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Review: Mangrove hybrid of *Rhizophora* and its parental species in Indo-Malayan region

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Abstract. *Setyawan AD, Ulumuddin YI, Ragavan P. 2014. Mangrove hybrid of* Rhizophora *and its parental species in Indo-Malayan region. Nusantara Bioscience 6: 69-81.* There was two putative hybrid species of mangrove in the Indo-Malayan region, namely *Rhizophora x annamalayana* Kathir. and *R. x lamarckii* Montrouz. *Rhizophora x annamalayana* is most recently known as a natural hybrid between *R. apiculata* and *R. mucronata*. At first, this plant is considered as *R. x lamarckii*, a well-known mangrove hybrid between *R. apiculata* and *R. stylosa*. Since *R. stylosa* is not distributed in India and Sri Lanka, the location where this species was first discovered, the name of the new hybrid species between *R. apiculata* and *R. mucronata* was corrected. Meanwhile, *R. x lamarckii* has long been known and is always found in habitat where its parents grew. Besides, the cross-breeding of *R. mucronata* and *R. stylosa* has never been reported. Both are sibling species that have identical morphological characteristics, thus the hybrid cross-bred species was not observed visually and can only be distinguished through genetic studies.

Keywords: *annamalayana*, *apiculata*, description, Indo-Malaya, *Rhizophora*

INTRODUCTION

There are approximately 70 species of mangrove plants distributed worldwide, divided into 20 genera (Spalding et al. 2010). Almost all mangrove species have been identified, named and classified, that the new species is commonly a hybrid of previously known species. The progress of molecular biology helps to solidify this hybrid species. Hybrids of mangrove species have been found in *Rhizophora, Sonneratia, Bruguiera, Lumnitzera* and *Heritiera* (Tomlison 1986; Zhou et al. 2005, 2008; Duke and Ge 2011; Guo et al. 2011; Ng and Chan 2012). Intermarriage also occurs among different mangrove species, but its frequency is relatively limited and generally produces sterile progeny (Chan 1996).

Rhizophora L. (Rhizophoraceae R.Br.) is the most successful-growth mangrove, with the widest extent of spread and the easiest to be found (highest abundance), grows in tropical and subtropical coastal areas, characterized by the stilt roots (Duke 2006a; Giesen et al. 2006). *Rhizophora* growing success is mainly supported by the ability to reproduce with the help of the wind, although it can also breed with the help of insects because the flowers have an odor, color, and nectar that can attract insects. *Rhizophora apiculata* Bl. has specialized wind pollination mechanisms; otherwise, *R. stylosa* Griff has less specialized and need insects for pollination (Tomlinson et al. 1979). *Rhizophora* is still actively evolving, where sterility barriers between species are easily traversed, thus it can give birth to some putative hybrid species, namely: *R. x lamarckii* Montrouz in the Malay Archipelago (Tomlinson and Womersley 1976), *R. x annamalayana* Kathir. in India and Sri Lanka (Kathiresan 1995, 1999), and *R. x selala* in Pacific islands (Tomlinson 1978; Duke 2010). Wind-pollination based breeding increases the frequency of putative hybrids (Tomlinson et al. 1979), especially *Rhizophora* pollen of different species have much in common morphology (Muller and Caratina 1977).

Rhizophora x annamalayana is the latest known mangrove species, as a natural hybrid between *R. apiculata* and *R. mucronata* Lam (Kathiresan 1995, 1999). Previously, it has been known *R. x lamarckii* which is a hybrid between *R. apiculata* and *R. stylosa* (Tomlison 1986). Meanwhile, hybrids between *R. mucronata* and *R. stylosa* were never reported. Both are sibling species with very similar morphological characteristics and genetic profile similar to 96.5% (Parani et al. 1997b). Formerly, *R. stylosa* is a variant with the name of *R. mucronata* var. *stylosa* (Griff.) Salvoza; thus to distinguish the two hybrids are difficult and can only be identified by DNA sequences (Ng et al. 2013).

Natural hybridization between species often occurs to maintain the genetic diversity and evolution that the plants can last a long time, although it can also occur as an introgression where progenies become weaker and sterile. *Rhizophora x lamarckii* and *R. x annamalayana* have so far been thought to be sterile and it always requires the presence of both parents (Duke and Blunt 1979; Chan 1996; Parani et al. 1997; Lo 2010; Ng and Chan 2012). In the hybrid species, *R. x annamalayana* pollen viability (3%) is much lower than both the parent (100% in *R. mucronata*, *R. apiculata* in 53%) (Kavitha and Kathiresan 2011, 2012). It denies the possibility that the parent species

of *R. stylosa* has been presented in India and gave birth of hybrid species before changed its distribution and was no longer found in the region (Schwarzbach and Ricklefs 2001). The accuracy of identification was instrumental in the successful restoration of mangrove forests (Ng and Szmidt 2013), where *Rhizophora* is widely used for this purpose (Setyawan et al. 2004).

In Indo-Malaya, *Rhizophora* consists of three species, i.e. *R. mucronata*, *R. stylosa* (two being closely allied or sibling species) and *R. apiculata*, and two putative hybrids, *R. x lamarckii* (*R. apiculata* x *R. stylosa*) and *R. x annamalayana* (*R. apiculata* x *R. mucronata*) (Duke 2006b). Although it has been widely published, both the name of the hybrid species was categorized as 'unresolved' names that it is not yet possible to assign a status of either 'accepted' or 'synonym' (The Plant List 2010). The five species can be found in Indonesia. *Rhizophora apiculata* and *R. stylosa* are the most common species. *Rhizophora mucronata* is less common, although its global distribution is much wider than the other two species (Hou 1992, Duke 2006b; Duke et al. 2010a, b, c). *Rhizophora x lamarckii* is only found in locations where both parents present. *Rhizophora x annamalayana* (Kathiresan 1995; 1999) is recorded only once in Lombok Island, West Nusa Tenggara, and is originally named as *R. x lombokensis* Baba & Hayashi (Baba 1994) (Figure 1).

In the coastal region of western Africa and America, *R. mangle* L. (syn. *R. samoensis* (Hochr.) Salvoza), *R. racemosa* G. Mey., and *R. harrisonii* Leechm. can be found and one hybrid is known as *R. x selala* (Salvoza) Toml. *Rhizophora harrisonii* has characteristics of both *R. mangle* and *R. racemosa* that it was initially thought to be the hybridization of the two, but recent molecular study makes it clear that it wasn't (Ceron-Souza et al. 2010). While in the Pacific islands, *R. mangle* var. *samoensis* and hybrid *R. x selala* (*R. mangle* var. *samoensis* x *R. stylosa*) there can also be found. The islands are the overlapping meeting point of *Rhizophora* of Indo-Malayan and *Rhizophora* of American (Tomlison 1986; Duke 2006b). Initially, *R. samoensis* is known as a separated species, but today the species is regarded as a variant of *R. mangle* (The Plant List 2010) (Figure 1).

The name of *R. x annamalayana* for a hybrid between *R. apiculata* and *R. mucronata* was firstly given by Kathiresan (1995) based on specimens grown in Pichavaram, Tamil Nadu, India. Kathiresan (1999) rewrite the publication, since the first paper was not accompanied by a complete description. The existence of *Rhizophora* hybrid species in this place have been previously indicated by Lakshmanan and Rajeswari (1983), Muniyandi and Natarajan (1985), Singh et al. (1987) and Subramonian (1993), but they called it *R. x lamarckii*, which is actually the name for a hybrid of *R. apiculata* and *R. stylosa*. The molecular studies support that *R. x annamalayana* is derived from hybrid of *R. apiculata* and *R. mucronata*, and not of *R. apiculata* and *R. stylosa* (Parani et al. 1997; Lakshmi et al. 2002). Based on the mitochondrial genome, *R. x annamalayana* is related closer to *R. apiculata* (Parani et al. 1997), on the other hand, with microsatellites; it is related closer to *R. mucronata* (Kumar et al. 2011).

Baba (1994) had previously named species from hybrid of *R. mucronata* and *R. stylosa* with the name of *R. x lombokensis*, based on specimens obtained from the Lombok Island, West Nusa Tenggara, Indonesia. However, the name is less developed and is not used in subsequent publications, despite the provisions of the International Code of Plant Nomenclature, a first-made name is prioritized (McNeill et al. 2005). At this time, the name of *R. x annamalayana* is widely used, but some authors write it as *R. x annamalai* (Lakshmi et al. 2002: Duke 2006b), because it is more proper to Latin grammar than the initial name. This hybrid species is also found in Merbok, the Malay Peninsula (Ong 2003).

