# An account of *Madhuca* (Sapotaceae) for the Flora of Singapore

## including a comparison of virtual and in-herbarium taxonomic methods

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Thesis submitted in partial fulfilment for the MSc in the Biodiversity and Taxonomy of Plants.

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August 2020

**CONTENTS**



Cover image: The only native representative of *Madhuca* in the Singapore Botanic Gardens: a tree of *M. malaccensis* growing in a remnant patch of rainforest (credit P. Leong).

**ABSTRACT**

An account of *Madhuca* (Sapotaceae) for the *Flora of Singapore* is presented, taking into consideration affinities with species found in the nearby state of Johor, Peninsular Malaysia. Six species are recognised, including 41 synonyms, and two lectotypes are provisionally designated. Two keys to the species are presented, one based on sterile characters and the other on fertile characters. For each species a full species description, image or illustration, specimen citation list and national conservation asssessment are provided. The conservation status of each species since the last national assessment in 2008 is upheld except for *Madhuca decipiens*, which after being rediscovered is now assessed as critically endangered rather than nationally extinct. An evaluation of the effectiveness and limitations of undertaking a virtual taxonomic study amid the global coronavirus outbreak with its reliance on online resources for research is discussed.

**ACKNOWLEDGEMENTS**

I am indebted to my supervisors, Peter Wilkie and Hannah Atkins for their valuable advice, precious wisdom, determined support and constant encouragement, without which this thesis experience would not have been such a joyful and enriching one. I can never thank you enough.

I wish to express my deepest appreciation to David Middleton for his guidance about the *Flora of Singapore* project and untiring responses to my numerous questions, and for generously providing me access to the Herbarium at the Singapore Botanic Gardens (SBG) midway through this project, which marked a true turning point for the findings in this study.

I am sincerely grateful to all the staff at the SBG Herbarium, especially Paul Leong for his beautiful *Madhuca* photos and formidable plant ID expertise, Serena Lee and Bazillah Mohd Ibrahim for the advice and support regarding SING/SINU records, Derek Liew for his wonderful patience in showing me the HerbScan setup and scanning several *Madhuca* specimens requested, Koh Sin Lan, Juriah binte Sabudin, Suganthara Davi for the multiple kindnesses, Lim Weihao and Paul Parasuraman Athen for sharing your amazing field expertise and being so generously persuaded to accompany me into the jungle to search for *Madhuca* trees, and Lua Hock Keong at the National Biodiversity Centre for conservation insights. Special thanks to Martin Pullan for troubleshooting all the issues I faced with PADME at incredibly short notice and setting up the image download function that proved infinitely useful. Also the wonderfully patient librarians at RBGE and SBG who either patiently scanned pages when students had no physical access to libraries, or quickly pointed me to the right shelves to save me time searching catalogues.

I am thankful to all my RBGE and UoE tutors for imparting the skills and knowledge that allowed me to undertake this thesis, especially Louis Ronse de Craene, Mark Hughes, David Harris, Colin Pendry, Axel Poulsen, Antje Ahrends, Pete Hollingsworth, Markus Ruhsam, Aline Finger, Chris Jeffree, Jen Farrar, Michael Möller, Crinan Alexander, Greg Kenicer, Peter Wilkie, Hannah Atkins, Catherine Kidner, Alex Twyford, Rebecca Yahr, Katherine Hayden, Joanne Taylor, David Mann, Mary Gibby, Kerry Walter, Neil Bell, Chris Ellis, Tiina Särkinen, Peter Moonlight, Toby Pennington, Martin Gardner, Philip Thomas, Caroline Lehmann, Richard Milne, Zoë Goodwin, Edeline Gagnon, Francisco Gutierrez, and Adolfo Jara. You have lit a botanical flame in me that I believe will never be extinguished. To my fellow MSc coursemates, thank you for all the amazing memories during this strange year, especially in Colombia, and I hope that we will be able to celebrate our graduation together some day, after the coronavirus pandemic has passed.

And finally, I am always grateful to my beloved husband for his unwavering support throughout all my endeavours, botanical and otherwise.

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# 1. INTRODUCTION

## *1.1 Aims of the Project*

The principal objectives of this research are to:

- Undertake a taxonomic study of *Madhuca* J.F.Gmel.[1] (Sapotaceae) to produce an account of the genus for the *Flora of Singapore*.

- Present a taxonomic history of the circumscription of the genus.

- Explore affinities of *Madhuca* species found in Singapore and those in the nearby Malaysian state of Johor, Peninsular Malaysia.

- Investigate the circumscription and taxonomic status of genera often confused or closely related to *Madhuca* in the region, in particular key vegetative characters of *Ganua* Pierre ex Dubard and *Payena* A. DC.

- In response to the worldwide coronavirus (COVID-19) outbreak, which has effectively shut down field studies, herbarium and laboratory work, evaluate the advantages and limitations of conducting taxonomic research solely using online resources.

- Make recommendations on how current efforts can be improved to maximise the utility of online resources for taxonomic study, to guide future research under similar conditions.

## *1.2 Introduction to Madhuca*

Sapotaceae is a medium-sized family made up of approximately 50 genera and 1,000 species of pantropical trees and shrubs with a worldwide distribution, but particularly abundant in the understoreys and canopies of wet, lowland forest in Asia and the Neotropics (Pennington, 1991, 2004). *Madhuca*, a genus within Sapotaceae, was first published by the German naturalist

[1] Per convention, the author of a genus or species is cited the first time it is mentioned in the thesis but only the name thereafter.

Johann Friedrich Gmelin in the 13th and last edition of *Systema Naturae*, in the same form and style as Carl Linnaeus' preceding records (Gmelin, 1791). *Madhuca* is an Indian plant name (Ng, 1972); in Sanskrit, 'madhu' means sweet or honey, and 'madhukar' means 'honey-maker' (Hanks et al., 2006). The type species is *Madhuca longifolia* J.F.Macbr. A more detailed account of the genus is given in section 1.3.

*Distribution*

*Madhuca* is primarily a Malesian genus with its centre of diversity in Borneo and the Malay Peninsula (Royen, 1960). While distributed from India, Sri Lanka, South China, Malesia to New Guinea (Fig. 1), about 70% of the approximately 100 *Madhuca* species may be found in Peninsular Malaysia and Borneo, around 30 and 40 respectively (Govaerts et al., 2001). Although Royen (1960) considered this concentration of *Madhuca* particularly remarkable, other large genera in the family such as *Palaquium* Blanco have a similar western Malesian distribution. In fact the distribution of Sapotoideae, one of the major clades of Sapotaceae that encompasses *Madhuca*, is centred in that region; the majority of species in Sapotoideae (ca. 300 out of 500) occurs in the Indo-Pacific, followed by Africa with half that species richness, then the Americas with half the number of Africa (Smedmark et al., 2006).

