* can be treated or renamed as *R.* × *lamarckii*. The above two contradictory statements show that molecular methods also do not provide the taxonomical distinction between *R.* × *lamarckii* and *R.* × *annamalayana*. The reason could be the lack of adequate information on morphological distinction between *R.* × *lamarckii* and *R.* × *annamalayana*. For instance, Lo (2003, 2010) collected specimens of *R.* × *annamalayana* from Sri Lanka, but the occurrence of *R.* × *annamalayana* is under dispute in Sri Lanka (Jayatissa *et al.*, 2002). Whereas Sahu *et al.* (2015) collected the specimens of the *R.* × *lamarckii* from three individuals at Havelock Island where all the possible parents coexist and Ragavan *et al.* (2011) suspected the occurrence of both the hybrids there. More importantly, in both the studies, morphological distinctions of the collected specimens were not described properly.

Lo (2003) noted that *R.* × *annamalayana* is morphologically dissimilar from *R. apiculata* and that *R.* × *lamarckii* has more similarity with *R. apiculata*. But the present study shows that both the hybrids are closely similar to *R. apiculata*, particularly in inflorescences with short peduncle, swollen bracteoles and bark texture. *R.* × *annamalayana* is distinguished from *R.* × *lamarckii* by its dark green broad leaves, ratio of length to width <1.8, small style <1.5 mm and occurrence of stamens in distinct whorls, while in *R.* × *lamarckii* leaves are narrowly elliptic, ratio of length to width >1.8, style > 1.5 mm, and 8-14 stamens are in a single whorl. However, occurrence of stamens in two distinct whorls is observed in specimens of *R.* × *lamarckii* too, but the frequency is lower than in *R.* × *annamalayana*. This suggests that the presence of stamens in two distinct whorls is characteristic of Indian *Rhizophora* hybrids and this kind of stamen arrangement is not observed in *Rhizophora* hybrids of other regions.

In this study *Rhizophora* hybrids were recorded from 10 sites (Table 4). The occurrence of *R.* × *annamalayana* in all the major mangrove areas of the ANI in this study shows that abundance and overlapping distribution of *R. apiculata* and *R. mucronata* in the ANI contributes to the high frequency of hybridization between them and occurrence of potential hybrid zone. *R.* × *lamarckii* was recorded only in Neil and Havelock Islands and its population is high at Neil Island; in Havelock only two individuals were identified. The low rate of hybridization between *R. apiculata* and *R. stylosa* in the ANI is attributed to the restricted distribution of *R. stylosa* in the ANI. Moreover *R. stylosa* is dominant in east IWP and the western distribution of *R. stylosa* is not well established, except for a little stand in Orissa and the ANI (Duke, 2006). In this study, *R. stylosa* was recorded in 10 sites, and among them its population was well developed in Neil and Havelock Islands, and in the other sites, only a few individuals were identified. In Neil Island, population density (individual per hectare) of *R. stylosa* is high (155.5) followed by *R. apiculata* (105.5); density of *R. mucronata* is comparatively low (16.6). In Havelock Island density of *R. apiculata* (361.1) and *R. mucronata* (166.6) is higher than that of *R. stylosa* (100).

As all possible parents were observed in Havelock Island, Manjery, Chidiyatapu and Kimous Bay, specimens of *Rhizophora* hybrids collected from the above mentioned places are not included in classificatory analysis. However, based on the key distinguishing characters like small style length and occurrence of stamens in two distinct whorls it was found that *Rhizophora* hybrids in Kimous Bay, Manjeri and Chidiyatapu are *R.* × *annamalayana*, in Havelock Island out of the eight individuals two are *R.* ×*lamarckii* and others are *R.* × *annamalayana* but in above mentioned places wide morphological variation among the hybrid individuals were noticed. Notable characters observed from these sites are bark having lenticels (Fig. 5A), leaves with acuminate tip (Fig. 5B) and laterally folded dark green leaves (Fig. 5C). Variations among the off-springs of the same hybridizing taxa are common in natural hybridization; Ng and Chan (2012) also reported wide variation among the hybrids in Malaysia.

Molecular studies show that both *R.* × *lamarckii* and *R.* × *annamalayana* appear to be F1s and no advance stage of hybridization is reported. In this study also no advanced reproductive stages were in both the hybrids, however one propagule was observed and collected from one individual

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Fig. 5 Variation in *Rhizophora* hybrids. A: Bark with lenticels. B: Leaves with acuminate tip. C: Laterally folded dark green leaf.

of *R.* × *annamalayana* at Danapur. The propagules look very similar to propagules of *R. apiculata*. The occurrence of propagule is a rare phenomenon in *Rhizophora* hybrids. So the hybrid zones are probably primary hybrid zones and strong post zygotic isolation occurs between hybridizing species. The occurrence of hybridization and strong post-mating isolation between parental species suggest that these species may be at the last stage of speciation and can achieve complete reproductive isolation *via* reinforcement (Dobzhansky, 1937).

CONCLUSION

Natural hybridization in the genus *Rhizophora* is most common. Hybridization and introgression not only facilitates speciation through gene flow between the species, but it can also reverse the process of speciation. Since mangroves are threatened by various anthropogenic threats and global climate change, it is crucial to understand the effect of this kind of evolutionary process on existing mangrove species. *Rhizophora* species are commonly used for restoration in the ANI as well as in India, and so it is important to know the taxonomical identity of the closely related species to avoid artificially promoting hybridization in mangrove restoration programmes. Though molecular methods are effective in assessing the hybridization and introgression, without taxonomical identity the results are not implemented in the field for conservation and management of this sensitive ecosystem. Thus, the detailed description of the morphological features of *R.* × *lamarckii* and *R.* × *annamalayana* provided in this study will provide better understanding of hybridization and speciation in *Rhizophora* species.

ACKNOWLEDGEMENTS

We are extremely grateful to the Department of Environment & Forests, Andaman & Nicobar Administration for providing necessary support in conducting the survey.

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