The main distribution of *R. x annamalayana* is the east coast of India (Pichavaram, Tamil Nadu), Sri Lanka and the Andaman and Nicobar Islands (Ragavan et al. 2011, 2014; Dahdouh-Guebas 2012). Meanwhile, the distribution of *R. x lamarckii* is much broader and its abundance is

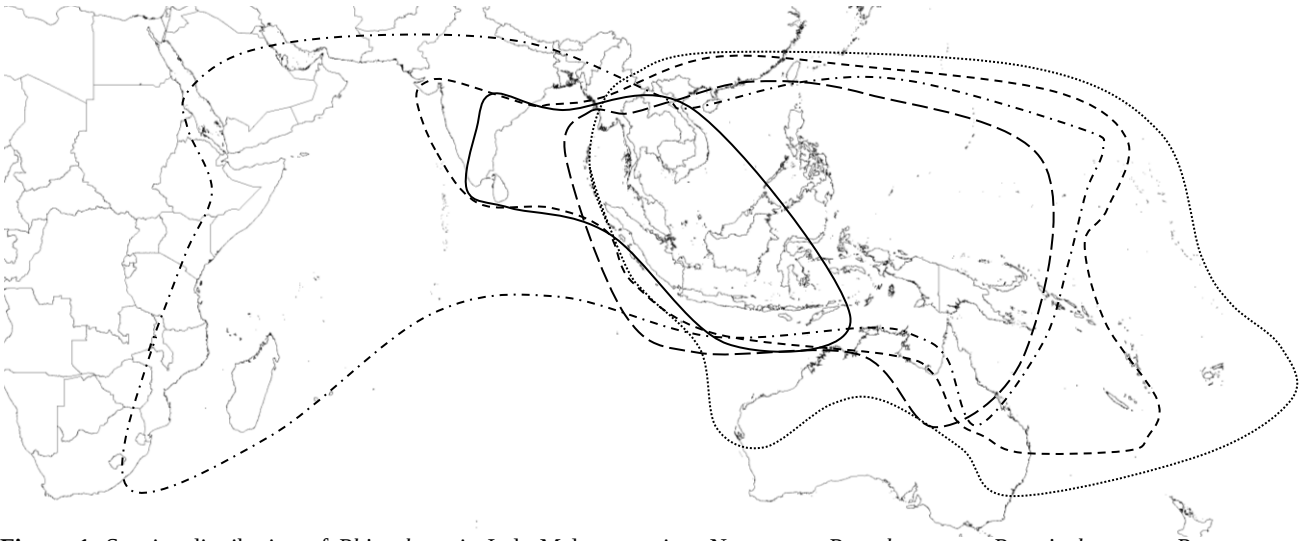

Figure 1. Species distribution of *Rhizophora* in Indo-Malayan region. Note: .....*R. stylosa*, - - - - *R. apiculata*, - . - . *R. mucronata*, — — *R. x lamarckii*, ——*R. x annamalayana* (Duke et al. 2002; Duke 2006b; Giesen et al. 2006; Setyawan and Ulumuddin 2012; Lo et al. 2014).

much higher than *R. x annamalayana*. The last species is only found abundantly in locations where *R. stylosa* is not present, while in locations where the three parents of *Rhizophora* are present, *R. x annamalayana* is far below *R. x lamarckii*. Since, the western distribution of *R. stylosa* does not reach these regions, except for a little stand in Orissa and Andaman and Nicobar state (Ellison et al. 2012), the hybridization is only occurred between *R. apiculata* and *R. mucronata*, but both hybrids are thought to be present in Andaman and Nicobar Islands (ANI), due to the presence of their three parents. *Rhizophora* hybrids are present in the mixed stands of *R. apiculata* and *R. mucronata;* in other places, the hybrids are present along with *R. apiculata, R. mucronata* and *R. stylosa*. Thus, it may be concluded that both *R. x lamarckii* and *R. x annamalayana* might be present in Andaman and Nicobar Islands. These hybrids are easily identified by their height, a large number of flowers with smooth bract and rare occurrence of propagules (Ragavan et al. 2014), and the presence of stamens in two distinct whorls i.e. outer longer stamens and inner smaller stamens (Ragavan et al. 2011).

Meanwhile, in the Malay Archipelago, there is plenty of *R. stylosa.* In many cases, tree density of *R. stylosa* is higher than *R. mucronata*, thus more frequent hybridization between *R. apiculata* and *R. stylosa* generate *R. x lamarckii*. Also, the nature of the style of *R. stylosa* is much longer than the style of *R. mucronata* that is thought to increase of the success of hybridization between *R. apiculata* and *R. stylosa* rather than the hybridization between *R. mucronata* and *R. apiculata* (Setyawan and Ulumuddin 2012).

MORPHOLOGY OF *RHIZOPHORA* HYBRIDS

Lo (2003, 2010) suggested that hybridization in *Rhizophora* is bidirectional and all the known *Rhizophora* in Indo-Malaya (*R. apiculata*, *R. mucronata*, and *R. stylosa*) would play a maternal parent. Thus, it is essential to find the taxonomic distinction between *R. stylosa* and *R. mucronata* for better understanding of *Rhizophora* hybrids. But, the occurrence of undefined intermediate individuals causes the uncertainty to distinguish *R. stylosa* and *R. mucronata*. The question is whether the intermediates are mixed genotypes between variants of one species or between genetically distinct, sibling species. On the current observation of ANI specimens (PR, 2014, pers. obs.), we have observed the intermediates between *R. stylosa* and *R. mucronata* only in place where both coexist. The intermediates are difficult to assign to either taxa but they can be distinguished from *R. stylosa* and *R. mucronata* by following ways, i.e. plenty of flowers less fruiting, more than 8 flowers per inflorescences, distinct leafy growth at base of bud and trichotomous inflorescence branches (Figure 2). Rest of the characters, i.e., style length, leaf shape, and color resembles either *R. mucronata* or *R. stylosa*. Thus, it may conclude that intermediates are variants of one species.

At the same time, we have observed some distinct specimens from sites where *R. stylosa* and *R. mucronata* coexist (Table 1). Some *Rhizophora* has highly leathery leaves with rounded apex, long style and lack of advanced stage of fruits. This specimen resembles *R. mucronata* by its broad leaves, and resembles *R. stylosa* by its long style (5 mm) and differs from *R. stylosa* and *R. mucronata* by its ovate leaves with rounded leaf apex, leathery texture, mostly 2-6 flowered inflorescences, large dimension of mature buds (1.7 cm L, 0.7 cm W)(Figure 3). Based on the above characters this specimen may consider as hybrids between *R. stylosa* and *R. mucronata*, but we have observed only one individual each at two sites with consistent morphological characters. Similarly, we have observed *Rhizophora* which has 2-4 flowered inflorescences with multiple numbers of joints in inflorescences this kind of inflorescences quit different among *Rhizophora* Other distinguishing characters are elliptic leaves folded laterally, intermediate (2-2.5 mm), large dimension of mature bud and occurrence few mature propagules (Figure 4).

In addition, some individuals resemble *R. stylosa* with plenty of flowers and lack of fruiting and *R. mucronata* like with narrow acute leaves, longitudinally fissured bark with plenty fruiting. These observations insist that *R. stylosa* and *R. mucronata* are distinct and they can hybridize. Thus, the intermediates may be hybrids between *R. stylosa*, and *R. mucronata* and hybridization is not restricted to F1 stage. The observation of hybrid between *R. stylosa* and *R. mucronata* by Ng et al. (2013) based on molecular analysis also insist the same. Moreover, Lo (2010) also mentioned that *R. mucronata* and *R. stylosa* are likely to have recently diverged and ISSR data well discriminate the two taxa as separate clusters. It is necessary to find the good specimen of *R. mucronata* and *R. stylosa* for better understanding of their role in hybridization (Figure 6).

Similarly, identification of good specimen of *R. x lamarckii* and *R. x annamalayana* is needed for their taxonomic distinction (Table 2; Figure 7). In places were only *R. apiculata* and *R. mucronata* present the hybrid individual exhibit consistent morphological characters, i.e. broadly elliptic leaves, L/W ratio is <1.8, ovate bud, 4 sided in cross-section, occurrence of stamens in two distinct whorls, light bark with finely fissured in both horizontal and vertical and small style. Similarly, hybrids from areas where only *R. apiculata* and *R. stylosa* present are consistent in following characters, i.e., narrowly elliptic leaves, L/W ratio is 2, ellipsoidal bud, slightly four-sided, occurrence of stamens in two distinct whorls, rough dark grey bark fissured in horizontal, long style. Thus, *R. x annamalayana* and *R. x lamarckii* are distinguished by leaf shape, L/W ratio, bud shape and dimension, peduncle length, bark texture, and style length. But, where all the parental species present the hybrids individuals do not exhibit consistent morphology characters (e.g., Ragavan et al. 2011) and this variation confirms the bidirectional hybridization and potential of all known *Rhizophora* as a maternal parent. The observation of *Rhizophora* with four stamens (Figure 5) and mature propagules from areas where *Rhizophora* hybrids present in mixed strands of *R. apiculata* and *R. mucronata* shows that hybridization is not restricted to F1 stage.