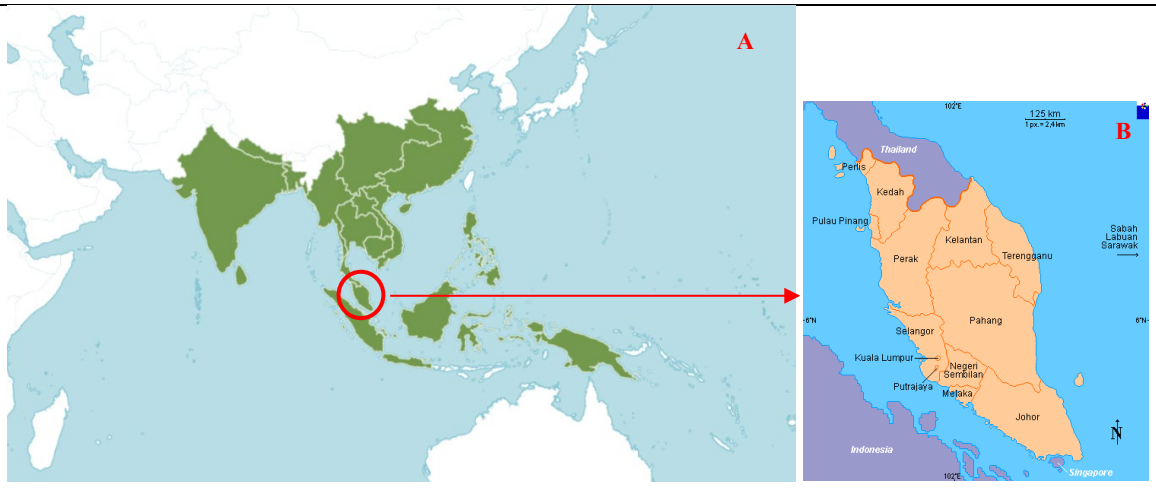



Figure 1: **A.** Distribution map of *Madhuca* J.F.Gmel. (reproduced from POWO). **B.** Map showing major states in Peninsular Malaysia (orange), Singapore, parts of Thailand and Indonesia (reproduced from FOTW)

*Uses*

In Malaysia, the attractive reddish timber of Sapotaceae has been integral to the silviculture industry, and *Madhuca*, *Palaquium* and *Payena* are the key genera used. Timber groups are

generally classified into ‘bitis’ or ‘nyatoh’ (Ng, 1972), where bitis, including *M. betis* J.F.Macbr. and *M. utilis* H.J.Lam, is an extremely strong hardwood used in heavy construction like shipbuilding, and nyatoh is a lightweight to medium-heavy hardwood, produced by *M. burckiana* H.J.Lam, *M. malaccensis* (C.B.Clarke) H.J.Lam, *M. motleyana* (de Vriese) J.F.Macbr. and *M. sericea* (Miq.) H.J.Lam (Fig. 2). Nyatoh enjoys popularity for fine-grained furniture, decorative panelling, veneers and parquet flooring (Ani & Barnett, 1999). However Wyatt-Smith (1954) observed that the trees of *Madhuca* were not sufficiently common for the timber to be of genuine commercial importance and the Malaysian Ministry of Plantation Industries and Commodities has focused more on quick growing tropical hardwoods for forest plantations, including *Acacia* Mill. species (Fabaceae) and *Khaya* A.Juss. species (Meliaceae) (Abd Latif et al., 2018).


Figure 2: Product images of Malaysian timber (Malaysian Timber Council).
**A.** Bitis **B.** Nyatoh

The type species, *Madhuca longifolia,* has long been known in India as the Mahua or butternut tree, where not just the seeds are an economically useful source of edible oils, but where the flowers, bark and leaves are also utilised in traditional medicine for ailments as wide-ranging as bronchitis, leprosy, diabetes or snake-bites (Yadav et al., 2012). Mahua flowers are even used as currency in some parts of India, where they are sold to obtain essential items such as food (Twari et al., 2011). Other than the Indian species *M. latifolia* J.F.Macbr. and *M. longifolia* that provide sources of alcohol and oil, *Madhuca* is of limited value as a source of gutta-percha (latex) or food, though the fruit of *M. obovatifolia* Merr. in the Phillipines is edible, and the seeds of *M. motleyana* can be used to produce fat for cooking despite the odour of bitter almonds (Burkill, 1966).

*Ecology*

Together with Burseraceae, Dipterocarpaceae and Fabaceae, Sapotaceae is a major family of large trees in Malaysia, and like most Sapotaceous genera, *Madhuca* can be found in primary forest to 1,650 m altitude and is common in freshwater swamps (Ng, 1972). *Madhuca motleyana* is a key species found in low-lying peat swamps in as many as seven Malaysian states while *M. hirtiflora* H.J.Lam, *M. sericea* (Miq.) H.J.Lam and *M. kingiana* (Brace ex King & Gamble) H.J.Lam are relatively widespread in lowland forest (Fig. 3), and *M. penangiana* H.J.Lam and *M. penicillata* H.J.Lam can be found on hills and some mountains (Wyatt-Smith, 1954).


Figure 3: Images of *Madhuca kingiana* in Singapore (credit: Yeoh Yi Shuen)
**A.** Forest tree **B.** Sapling on forest floor

There have been few studies on the pollination biology of *Madhuca* species in Southeast Asia, but in India, the flowering *M. longifolia* is known to be visited by monkeys, squirrels and birds (Kundu et al., 2012), and both pollination and seed dispersal for *M. latifolia* were found to be performed by pteropodid bats (Mahandran et al., 2018).

Royen (unpublished[2]) noted that some nuts of *Madhuca* species including *M. motleyana*, were dispersed by freshwater, "…(falling) into the streams in Malayan and Bornean forests and are drifted down, often in great abundance. As they float the Malays and Dayaks catch them in nets for trading purposes."

[2] Pieter van Royen was a co-worker of Herman Johannes Lam, director of the Rijksherbarium between 1933 and 1962, and revised several large genera within Sapotaceae including *Madhuca* (Royen, 1960). He had worked on an account of the family for Flora Malesiana, containing around 16 genera and 260 species, which remains unpublished (Wilkie, 2011).

### *1.3 Taxonomic History of Madhuca*

*Major synonyms: Bassia* J.Koenig and *Ganua* Piere ex Dubard

Many *Madhuca* species in its current circumscription were formerly recognised in the genus *Bassia* (Linnaeus, 1771). Linnaeus described the type species, *Bassia longifolia* L.*,* as a tall tree with entire, ovate-lanceolate leaves clustered at the ends of curving branches, with axillary inflorescences and flowers that were simple, narrow, elongated and pendulous (Fig. 4).