Table 1. Diagnostic characters between *R. x annamalayana* and *R. x lamarckii* of Andaman and Nicobar Islands specimens

Characters	*R. stylosa*	*R. mucronata*
Leaf shape	elliptic, broader towards the apex	ovate, broader at base
Leaf apex	acute	broadly acute
Leaf base	cuneate	rounded
Leaf mucro	spike	spike
Leaf L/W	2.02	1.6
Bark	Dark grey to black smooth finely fissured	Brown to bark grey rough friable horizontally fissured
Petiole L	3.35	2.61
Petiole W	0.23	0.31
Inflorescence branch no.	3	3
No. of flowers per inflorescences	2 to 8	2 to 8
Bract condition	smooth	smooth
Bud L	1	1.47
Bud W	0.43	0.8
Bud L/W	2.39	1.81
Mature bud X section	rounded	rounded
Bud shape	ellipsoidal	ellipsoidal
Peduncle L	3.9	3.15
Peduncle W	0.2	0.3
Petal L	0.8	0.8
Petal W	0.3	0.3
Petal X section	folded	folded
Petal margin	hairy	hairy
Stamen no.	8	8
Style L	4	0.1
Fruit L	2.5	4.5
Fruit W	2	3
Fruit L/W	1.25	1.5
Hypocotyl L	30	51
Hypocotyl W	1.5	1.7
Collar L	1	1.5

Table 2. Diagnostic characters between *R. x annamalayana* and *R. x lamarckii* of Andaman and Nicobar Islands specimens

Characters	*R. x annamalayana*	*R. x lamarckii*
Leaf L	12.39	13.08
Leaf W	7.4	6.45
Leaf L/W	1.67	2
Leaf shape	broadly elliptic	elliptic
Leaf apex	acute	acute
Leaf base	cuneate	attenuate
Leaf mucro	spike	spike
Leaf mucro L	0.34	0.45
Petiole L	2.17	2.39
Petiole W	0.35	0.3
Inflorescence branch no.	1	1
No. of flowers per inflorescences	2 to 4	2 to 4
Bract condition	smooth	smooth
Bud L	1.44	1.65
Bud W	0.86	0.8
Bud L/W	1.68	2.06
Mature bud X section	four-sided	slightly four-sided
Bud shape	ovate	ellipsoidal
Peduncle L	1.3	1.85
Peduncle W	0.5	0.4
Petal L	1.08	1
Petal W	0.36	0.3
Petal X section	curved	curved
Petal margin	slightly hairy	slightly hairy
Stamen No	8 to 16	8 to 16
Style L	0.12	0.3
Fruit L	4	[none]
Fruit W	2.3	[none]
Fruit L/W	1.73	[none]
Hypocotyl L	29	[none]
Hypocotyl W	1.5	[none]
Collar L	1	[none]

Note: Measurement in cm, L = length, W = width.

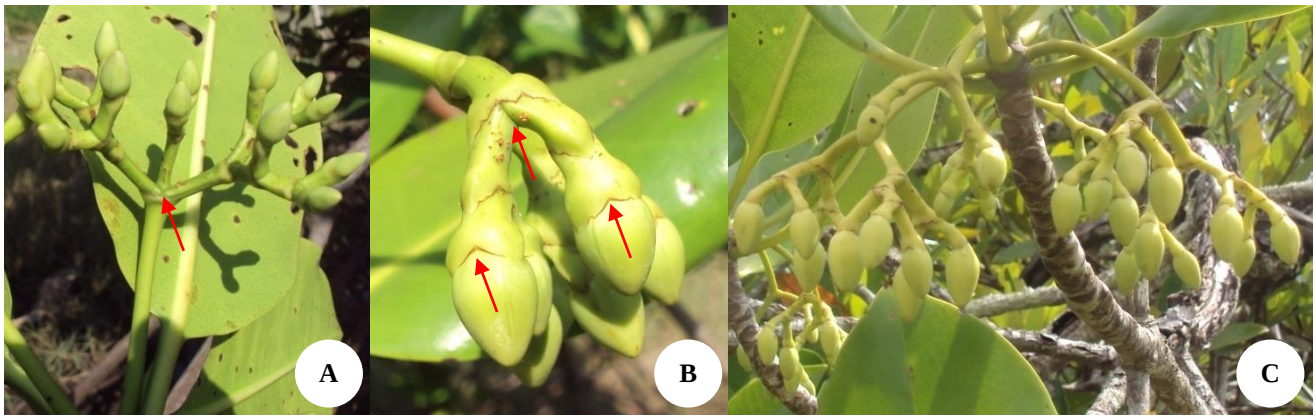

Figure 2. The intermediates between *R. mucronata* and *R. stylosa*. (A) Inflorescence with trichotomous branch, (B) Buds with distinct leafy growth at the base and branching points, (C) Inflorescences with more than 8 flowers.

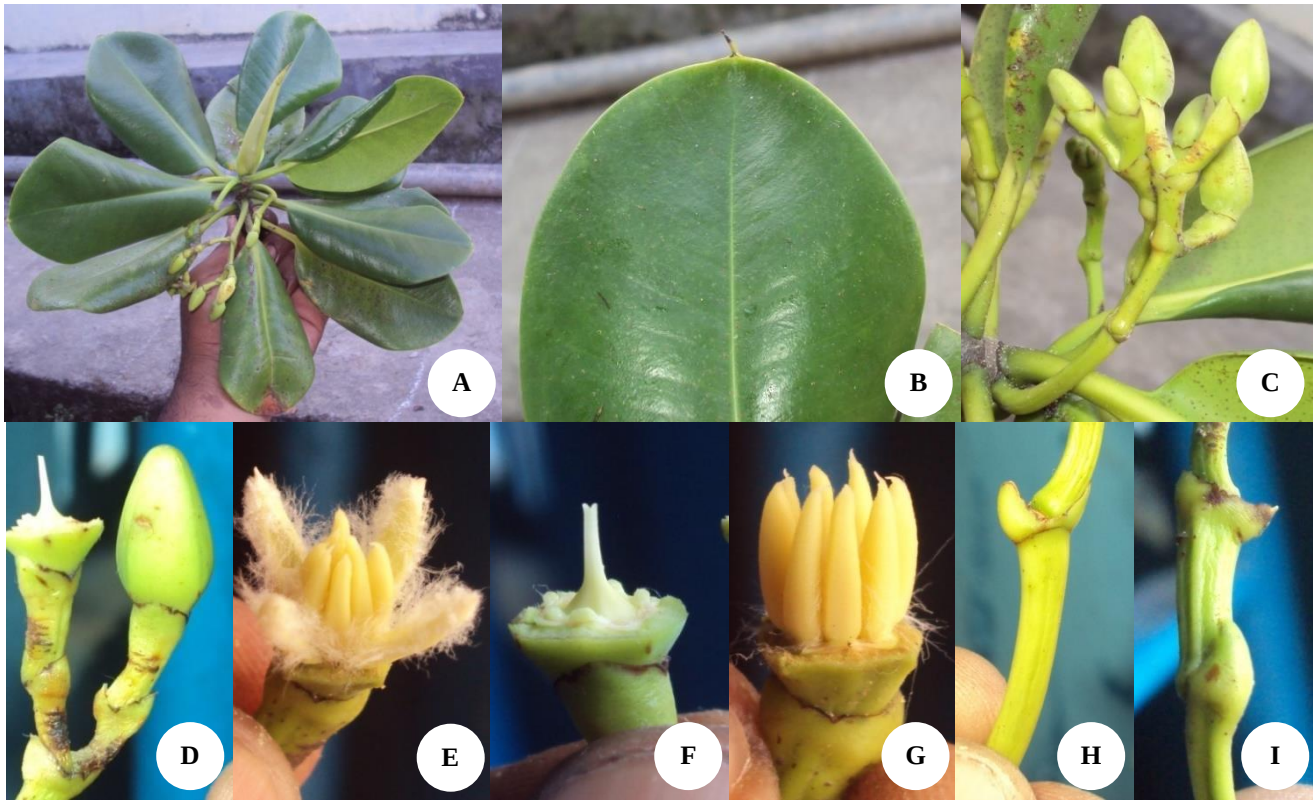

Figure 3. *Rhizophora* with ovate leathery leaves and long style. A. Branchlet, B. Rounded apex, C. Inflorescences, D. Mature bud, E. Stamens and highly hairy folded petals, F. Long style, G. Stamens, H. Two leafy outgrowth at branching point, I. Single leafy outgrowth at first joint.