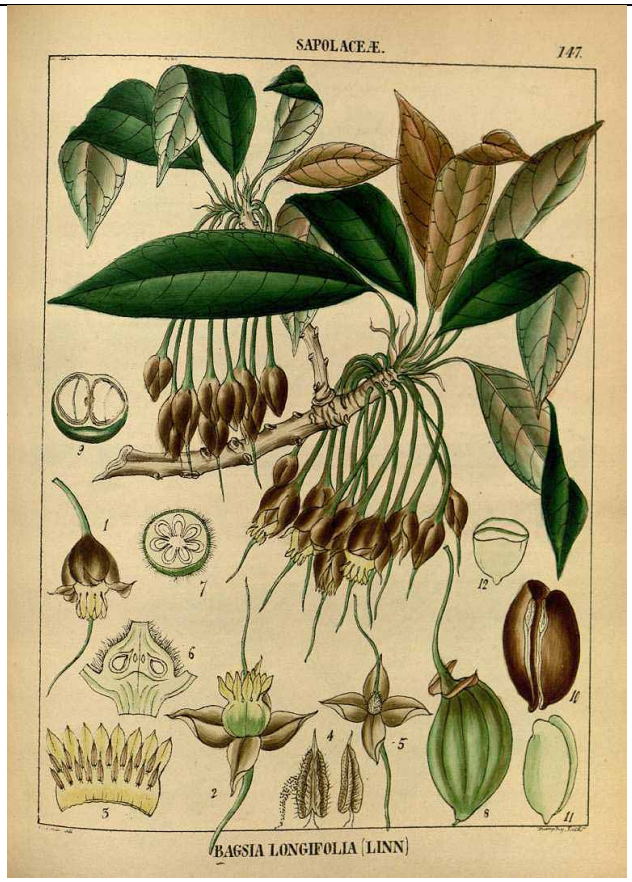



Figure 4: Illustration of *Bassia longifolia* (Reproduced from Wight, 1850).

However, Macbride (1918) explains clearly why Linnaeus' naming of *Bassia longifolia* was illegitimate, since *Bassia* Allioni (now in Amaranthaceae) had been validly published earlier in 1766. Engler (1890) rightly replaced *Bassia* in his account of Sapotaceae, unfortunately the name that he used, *Illipe* F.Muell., was also incorrect since Koenig's reference to *Illipe* in Linnaeus (1771) was not to confer a name to the genus, but to explain the vernacular Tamil name of the tree known to the native inhabitants of the Malabar coast. Indeed, as the publication of the genus *Illipe* (Mueller, 1884) was under the mistake that Koenig had changed the name

of that genus to *Illipe*, King & Gamble (1906) thus reverted to *Bassia* Koenig when they published their revision of Sapotaceae. However, recalling the nomenclatural validity of the earlier name *Bassia* Allioni, Macbride (1918) rightly reiterates that the first available name for the species within *Bassia* J.Koenig has to be *Madhuca*.

*Ganua* Pierre ex Dubard (1908) had largely been kept a separate genus until subsumed into *Madhuca* in the generic monograph of Sapotaceae by Pennington (1991). The Malay native name for latex, 'ganu', provides the derivation for *Ganua* (Ng, 1972). Dubard described some of the key features of *Ganua* as very low inserted ovules, imperfectly closed cells of the conoidal ovary, a thin pericarp and a differential leaf nervation. Lam (1925, 1927) expanded the genus, adding new species found in Malaysia and Singapore. In the last major revision of *Ganua*, Assem (1953) states that the genus is distinguished by "…terminal vegetative bud often with conspicuous bud scales, often with stipules; tertiary venation mostly longitudinal; sepals mostly with distinct dark hair tufts; ovary gradually contracted into the hollow style, septa almost always imperfect, leaving the basal placentra free; pericarp thin and dry; testa of seeds thin, scar linear; albumen membranous." However, these characteristics have been called into question, particularly given the close relationship between *Ganua* and *Madhuca* (Tab. 1). Earlier accounts by King & Gamble (1906) as well as Ridley (1923) had already united *Ganua* and *Madhuca* from the Malayan Peninsula under *Bassia*. Despite retaining *Ganua* in his family revision, Ng, a Malaysian field botanist, expressed doubt over Assem's definition of *Ganua*, observing that species of both *Ganua* and *Madhuca* had reticulate tertiary nerves, and that Assem's distinguishing characters were "…clumsy and in practice extremely difficult to apply" (Ng, 1972). These doubts were supported by Pennington (1991), who recognised *Ganua* as a synonym of *Madhuca* after comparing the 18 species of *Ganua* described by Assem with all species of *Madhuca.* In this comparison he showed that the generic characters on which *Ganua* were based were inconsistent and no longer tenable: notably, 11 species of *Ganua* had reticulate tertiaries, the most frequent arrangement in *Madhuca*, and that tufts of hair at the apex of the sepals, the linear seed scar and thin layer of endosperm occurred in both *Ganua* and *Madhuca*. Pennington and Ng also neither found nor replicated the description of 'bud scales' by Assem.

Recent phylogenetic studies (Richardson et al., 2014) support the placement of *Ganua* in *Madhuca*: Fig. 8 shows most of the *Madhuca* species sampled occuring in two major clades (K and L) and that species previously in *Ganua* (namely *G. curtisii* H.J.Lam*, G. kingiana* (Brace) Assem and *G. motleyana* Pierre ex Dubard; now *M. curtisii* Ridl., *M. kingiana* and *M.*

*motleyana*) do not form a separate clade but are scattered within the clades containing *Madhuca* species.

Table 1: Selected characters used to distinguish *Ganua* and *Madhuca* in historical keys and taxonomic accounts (Ng, 1972; Kochummen, 1997)

| Genus | Common | Leaves | Veins | Stipules |
|---|---|---|---|---|
| ***Madhuca*** | Tertiary nervation of leaves not descending; spiral leaf arrangement on all shoots, 4 sepals, thick cotyledons, thin/absent endosperm. | Woolly or velvety on underside (some species) | Not looping | Small, indistinct, dropping early (*M. kunstleri* H.J.Lam) |
| ***Ganua*** | | Completely glabrous or woolly on stalk or midrib only | Looping at margin | Small, indistinct, dropping early (some species)<br><br>Large, 0.5-2.8 cm, scale-like, conspicuously covering twig tips and often persisting along twigs (some species) |

*Generic limits, subgeneric classifications and intergeneric relationships*

Such convolutions in generic delimitation are not uncommon in Sapotaceae, given the numerous overlapping morphologies amongst a large number of taxa. Pennington (1991) noted that "characters unique to a genus are extremely rare in the Sapotaceae, so the use of single characters to define genera causes instability, depending which character is selected". Lam (1925), too, asserted that "no one will confound a characteristic *Payena* with the type of a *Madhuca*, but the boundaries of each of the genera accepted are extremely vague and to a high degree suspending from the individual taste of the author".

Lam (1925, 1927) subdivided *Madhuca* into two sections, section Dasyaulus and Kakosmanthus. These were based on the presence of a tertiary nerve parallel to the secondary nerves, reaching the margin of the leaf in Dasyaulus, and absent in Kakosmanthus. However, Royen (1960) disregarded this subdivision, noting the inconsistency manifested by *M. korthalsii* H.J.Lam in section Kakosmanthus where tertiary nerves toward the margin are present. Subsequent authors such as Ng (1972) also did not follow Lam's sections.

This difficulty in establishing unique morphological features or discrete diagnostic characters has been manifested by extremely diverse classification schemes, ranging from Baehni's (1965) monograph recognising 63 genera, six tribes and three subfamilies, to Aubreville's (1964) account containing almost double the number of genera (122), 15 tribes and four subfamilies. In Pennington's (1991) classification, which is the most comprehensive and recent

family synthesis based on morphology, 53 genera, five tribes and three subtribes are recognised.

*Madhuca* falls within the tribe Isonandreae (Tab. 2, Fig. 5), the other tribes being Chrysophylleae, Omphalocarpeae, Mimusopeae and Sideroxyleae. The similarities of the staminode-lacking genera in Pennington's Isonandreae (*Aulandra* H.J.Lam*, Burckella* Pierre*, Diploknema* Pierre*, Isonandra* Wight*, Madhuca, Palaquium,* and *Payena*) follow earlier tribal circumscriptions, and overlap with Lam's (1939) Madhuceae (*Aesandra* Pierre ex L.Planch*, Burckella, Diploknema*, *Madhuca, Ganua, Payena, Tropalanthe* S.Moore) and Aubreville's (1964) Madhuceae (*Aesandra, Burckella, Chelonespermum* Hemsl.*, Ganua, Isonandra, Madhuca, Payena*). However, Pennington's careful consideration of relevant suites of characters is an improvement upon earlier versions, in particular Lam's lack of first hand knowledge of American or African species, and Aubreville's sprawling monograph where numerous genera were mostly defined upon single variable characters.

Important characters used in contemporary morphology-based classifications of the Sapotaceae include the number of corolla lobes vs. calyx lobes, the presence or absence of corolla lobe appendages and the presence or absence of staminodes (Pennington, 1991). Baehni's (1938, 1965) treatments were notable in that unlike all previous classifications, he placed primary emphasis on the position of the seed scar (lateral or basal). James Sinclair, former Curator of the Herbarium at the Botanic Gardens in Singapore, known for his many collections and repeated trips to study tree phenology, made an energetic rebuttal of Baehni's inclusion of *Payena* species into either *Madhuca* or *Isonandra*, stating that Baehni "has been carried away" by seed character (Sinclair, 1967). For one of Baehni's *Isonandra* species, Sinclair convincingly recounts that he checked and collected 22 seeds from the tree (actually *Palaquium obovatum* Engl.), finding that "every one of these has the scar extending along the entire length of the seed almost from end to end and in no case did the scar terminate three quarters way up as shown by Baehni".

Table 2: Combination of characters used in the diagnosis of genera in Isonandreae (Pennington, 1991)

| Genus | Leaves | Calyx | Corolla | Stamens | Ovary | Seed scar | Endosperm |
|---|---|---|---|---|---|---|---|
| ***Madhuca*** | Spirally arranged | Biseriate 2 x 2 free | (6-)8-12(-17) | (12-)14-36(-43) | Glabrous | Long narrow adaxial | Present or absent |
| ***Aulandra*** | Spirally arranged | Biseriate 2 x 3 free or united at base | 6 | 18-19 | Hairy | Broad adaxial covering 2/3 of surface | Absent |
| ***Burckella*** | Spirally arranged | Uniseriate 4 partly united | 8(-9) | 16-18(-30) | Hairy or glabrous | Covers at least 1/2 of surface | Absent |
| ***Diploknema*** | Spirally arranged | Uniseriate (4-)5(-6) free or partly united | 8-16 | (10-)16-30(-80) | Hairy or glabrous | Broad or narrow adaxial scar | Present or absent |
| ***Isonandra*** | Spirally arranged | Biseriate 2 x 2 ± free | 4(5) | 8(-10) | Hairy | Long narrow adaxial | Copious |
| ***Palaquium*** | Spirally arranged | Biseriate 2 x 3 free or slightly united | (5)6 | 12 | Hairy | Broad adaxial | Usually absent |
| ***Payena*** | Alternate and distichous, sometimes spirally arranged | Biseriate 2 x 2 ± free | 7-9 | 13-20(-30) | Hairy or glabrous | Long narrow adaxial | Copious |

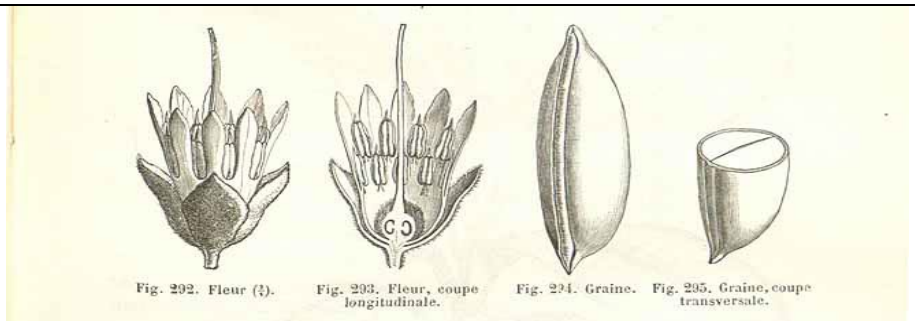



Figure 5: Illustrations of *Madhuca longifolia* flower and longitudinal section, seed and transverse section (Reproduced from Baillon, 1891).

### *1.4 Molecular Advances in Sapotaceae Classification*

Set against this complex and often contradictory morphological background, molecular studies have advanced our understanding of the family's circumscription, though phylogenetic relationships for all genera have not yet been completely resolved.

*Isonandreae: from paraphyly to monophyly?*

The first family-wide phylogenetic studies, based on the chloroplast coding region *ndh*F (Anderberg & Swenson, 2003) and then a combined analysis using molecular and morphological data (Swenson & Anderberg, 2005), determined that Pennington's (1991) tribal circumscription of Isonandreae was paraphyletic. In these early phylogenetic results, one well-supported clade corresponded to Mimusopeae and parts of Isonandreae (*Madhuca*, *Payena* and *Palaquium*), and another moderately-supported clade contained the remaining representative genera of Isonandreae (*Burckella*, *Diploknema*). The phylogenetic relationships between these clades were not resolved (Fig. 6). Monophyly was recovered for several genera including *Diploknema* and *Payena,* although with very little sampling, but not *Madhuca*, which was represented by just one species, *M. microphylla* (Hook.) Alston.

Echoing earlier classifications, Swenson & Anderberg (2005) did not find any single unique morphological character in their tribal diagnosis, and they proposed a now widely accepted three-subfamily classification of Sapotoideae, Sarcospermatoideae and Chrysophylloideae, in line with the main clades recovered in their phylogenetic work. The subfamily Sapotoideae includes the tribes Sideroxyleae and Sapoteae, the latter of which contains *Madhuca*, *Payena* and *Palaquium* from Pennington's tribe Isonandreae, as well as subtribes Mimusopinae and Manilkarinae (Fig. 6). The rest of the Isonandreae genera, *Burckella* and *Diploknema*, were treated as tribus insertae sedis, and *Aulandra* and *Isonandra* were not sampled, although Swenson & Anderberg (2005) considered they probably belonged to Sapotoideae.