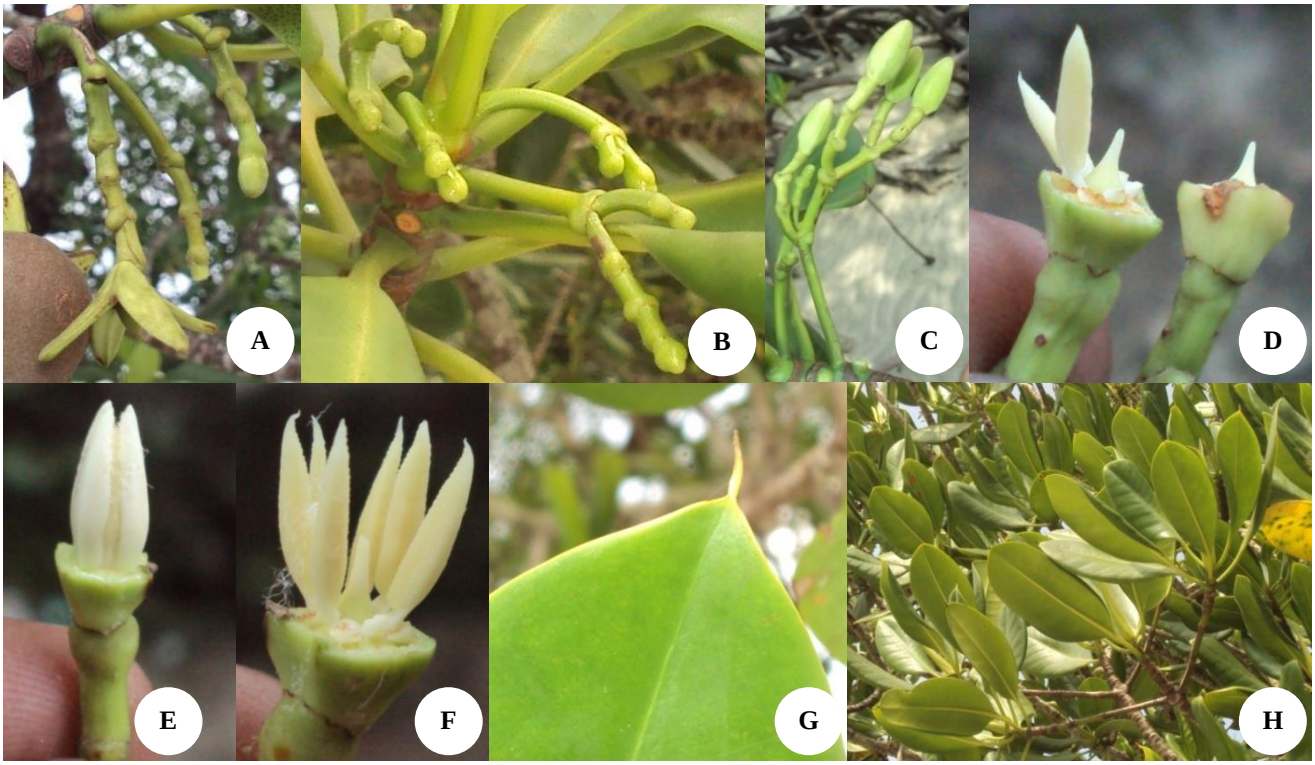

Figure 4. *Rhizophora* having inflorescences with multiple joints (A, B, C); D. Style, E. Petals, F. Stamens, G. Long mucronate, H. Branchlet with laterally folded leaves.

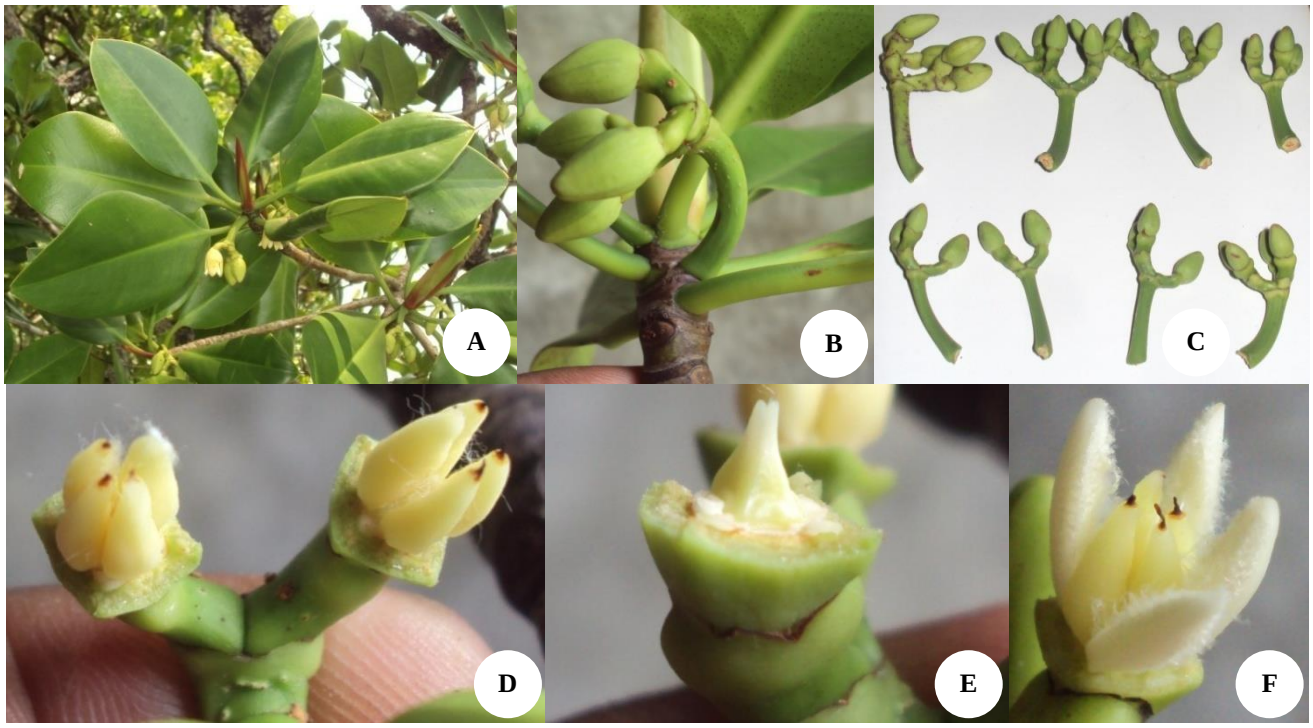

Figure 5. *Rhizophora* with four stamens. A. Branchlet with dark green elliptic leaves, B. Inflorescence with short peduncle, C. Inflorescences with 2-6 flowers, D. Flowers with 4 stamens, E. Four sided ovary with small style (1 mm), F. Hairy thick leathery folded petal.

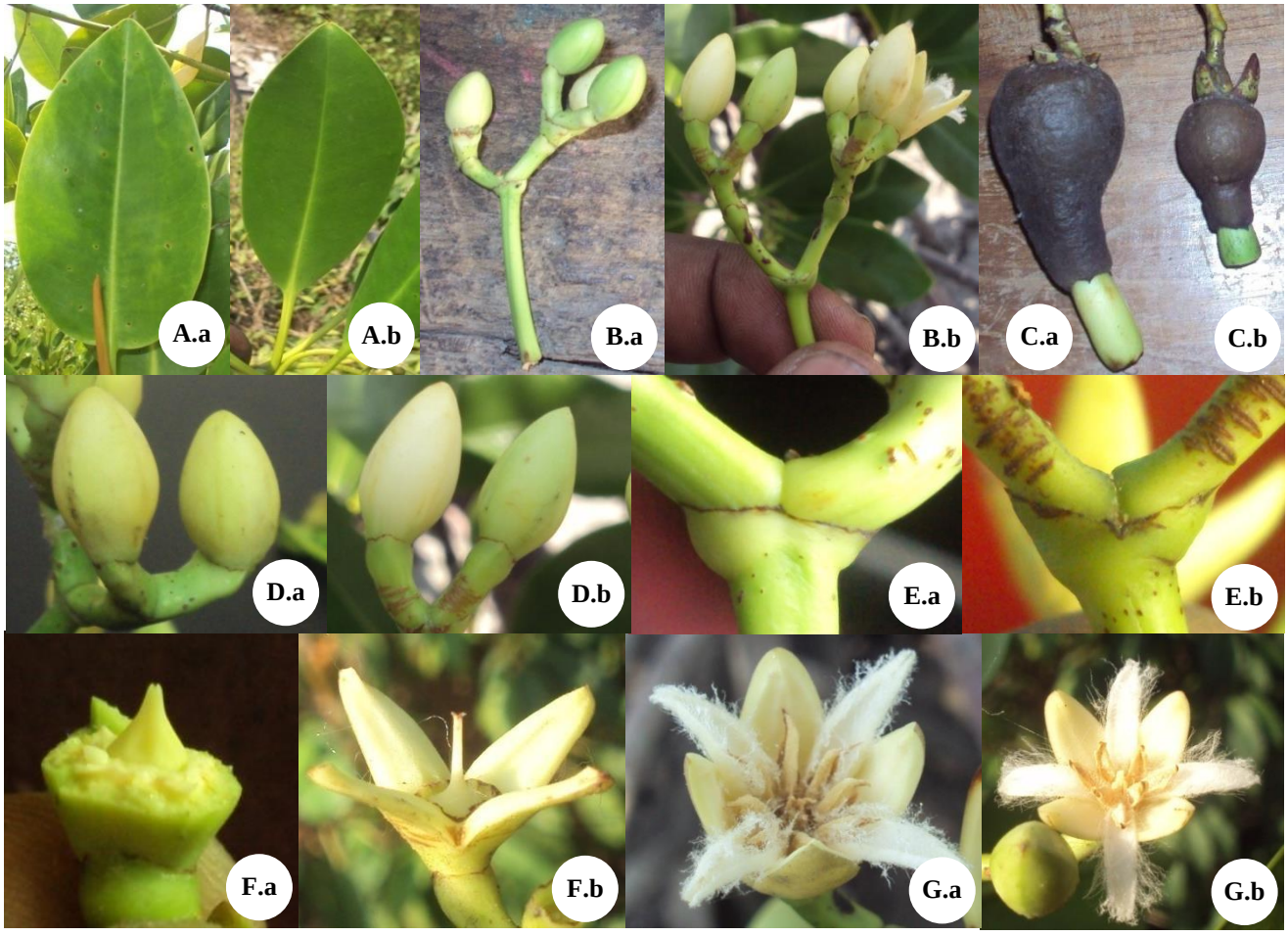

Figure 6. Morphological distinction between *R. mucronata* (left/a) and *R. stylosa* (right/b) of Andaman and Nicobar Islands. A. Leaves, B. Inflorescent, C. Hypocotyl, D. Flower buds, E. Dichotomic branching, F. Styles, G. Flowers

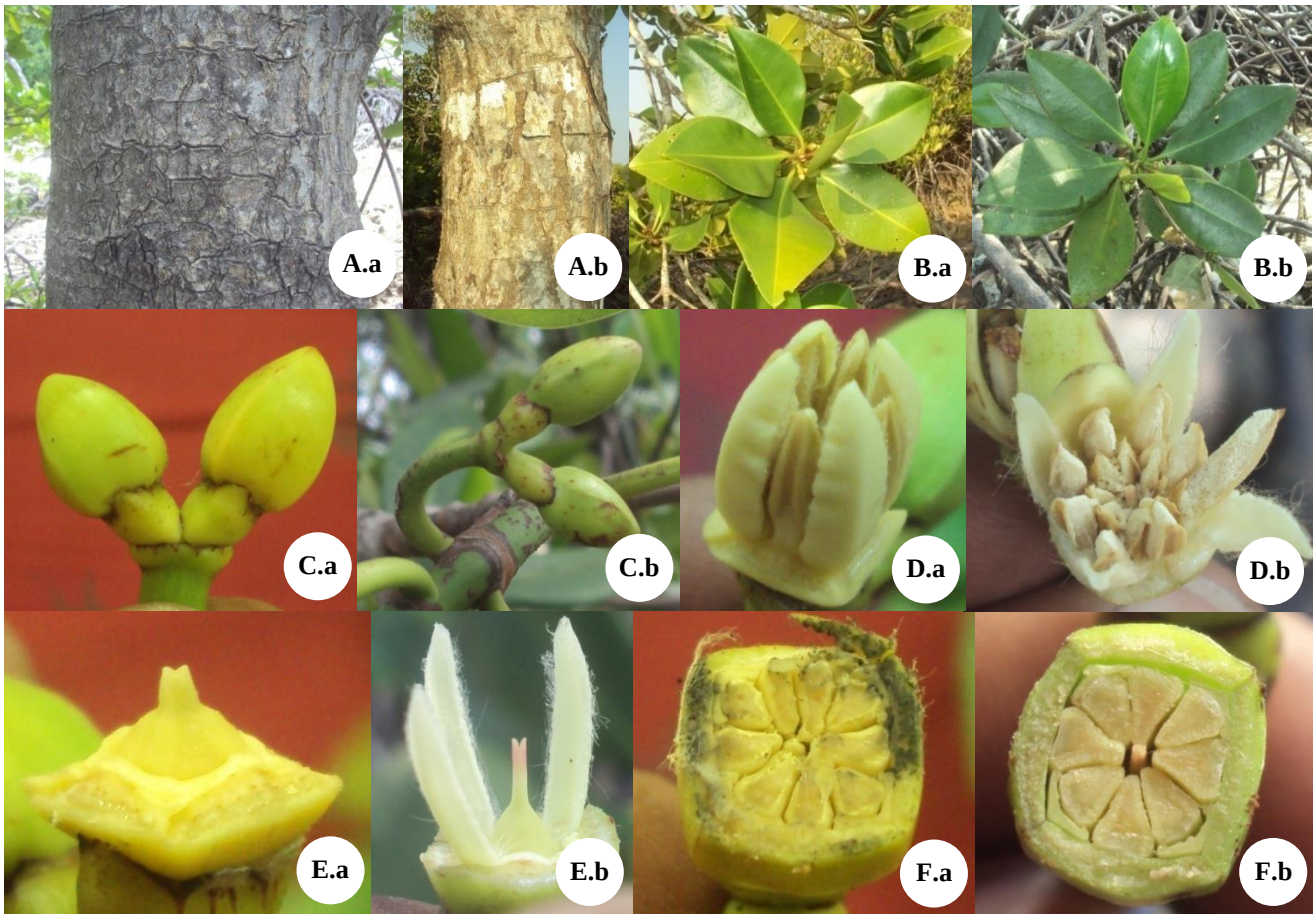

Figure 7. Morphological difference between *R. x annamalayana* (left/a) and *R. x lamarckii* (right/b) of Andaman and Nicobar Islands. A. Bark, B. Leaves, C. Mature bud, D. Stamens in two rows, E. Style length, F. Bud cross-section.

KEY OF IDENTIFICATION

Rhizophora Linnaeus, Sp. Pl. 1: 443. 1753.

Tree or shrub with aerial roots (pneumatophore), which is usually with branches and several meters high from the trunk. Stipules are reddish, sessile, leaf-like, interpetiolar, lanceolate. Stem is medium to high; up to 30-40 m, generally 5-8 m. Stem diameter above the aerial root is 15-35 cm and above the substrate is 0.5 to 7 m. Stem internodes are hollow. The bark is gray to dark-gray and longitudinally fissured, sometimes it is red-brown and smooth. Mature aerial roots stick up 1-2 m, long and slender (*R. stylosa*) or big and strong (*R. mucronata*).

Leaves are opposite or distichous, cauline, leathery, petiolate, simple, light or dark green, obovate, margins revolute, 6-19 cm long, 3-10 cm wide. Petiole is 1-4 mm. Leaf tip is mucronate, 1-7 mm long. Leaf blades are glabrous, elongated middle veins, hard to drop, leaf edge is blunt or serrate near top; elliptic, or obovate (usually elliptic to obovate); pinnately veined (midrib extended into a caducous point); margin is entire or serrulate near apex. Upper surface of the leaves is smooth, shiny. On undersurface, there are spots cork, evenly dispersed, not obtrusive, but are absent in *R. apiculata* and *R. x lamarckii* of the southern Papuasia and northern Australia.

Inflorescences axillary, dense cymes (simple or di- or trichasial); pedunculate, with little to many nodes, 1-2 branching and 1-many flower buds. Flowers are ebracteate; bracteoles forming a cup just below flower; usually 4 or 5 merous. In *R. mucronata*, *R. stylosa*, *R. x annamalayana*, *R. x lamarckii*, and *R. apiculata* consecutive interest lies in node of 1-3, 1-5, 3-5, 3-6, and 6-11 of apical buds. Perianth is with distinct calyx and corolla; 6-32; 2-whorled; isomerous. Calyx tube is ovate (to narrowly ovate), adnate to ovary, persistent; lobes 5-8. Petals tube adnate to the ovary, ovate; sessile, alternating with the calyx, lanceolate; blunt-lobed; valvate; tubular; regular; commonly fleshy (or leathery); persistent. Petals are pale yellow, lobes 4, lanceolate. Flower buds obovate, green to yellowish green, 1-2 cm long, ~1 cm wide.