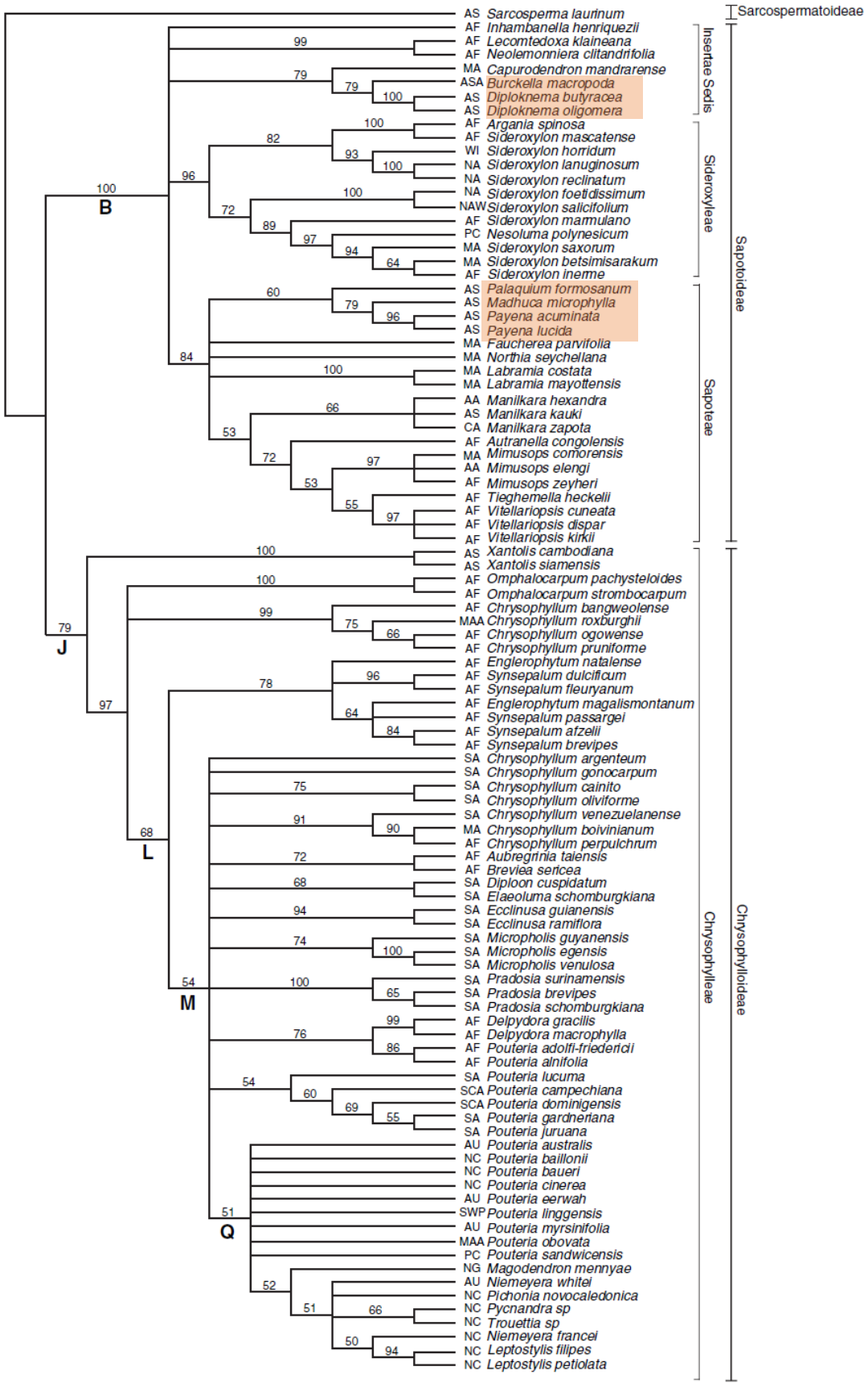



Figure 6: The revised system of Sapotaceae classification to subfamilies and tribes, reproduced from Swenson & Anderberg (2005). Jackknife support for groups are indicated above the branches. Isonandreae genera (Pennington, 1991) are highlighted in orange .

Subsequent to Swenson & Anderberg's (2005) major re-classification of Sapotaceae, Smedmark et al. (2006) used an enhanced chloroplast sequencing dataset, with *ndh*F in addition to the regions *psb*M-*trn*D, *trn*H-*psb*A, *trn*C-*trn*D, and *trn*C-*psb*M, to further illuminate subfamily relationships within Sapotoideae. This time, more than one species of each genera was included to better test monophyly. *Madhuca* was represented in addition to *M. microphylla* with *M. hainanensis* Chun & F.C.How and *M. longifolia*. Unfortunately (and partly due to still-limited taxon sampling) the relationships between genera within Isonandreae remained largely unresolved (Fig. 7) .

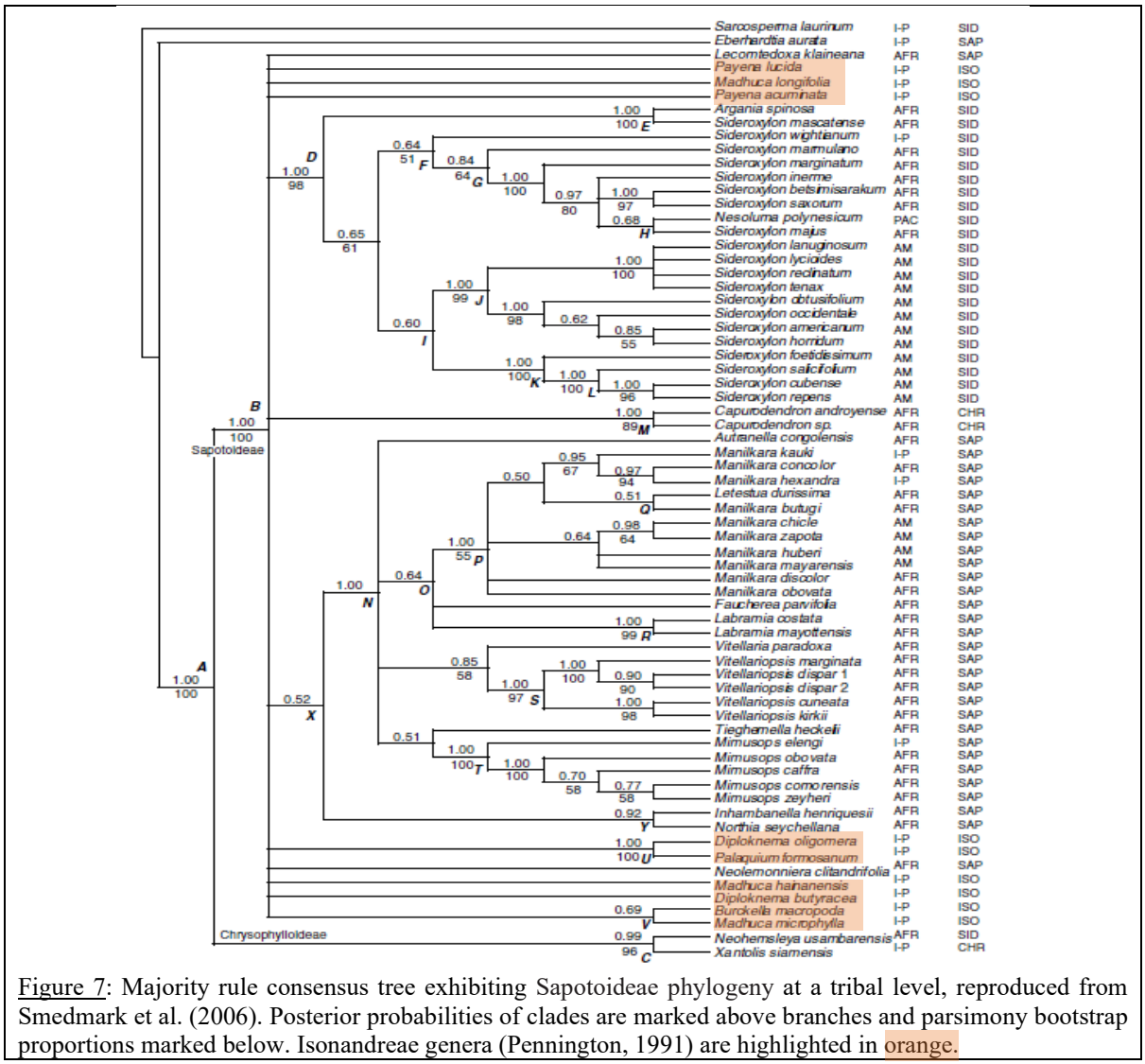



Figure 7: Majority rule consensus tree exhibiting Sapotoideae phylogeny at a tribal level, reproduced from Smedmark et al. (2006). Posterior probabilities of clades are marked above branches and parsimony bootstrap proportions marked below. Isonandreae genera (Pennington, 1991) are highlighted in orange.

Richardson et al. (2014), in a study focusing on diversification rates in Isonandreae, included a phylogenetic analysis with increased sampling, (46 nuclear and plastid sequences (ITS, *trn*H-*psb*A, *trn*C-*trn*D, *trn*C-*psb*M and the 3' end of *ndhF*) for 80 out of the approximately 200

species of Isonandreae), strongly supported the monophyly of the tribe Isonandreae. Generic limits within the tribe, however, still require further scrutiny. Although there is a strongly-supported clade consisting of most of the *Madhuca* species (K–L in Fig. 8), another clade indicates that *Madhuca, Isonandra* and *Diploknema* (G–J in Fig. 8) are polyphyletic. Furthermore, *Aulandra longifolia* H.J.Lam and *Diploknema butyracea* (Roxb.) H.J.Lam are nested within *Palaquium*.

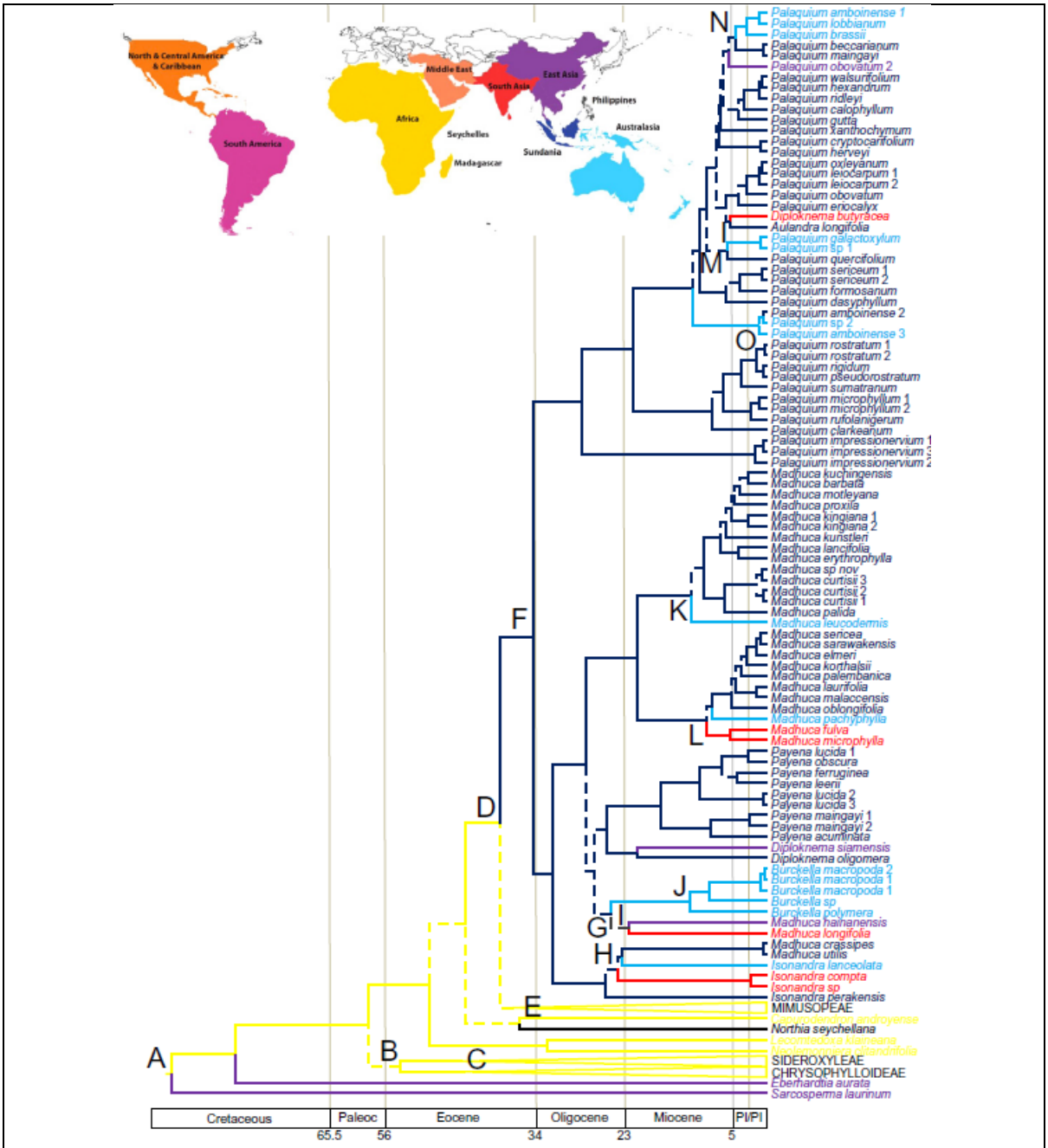



Figure 8: Maximum clade credibility tree indicating strong support for the monophyly of Isonandreae, and showing the relationships to other major clades, reproduced from Richardson et al. (2014). The broken lines represent nodes with posterior probability values < 0.95. The dark blue lines, representing Sundania, indicate the proliferation of Isonandreae species from that region as a result of the phylogeographical analysis.

A notable outcome of these phylogenetic studies is that virtually all 'important' morphological characters, including the number and arrangement of sepals, the number of petals relative to sepals, or the presence or absence of staminodes, are not reliable characters for classifications. Swenson & Anderberg (2005) demonstrated many such characters as homoplasious: for instance, staminodes are plesiomorphic, being lost multiple times in certain clades and reappearing in others. This has since guided subsequent taxonomic decisions, and Mackinder et al. (2016) reiterated that staminodes are no longer a character upon which a monophyletic genus in Sapotaceae can be based.

*Floral development in Sapotaceae*

Kumpers et al. (2016) mapped floral structures in Sapotaceae onto an up-to-date phylogeny to study evolutionary trends. Stable synapomorphies for certain clades were found to justify coordinated fluctuations in merism (Fig. 9). Three scenarios were presented: (i) a merism increase impacting organs more or less equally (applicable to *Palaquium*); (ii) an increase in petals, stamens and carpels without affecting sepals (*Payena* and *Madhuca*); or (iii) increased carpels independent of other organs (*Burckella*). A major finding was that throughout Sapotaceae except for genera in Isonandreae, the antesepalous stamen whorl was lost, and that the two fertile stamen whorls in Isonandreae demonstrated either a plesiomorphy or reversal.