Corolla lobes are 4, lanceolate stripe, pink to white, furred, ~10 mm long, ~2 mm wide. Stamens are 7-12, yellow; filaments are much shorter than anthers or absent; free of one another; anthers are connivent; dorsifixed; dehiscing by longitudinal valves, introrse, locules many, dehiscing by an adaxial valve; filaments are light green, rounded, 0.5-6 mm above receptacle, two forked tip. The bud of *R. x annamalayana* is longer than *R. x lamarckii* (<1.7 mm). *R. mucronata* bud is longer (> 2 mm) than *R. stylosa* (<2 mm). Ovary is inferior, 2-lobed, apically partly

surrounded by a disk, free part elongating after anthesis; style 1, sometimes very short; stigmas are 4.

Bracts form a bowl just below the flower. Mature bracts of buds are green, slender (*R. mucronata*, *R. stylosa*), green, swollen (*R. x annamalayana*, *R. x lamarckii*) or bright green, swollen (*R. apiculata*). Peduncles 1-7 cm long, ~3 mm wide. Bracteoles in *R. mucronata* and *R. stylosa* are slender (length far exceeds its width) at the base of mature shoots, while the other is as wide as its length or wider than its length. Bracteoles of *R. apiculata* are swollen (wider than its length), corky brown, fused inflorescence, nodes of mature buds and flower are in axillary panicles, at 6-11 nodes below the apical bud, far below the leaves on leafy shoots.

Fruit is brown, ovoid, ovoid-conic, or pyriform. Fertile seed is one in each fruit; germination is viviparous; hypocotyl is protruding to 78 cm before propagule falls. Mature fruit is pear-shaped, elongated, narrowed at the middle, smooth brown surface, elongated petal lobes (when hypocotyl will emerge). In *R. apiculata*, *R. mucronata*, *R. stylosa*, *R. x lamarckii*, and *R. x annamalayana*, mature fruit is respectively located in the leaf axil at 8, 3-5, 4-7, 7 (rare), and 5 (rare), below the apical bud.

Hypocotyl is slender, cylindrical, elongated, green, and smooth with spots of small brown irregular lenticels, half of the distal width is quite broad, the distal tip is generally thorny, but is commonly rounded to blunt at *R. apiculata*. Mature hypocotyl on *R. apiculata*, *R. mucronata*, *R. stylosa*, *R. x lamarckii*, and *R. x annamalayana*, are respectively located in the leaf axil at 9-13, 4-10, 4-9, none, and 8-9 (rarely) below the apical bud. Hypocotyl size is varied and inconsistent in each species, 14-80 cm long, 1-2 cm at its widest point, and 0.5-1.5 cm wide at the collar; hypocotyl elongated to ~75 cm before propagule fall (Ding Hou 1958; Ko 1983; Tomlinson 1986; Duke, 2006; Gathe and Watson 2008). Summary of morphological comparisons is shown in Table 3 and Figure 8.

Nine species, tropics, and subtropics; five species in Indo-Malaya, include Indonesia.

1a. Peduncle is shorter than petiole, thick, on leafless stems; flowers are 2 per inflorescence; bracteoles united, cup-shaped; petals are glabrous; stamen is 9-15.

2a. Bracts are corky brown, flower are hairless ..*R. apiculata*
2b. Bracts are smooth green

3a. Flowers sterile; hypocotyl not formed..... ..... *R. x lamarckii* (*R. apiculata* x *R. stylosa*)
3b. Flowers generally sterile; stamens in two distinct whorls; hypocotyl rarely formed .... *R. x annamalayana* (*R. apiculata* x *R. mucronata*)

1b. Peduncle is usually as long as (or greater than) petiole, slender, in leaf axel; flowers are more than 2 per inflorescence; bracteoles are united at base; petals are pubescent; stamen is 6-8.

4a. Style is less than 2.5 mm (0.5-1.5 mm); anthers are sessile ..... *R. mucronata*
4b. Style isomer than 2.5 mm (4-6 mm); anthers are on a short but distinct filament ..... *R. stylosa*

Table 1. Morphological comparison of *Rhizophora* in Indo-Malaya region.

Part of plant	*R. apiculata*	*R. mucronata*	*R. stylosa*	*R. x lamarckii*	*R. x annamalayana*
Stem	Dark gray with shallow grooves	Dark gray with deep grooves	Reddish brown without grooves	Gray with grooves	Brown with grooves
Leaves	Petiole 1.5-3 cm, midrib on undersurface with a reddish tinge, lamina elliptic-oblong to sub-lanceolate, tip with shoot elongation, the undersurface with clearly black spots	Petiole 2.5-4 cm, midrib on undersurface pale green, lamina broadly elliptical to round elongated, tip with prominent mucronate spurs, undersurface with prominent black spots	Petiole 2.5-3.5 cm, midrib on undersurface pale green, lamina elliptic-wide, tip with prominent mucronate spurs, undersurface with conspicuous black spots	Petiole 2-3 cm, midrib on undersurface light green, lamina obovate-elliptical, tip with prominent mucronate spurs, undersurface with black spots that tight on mature leaves	Petiole 2-3.5 cm, midrib on undersurface light green, lamina obovate-elliptical, tip with clear mucronate spurs, undersurface with clearly black spots
Inflorescence	Always with a pair of buds, arise from the strong peduncles	Branched 2-4 times, 4-8 flower buds appear on long peduncles	Branched 2-4 times, 4-8 buds appear on the elongated peduncles	Branched 1-2 times, 2-4 flower buds appear on short peduncles	Branched 1-2 times, 2-4 flower buds appear on short peduncles
Flowers	Petals glabrous, style 1 mm. Flower on very short stalks.	Petals hairy, style short, 0.5-1.5 mm. Flower on long branching stalks with short style.	Petals hairy, style elongated, 4-5 mm. Flowers on long branching stalks with long style.	Petals slightly hairy, style medium, 2-3 mm	Petals slightly hairy, style short, 1 mm
Fruits	Brown when ripe, 2-2.5 cm. Fruit on very short stalk almost stuck to the branch.	Dark brown when ripe, ovate, 2.5-3.5 cm. Fruit large compared to sepals.	Brown when ripe, ovate, 2 cm. Fruit not thus large compared to sepals.	Sterile	Generally sterile
Propagule	Hypocotyl cylindrical, rounded elongated with blunt ends, up to 30 cm, slightly red color	Hypocotyl cylindrical, warty with pointed tip, up to 30-60 cm, yellow. Very long hypocotyl.	Hypocotyl cylindrical, warty with pointed tip, up to 30 cm, yellow	Sterile	Rarely formed

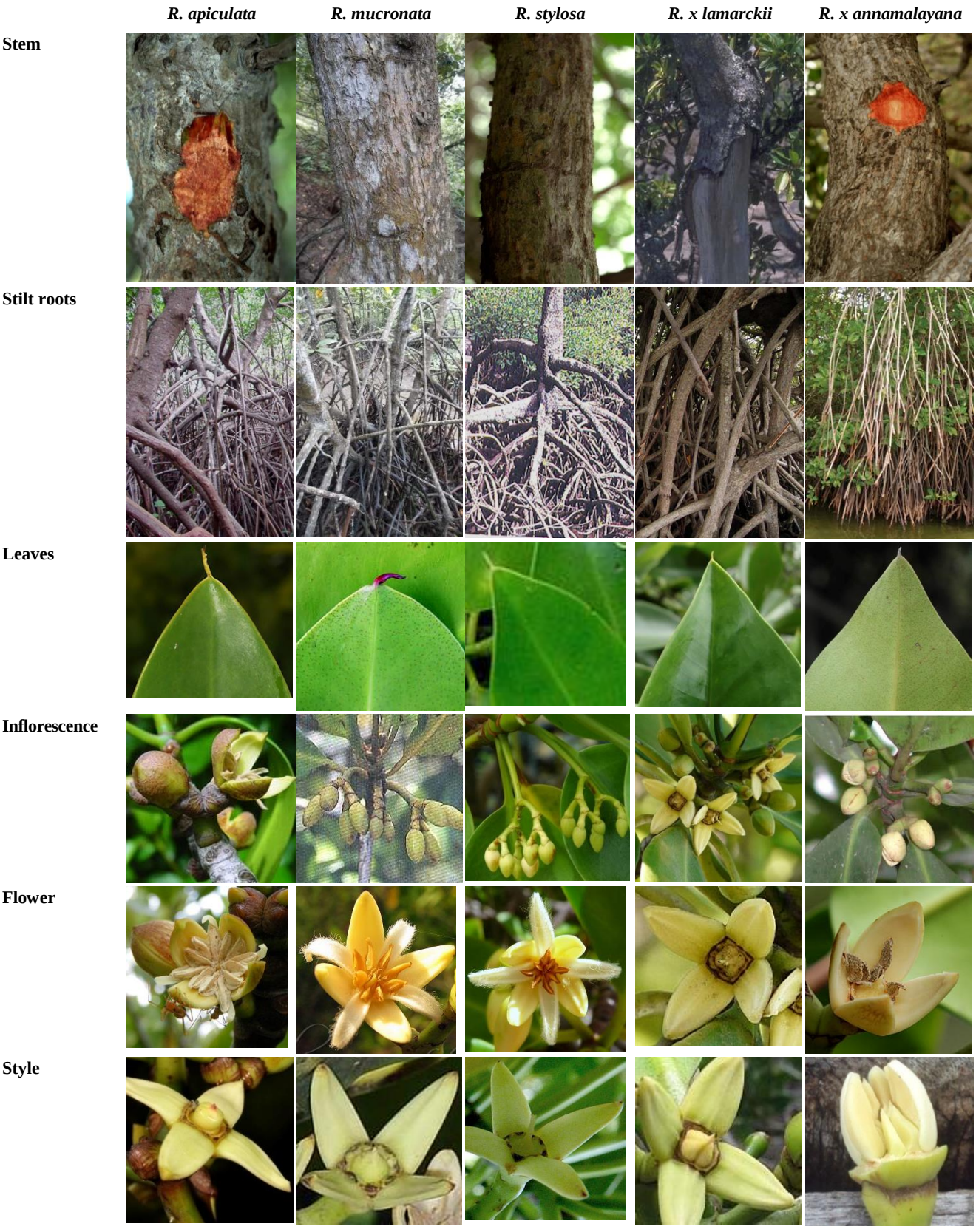
R. apiculata
R. mucronata
R. stylosa
R. x lamarckii
R. x annamalayana
Stem
Stilt roots
Leaves
Inflorescence
Flower
Style