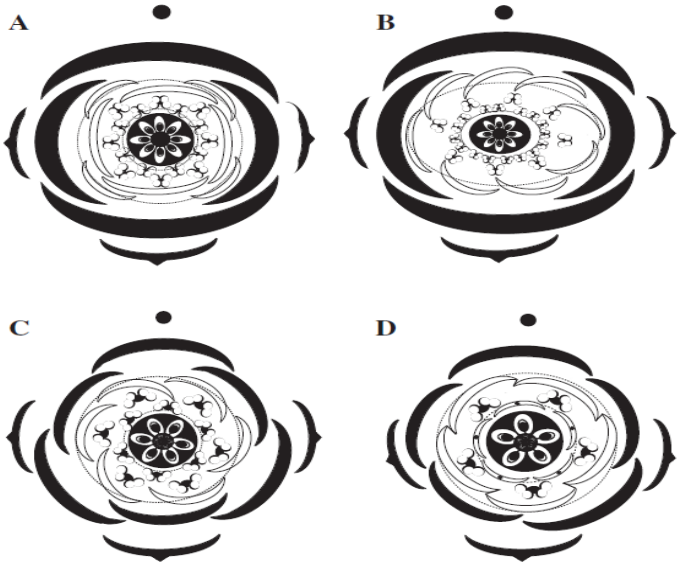



Figure 9. Floral diagrams of selected Sapotaceae species, including from Isonandreae (reproduced from Kumpers et al., 2016). A. *Payena leerii* Kurz; B. *Madhuca malaccensis*; C. *Palaquium amboinense* Burck; and D. *Sideroxylon inerme* L. showing that antesepalous stamens are sterile-like in all clades other than Isonandreae. The uppermost black dot on each diagram represents the main shoot axis; black arcs, sepals; black arcs with middle triangles, bracts/bracteoles; white arcs, petals; white arcs with middle black dots, staminodes; broken lines, stamen-petal tube limits.

*Diversification rates in Sapotaceae*

Having a relatively well-sampled molecular phylogeny of the Sapotoideae has allowed estimations of diversification rates to be made, although different studies have shown varying node ages and ancestral ranges. One reconstruction of the crown node for Isonandreae, inclusive of the largest clade of *Madhuca* (K–L in Fig. 8), demonstrated the most probable origination from Sundania, with an age of ca. 36.5 Ma (Richardson et al., 2014). In contrast, Armstrong et al. (2014) estimated an age of ca. 52 Ma for Isonandreae with Africa having the highest ancestral range probability. These differences are reflective of study-dependent fluctuations in the mean of the crown-group node for Sapotaceae: from 107 Ma, to 84.5 Ma, to only 58.3 Ma (Armstrong et al., 2014, Richardson et al., 2014, and Rose et al., 2018 respectively).

The most recent study (Rose et al., 2018) produced a clear geographic signal for Indo-Malaysia as the ancestral range for Sapotaceae, and demonstrated that Sapoteae, where *Madhuca* is now nested, has historical pan-Indian connections through Australasia, Indo-Malaysia and the Afrotropics. Similar to the rest of Ericales, Sapotaceae saw rapid speciation later in the history of the order, which for certain genera such as *Madhuca*, *Payena* and *Palaquium*, occurred within an Indo-Malaysia range (Fig. 10); this finding helps to shed light on today's concentrated Malesian distribution of *Madhuca*, and is not wholly inconsistent with the suggestion by Richardson et al. (2014) that Southeast Asia acted as a more vibrant epicentre of speciation than the Neotropics for Isonandreae.

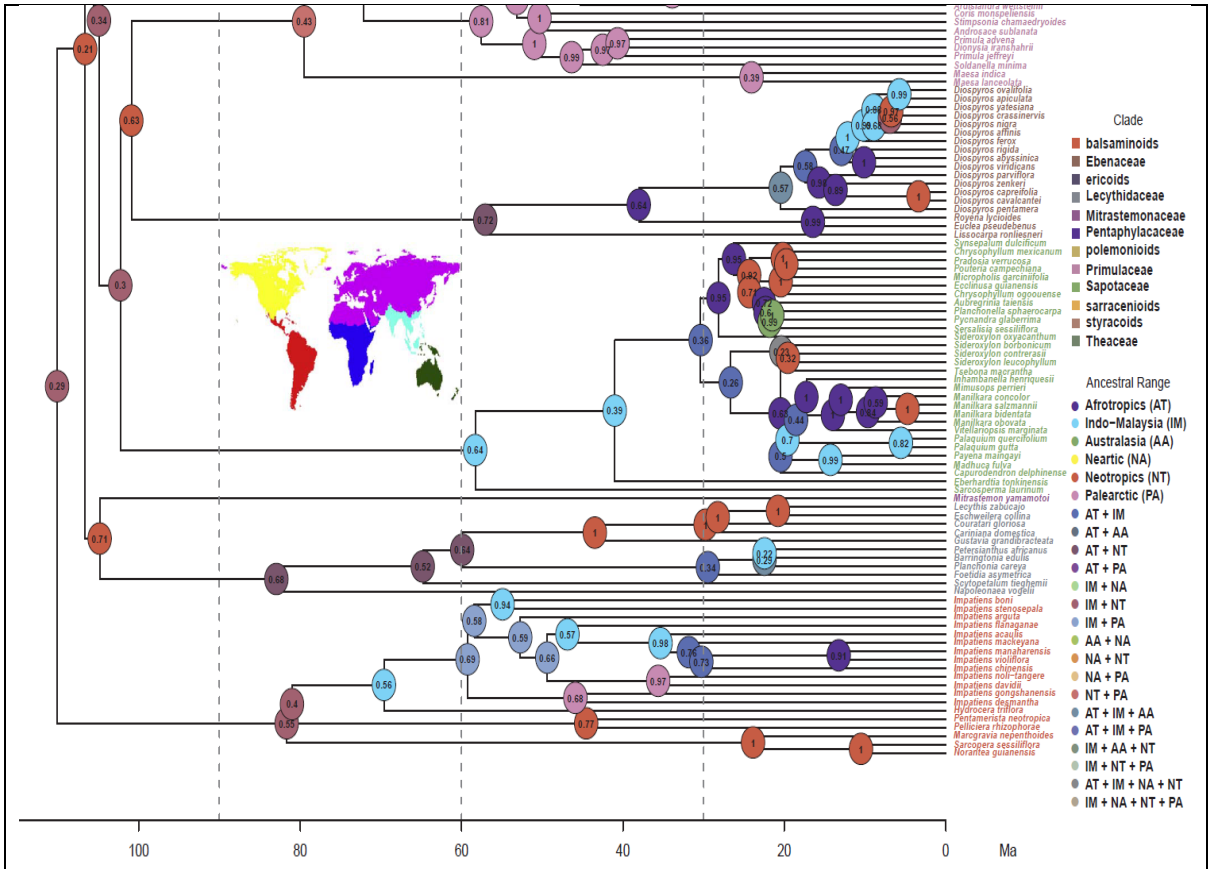



Figure 10. Circles at nodes indicate the most likely ancestral range for major Ericales clades (Sapotaceae species are in green), with the probability indicated within the circles. Chronogram reproduced from Rose et al. (2018).