Figure 8. Morphological comparison of *Rhizophora* in Indo-Malayan region. (Photo source from P. Awale, N.C. Duke, J.L.T. Kwong, P. Ragavan, R. Tan, R. Yeo, P.B. Pelser & J.F. Barcelona, etc.).

DESCRIPTION

***Rhizophora apiculata* Blume, Enum. Pl. Javae 1: 91. 1827.**

Syn. *Mangium candelarium* Rumph., *Rhizophora candelaria* DC, *Rhizophora conjugata* (non Linné) Arn., *Rhizophora lamarckii*, *Rhizophora mangle* (non Linné).

Local names. Bakau, bakau minyak, bangka minyak, donggo akit, jangkar, abat, bangkita, bangkita baruang, kalumagus, kailau, parai (Ind.); bakau minyak, bakau tandok, bakau akik, bakau puteh, akik (Mal.); bakauan lalaki, bakauan, bakau, uakatan bakad, bakhau, bakhaw, uakatan, bakauan lalake (Philip.), duoc (Viet.), kongkang, kongkaang bai leu (Thai.), kongkang-slektoch (Camb.)

Description. Trees or shrubs are erect, 3-6 (-30) m tall, and 50 cm d.b.h. Stilt-roots are up to 5 m up the stem. Bark is dark grey and chequered, usually with vertical fissures. Stipules are 4-(6)-8 cm, dropped early. Leaves are crowded at twig tips, opposite, simple, penniveined but venation barely visible, glabrous, narrowly elliptic, and leathery; are dark green with a distinct light green zone along the midrib, tinged reddish underneath. Petiole is 1.5-3.5 cm, usually tinged reddish; and is flanked by leaflets at its base, 4-8 cm. Leaf blade is elliptic-oblong to sublanceolate, 7-19 × 3-8 cm, abaxial midvein reddish, base broadly cuneate, apex acute to apiculate. Undersurface leaves are with reddish-brown spots (cork warts), except for population from southern Papuasia and northern Australia. Inflorescences are 2-flowered cymes; peduncle is 0.7-10 mm. Flowers are ca. 2 cm diam., sessile, yellow-red, placed in axillary bundles, stalk 1.4 cm long. Calyx lobes are ovate, concave, 1-1.4 cm, apex acute. Sepals are 4, yellow-red, persistent, in a recurved form on the end of the fruit. Petals are lanceolate, flat, 6-8 mm, membranaceous, glabrous, white. Petals are 4, yellow-white, membranous, flat, hairless, 9-11 mm long. Stamens are mostly 12, 4 adnate to base of petals, 8 adnate to sepals, 6-7.5 mm; anthers are nearly sessile, apex apiculate. Ovary is largely enclosed by disk, free part 1.5-2.5 mm; style is ca. 0.8-1 mm. Fruit ca. is 2.5 × 1.5 cm, apical half narrower, contain one fertile seed. Hypocotyl is cylindric-clavate, green with purple, club-shaped, ca. 1.8-3.8 × 1-2 cm, blunt before falling. Flowers and fruits throughout the year (Qin and Boufford 2007; Setyawan and Ulumuddin 2012).

Ecology. Grows on the deep muddy soil, gently, which is flooded by normal high tide. Avoids harder substrate mixed with sand. Also prefers tidal waterways with permanently strong freshwater input. Its stilt root branching is likely to be abnormal, caused by beetle damage on root tip. Crabs can inhibit the growth of seedlings due to gobble or peeling hypocotyl skin. Grows slowly, but is blooming throughout the year. Grows up to form a dominant 90% of the vegetation in an area. Grows abundantly in Southeast Asia and are unevenly distributed in Australia (Giesen et al. 2006).

Distribution. South China (Guangxi, Hainan), Cambodia, India, Indonesia, Malaysia, Myanmar, Philippines, Sri Lanka, Thailand, Vietnam; East Africa, North Australia, New Guinea, Micronesia, West Pacific Islands.

Conservation status. Least Concern ver 3.1.

Uses. It is heavy to very heavy wood, and very hard that it requires careful treatment, thus it would not break, but it can be worked out with good results. It is used for pile, beams, and outrigger boats, home interior, furniture, firewood and charcoal. The bark contains up to 30% tannins. Stilt root branching is used to make the anchor, after weighted with stones. It is sometimes planted along the pond to protect levees and dikes. It is used for mangrove rehabilitation and plantation forests (Giesen et al. 2006).

Notes. The leaves of Indo Malayan *Rhizophora* species typically have small reddish-brown spots (cork warts) on their undersurfaces. Spots are present on *R. apiculata* from India to Southeast Asia and northern Papuasia. However, in southern Papuasia and northern Australia, the spots are absent in *R. apiculata* and the hybrid *R. x lamarckii* (Duke et al. 2002).

***Rhizophora mucronata* Lamarck ex Poiret, Encycl. 6: 189. 1804.**

Syn. *Mangium candelarium* Rumph., *Rhizophora candelaria* Wight & Arn., *Rhizophora latifolia* Miq., *Rhizophora longissima* Blanco, *Rhizophora macrorrhiza* Griff., *Rhizophora mangle* (*non* Linné) Roxb., *Rhizophora mucronata* var. *typica* Schimp.

Local names. Bangka itam, dongoh korap, bakau hitam, bakau korap, bakau merah, jangkar, lenggayong, belukap, lolaro (Ind.); bakau kurap, bakau belukap, bakau gelukap, bakau jangkar, bakau hitam (Mal.); bakau, bakauan-babae, bakhau, bakhaw, bangkau, bakauan babe (Philip.), koriki, pabo, togo, tortor, totoa (PNG), dong (Viet.), kongkaang bai yai, kongkang (Thai.)

Description. Trees or shrubs are erect, and up to 27(-30) m, d.b.h. above highest stilt root is up to 70 cm in diam.; bark is dark to almost black, horizontally fissured. It has both stilt roots and aerial roots growing from lower branches. Stipules are 5.5-8.5 cm. Petiole is 2.5-4 cm. Leaf blade is broadly elliptic to oblong, 8.5-23 ×5-13 cm, leathery, base cuneate, apex blunt to acute. Petiole is green, 2.5-5.5 cm long, leaflets are at the base of petiole 5.5-8.5 cm. Inflorescences are forked 2-3 times, 2-5(-12)-flowered cymes; peduncle is 2.5-5 cm. Flowers are sessile. Calyx lobes are ovate, 9-14 × 5-7 mm, deeply lobed, pale yellow. Petals are lanceolate, 7-9 mm, fleshy, partly embracing stamens, margins pilose (densely hairy margins). Stamens are 8, 4 borne on base of petals, 4 borne on sepals, 6-8 mm; anthers sessile. Ovary emerges far beyond disk, free part elongate-conic, 2-3 mm; style is 0.5-1.5 mm. Fruit is dull, brownish green, elongate-ovoid, 5-7 × 2.5-3.5 cm, basally often tuberculate, apically slightly contracted. Hypocotyl is cylindrical, 30-65 cm long, up to 2 cm wide (Qin and Boufford. 2007; Setyawan and Ulumuddin 2012).

Ecology. Grows up in an environment similar to *R. apiculata*, but is more tolerant to sandy and harder substrate. Generally grows in clusters near or on the banks of creeks and tidal estuaries, rarely far from the tides. Optimal growth occurs in deep submerged areas, on the hard ground and rich in humus. This species is one of the most important and widespread mangrove. Flowering occurs throughout the year. Seedlings are often eaten by crab, preventing new growth. Seeds dried in the shade for a few days before planting are less favorable for crab. This process is likely to cause the accumulation of protective tannins. The presence is very abundant (Giesen et al. 2006).

Distribution. Taiwan, Cambodia, India, Indonesia, Japan (Ryukyu Islands), Malaysia, Myanmar, Pakistan, Philippines, Sri Lanka, Thailand, Vietnam; East Africa, Madagascar, Southwest Asia, North Australia, New Guinea, Micronesia, West Pacific Islands. Introduced to Hawaii. Widely distributed in Southeast Asia.

Conservation status. Least Concern ver 3.1.

Uses. It is heavy to very heavy wood, and very hard and strong; shrinks a lot and somewhat is difficult to work on because of its hardness. It is used for firewood and charcoal. The tannin of the bark is used for tanning and dyeing, especially to strengthen the fishing lines and rigging. Sometimes it is used to treat hematuria. It can be grown in fish ponds to protect the levees and dikes, and can be used to make fish traps (Giesen et al. 2006).

***Rhizophora stylosa* Griffith, Not. Pl. Asiat. 4: 665, 1854.**

Syn. *Rhizophora lamarckii*, *Rhizophora mucronata* Lamarck var. *stylosa* (Griffith) Schimper.

Local names. Typically the same as the name of *R. mucronata*, namely: bakau (Ind. and Mal.); bakau pasir (Sing.); bakauan bato, bakhaw, bangkau (Philip.).

Description. Small trees or shrubs are erect and has multi- or single-trunked, often less than 8 m up to 10 m tall. Bark is reddish or pale gray, smooth to rough, fissured; it is 10-15 cm at d.b.h.; stilt-roots are up to 3 m long, and aerial roots emerge from the lower branches. Leaves are broadly elliptic; leaf blade is obovate, 6.5-12.5 × 3-4(-5.5-7.5) cm, base broadly cuneate, apex mucronate, leathery, with a regularly-spotted under surface and appointed tip. Petiole is 1-3.5 cm, with 4-6 cm long leaflets at its base. Inflorescences are axillary, flowers are forked 3-5 times, with 2- to many (up to 32) flowered; peduncle is 1-5 cm. Pedicel 5-10 mm, terete; bracteoles are brown, connate. Calyx lobes are pale-yellow, still present on the fruit, but are then recurved, lanceolate to oblong-lanceolate, 9-12 × 3-5 mm. Petals are white-yellow, 0.8-1.2 cm, involute, margin densely villous/woolly. Stamens are usually 8; filaments are short but distinct; anthers are 5-6 mm. Ovary is emerging beyond disk, free part and shallowly conic and less than 1.5 mm; style is 4-6 mm; stigma lobes are 2. Fruit is green-brown, conic, pear-shaped, 2.5-4 × ca. 2 cm. Hypocotyl is cylindrical (often mistaken for the 'fruit'), 20-40 cm, apex acute. Flowers and fruits are produced throughout the year (Qin and Boufford 2007; Setyawan and Ulumuddin 2012).

Ecology. It can grow on different tidal habitats, such as mud, sand, coarse gravel and pebbles, but prefers a tidal river bank, and is also a pioneer species in coastal areas or outer part of the mangrove ecosystem. One distinctive niche is its ability to grow as the mangrove edges on small coral islands, growing on the coral substrate. This species produces flowers and fruit throughout the year. Abundance slightly common to common.

Distribution. China (Guangdong, Guangxi, Hainan), Taiwan, Cambodia, Indonesia, Japan (Ryukyu Islands),

Malaysia, Philippines, Singapore, Vietnam; North Australia, New Guinea, Pacific Islands.

Conservation status. Least Concern ver 3.1.

Uses. It can be used as wood buildings and utensils, firewood and charcoal. Australian Aborigines use it to make boomerangs, spears and ceremonial objects. Palm wine with low alcohol content and herbs to treat hematuria can be made from its fruit.

***Rhizophora x lamarckii* Montrouz. Mém. Acad. Roy. Sci. Lyon, Sect. Sci. sér. 2, 10:201. 1860**

Rhizophora x lamarckii is a hybrid of *R. apiculata* and *R. stylosa*. This species has much in common with both parents.

Description. Trees or shrubs are erect and up to ca. 25 m, often with several trunks; bark is light brown, smooth to dark grey, rough, and often horizontally fissured. Stilt roots extend to 2(-6) m above the ground, extend downwards from branches. Stem base is diminished below the stilt roots. Leaves are simple, opposite, obovate-elliptic to elliptic, bright yellowish-green, waxy above and dull below, 7-15 cm long, 3-8 cm wide, yellow-green, with a pointed apex and mucronate spike to 6 mm long, and are not evenly spotted below (but old leaves are often liberally wound-spotted); petiole is 1-4 cm long. Inflorescence is axillary, 2-4-flowered (occasionally 1), borne within the leafy shoot; yellow-green or cream flowers which are held within leaf clusters; peduncle is 1-3 cm long, green, smooth; bracteoles are partly united, smooth, yellow-green except a brown crenulate rim. Flowers have 4 calyx lobes and 4 slightly hairy white petals. Petals are ~10 mm long; margins slightly incurved, sparsely hairy. Stamens are variable, usually 9-11; anthers sessile. Upper part of ovary is shallowly conical; style are ~2.5 mm long; stigma minutely 2-lobed. Fruit is rarely found beyond the immature fruit stage. Fruit is shiny, brown-olive, inverted pear-shape, pyriform, 2.5-3 cm long. Hypocotyl is rarely developed, smooth, green, 14-28 cm long, narrowly club-shaped, rounded at apex (Chan 1996; Duke 2006; Setyawan and Ulumuddin 2012).

Ecology. It lives in habitat that same with that *R. apiculata* and *R. stylosa* live.

Distribution. Indonesia, India, Malaysia, North Australia.

Conservation status. This hybrid species has not yet been assessed for the IUCN Red List.

Uses. The wood is used as fire-wood, for construction and charcoal making.

***Rhizophora x annamalayana* Kathiresan, Environ. Ecol. 17 (2): 500, 1999**

Rhizophora x annamalayana is a hybrid of *R. apiculata* and *R. mucronata*. This species has much in common with both parents.

Syn. *Rhizophora* x *annamalai* K.Kathiresan (= *R. apiculata* x *R. mucronata*)

Description. Trees are erect, about 25 m tall; bark brown, with vertical fissured. Leaves are simple, opposite, with short stalks, ovate to elliptical widened, tip apiculate, base cuneate, entire, coriaceous, 10-15 x 5-9 cm. Inflorescence is axillary cyme. Flowers are 2-4, white or cream, hermaphrodite. Petals are 4 lobes, hairy. Stamens are 12 -15, sometimes are very small, staminodium or filamentous. Fruits brown, obpyriform. Hypocotyl is 30-50 cm, smooth, cylindrical.

Ecology. It is commonly found at the top of the tidal area and rarely at the mid-tide.

Distribution. Sri Lanka, India (Pichavaram of Tamil Nadu and Andaman and Nicobar Islands), Malaysia (Merbok, Kedah), Indonesia (Lombok, West Nusa Tenggara).

Conservation status. This hybrid species has not yet been assessed for the IUCN Red List.

Uses. Bark is used as a source of tannin and petroleum coke substitute for calcium carbide, and is used as firewood and medicine; tannins from the bark are used as an insect repellent. The leaves are used as animal feed. Stem with complicated stilt roots is effectively used as a tidal wave breaking to prevent abrasion and forms ideal niches for various species of fauna.

CONCLUSION

In the Indo-Malayan region, there are three species of *Rhizophora* namely: *R. apiculata*, *R. mucronata*, and *R. stylosa* and two putative hybrid species, namely *R. x lamarckii* (*R. apiculata* and *R. stylosa*) and *R. x annamalayana* (*R. apiculata* and *R. mucronata*). Genetically, there is also a hybrid of R. *mucronata* and *R. stylosa*, but because both are sibling species and have very similar morphologic characteristics, the progeny is morphologically indistinguishable from the parent.

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