# 2. MATERIALS AND METHODS

Due to the COVID-2019 pandemic and related institutional lockdowns, project work was conducted between 14 May and 6 July 2020 using information only accessible online or stored on computer hard drives. Post 6 July, physical access to the collections in the Herbarium of the Singapore Botanic Gardens (SING) was available.

## *2.1 Taxonomic Investigation*

### *2.1.1 Sources of Information*

A list of *Madhuca* species names recorded as occurring in Singapore and Johor was compiled from Chong et al. (2009) and Turner (1995).

Relevant literature was accessed through online sources such as the Biodiversity Heritage Library (biodiversitylibrary.org) and the Botanicus Digital Library (botanicus.org). This was guided by citations in the World Checklist of selected plant families (wcsp.science.kew.org), the International Plant Names Index (ipni.org), the Tropicos database (tropicos.org) and previous taxonomic work on *Madhuca* and *Ganua* (e.g. Assem, 1953; Royen, 1960; Ng, 1972; full reference listings are in the taxonomic treatment). Where literature could not be found online, staff at RBGE kindly shared previously-scanned personal copies or provided scans of relevant pages whenever they were able to access hardcopies from the RBGE Library.

The JSTOR Global Plants database (jstor.org/global-plants/) provided access to images of types, accompanied by information including the collector name, date and location (where known), the herbarium location of the specimen and barcode (if available). The types of names accepted in the taxonomic treatment presented in this thesis were located and examined. Types for heterotypic synonyms were not examined unless they were relevant to the distribution covered in this thesis (Singapore and Johor).

General specimen records of *Madhuca* species from Singapore and Johor were extracted from the Sapotaceae Resource Centre (Wilkie et al., 2008–). This website shares data and images from various herbaria compiled by a range of Sapotaceae researchers and entered into the

RBGE PADME database. The website currently provides access to more than 45,000 specimen records.

Information on all herbarium specimen images of *Madhuca* from Singapore, including collector, collector number, date of collection, locality, geographical coordinates (latitude and longitude) was captured in an excel spreadsheet, and cross-checked with existing entries in the PADME database. Erroneous entries were corrected, missing data was entered, new images attached to records, and coordinate information added. Coordinate information was sourced from Chen et al. (2014) for Singapore localities and Hamidah et al. (2011) for Peninsular Malaysia.

A list of collector details (name and number) was compiled for inclusion in the exsiccatae of the flora account. These are recorded as they appear on the herbarium labels, rather than using prior knowledge to record them under the person coordinating the collection programme. This considers the common historical practice of prominent botanists having collectors. In some taxonomic accounts, labels stating the collector name have been converted to the name of the botanist whom the collector was working for. For instance, Mat (a short reference for Ahmad bin Hassan) was a known collector for Ridley (Sinclair, 1967), and past treatments such as Royen (1960) frequently ignored Mat's name written on the label, instead recording Ridley as the collector. The alternative approach, which is followed in Ng (1972) and here, is to record what is written on the label and recognise the actual collector.

A list of SINU herbarium records of *Madhuca* collected in Singapore was obtained from staff at the National University of Singapore (Appendix 1), however visitor access to examine specimens remained prohibited throughout the duration of this project.

### *2.1.2 Digital Specimen Images*

Digital images of *Madhuca* specimens collected from Singapore and Johor were viewed from the following herbaria: SING, SAN, SAR, KEP, K, E and L (Herbarium acronyms follow Index Herbariorum, Thiers (continuously updated)). These images were accessed via a range of sources including the JSTOR Global Plants database, the BioPortal database of the National Herbarium of the Netherlands, the RBGE Herbarium Catalogue and the Sapotaceae Resource Centre. Officially-scanned images of *Madhuca* species collected in Singapore and held at SING

were provided directly by herbarium staff. Images of specimens held at SINU were not available due to institutional closures.

Images from institutional digitisation initiatives, individual researchers (via PADME) and global data compiling sites were assessed for their utility in capturing important taxonomic detail. The following criteria were used: quality of image resolution (i.e. above 300 pixels/dots per inch - dpi), presence of scale bar, availability of a virtual measuring tool, presence of a colour chart, quality of specimen lighting (i.e. without borders and shadows) and consistency of image (i.e. height horizontally above specimen). Based on these criteria the utility of a specimen image was rated as high, medium or low. Institutional scans (usually professionally produced) with resolution of at least 300 dpi, scale bars and/or virtual measuring tools would automatically be rated as high, due to the ability to capture qualitative and measurable macro-morphological characters in the taxonomic description. Medium-ranked images would capture no measurements, but contain information on qualitative macro-morphological characters and collection details that would contribute at least five aspects (e.g. leaf shape, number of secondary veins, number of flowers on inflorescence, collector notes on ecology or colour) to the taxonomic description. Low-ranked images would capture less than three aspects. Flowering or fruiting specimens often differentiate medium- or low-ranked images, since there would be additional fertile characters to describe (e.g. number of flowers on inflorescence, shape of fruit or seed).

### *2.1.3 In-herbarium Analysis*

After the Herbarium facilities at the Singapore Botanic Gardens were opened to visitors from 6 July 2020, SING specimens could be examined using a stereo dissecting microscope (Olympus SZX7) and light attachments. Venation patterns were recorded when using a light source to better discern indentations and shadows. Photographs of material seen from a microscope were taken with a smartphone camera (iPhone 8 Plus).

As micro-morphological characters or hidden areas such as fertile parts or indumentum could not usually be described from specimen images (even professionally-scanned images), flowering and fruiting specimens located in SING were prioritised for examination once access to the herbarium was possible. While it would have been preferred to measure at least five specimens of each species with flowers or fruits, it was not possible given the limited

collections from Singapore in SING. Even when specimens contained fertile material, some were either too degraded or sparse to sufficiently capture relevant details. Hence measurements from Singapore collections were supplemented and compared with those in Johor and other states in Peninsular Malaysia (where Johor specimens were lacking) held in the SING herbarium.

### *2.2 Species Concept*

As currently there is a lack of sufficient phylogenetic information (e.g. complete ITS data) to delineate *Madhuca* species, this account utilises a morphological species concept, with phenetic criteria to delimit species separated by a discontinuity in characters (Crisp & Weston, 1993).

### *2.3 Morphological Character Assessment*

Images from initial online resources were sorted virtually into taxon piles; this was replicated when access to actual specimens was possible in the SING herbarium.

A matrix of morphological characters was compiled for each specimen. Morphological definitions (Fig. 11–12) follow Beentje (2016), and details pertaining to leaves, particularly venation (Fig. 13) follow the Leaf Architecture Working Group (1999) and Hickey (1979). Important definitions used intensively (Fig. 11–13) are reproduced from the Leaf Architecture Working Group (1999) and Beentje (2016).

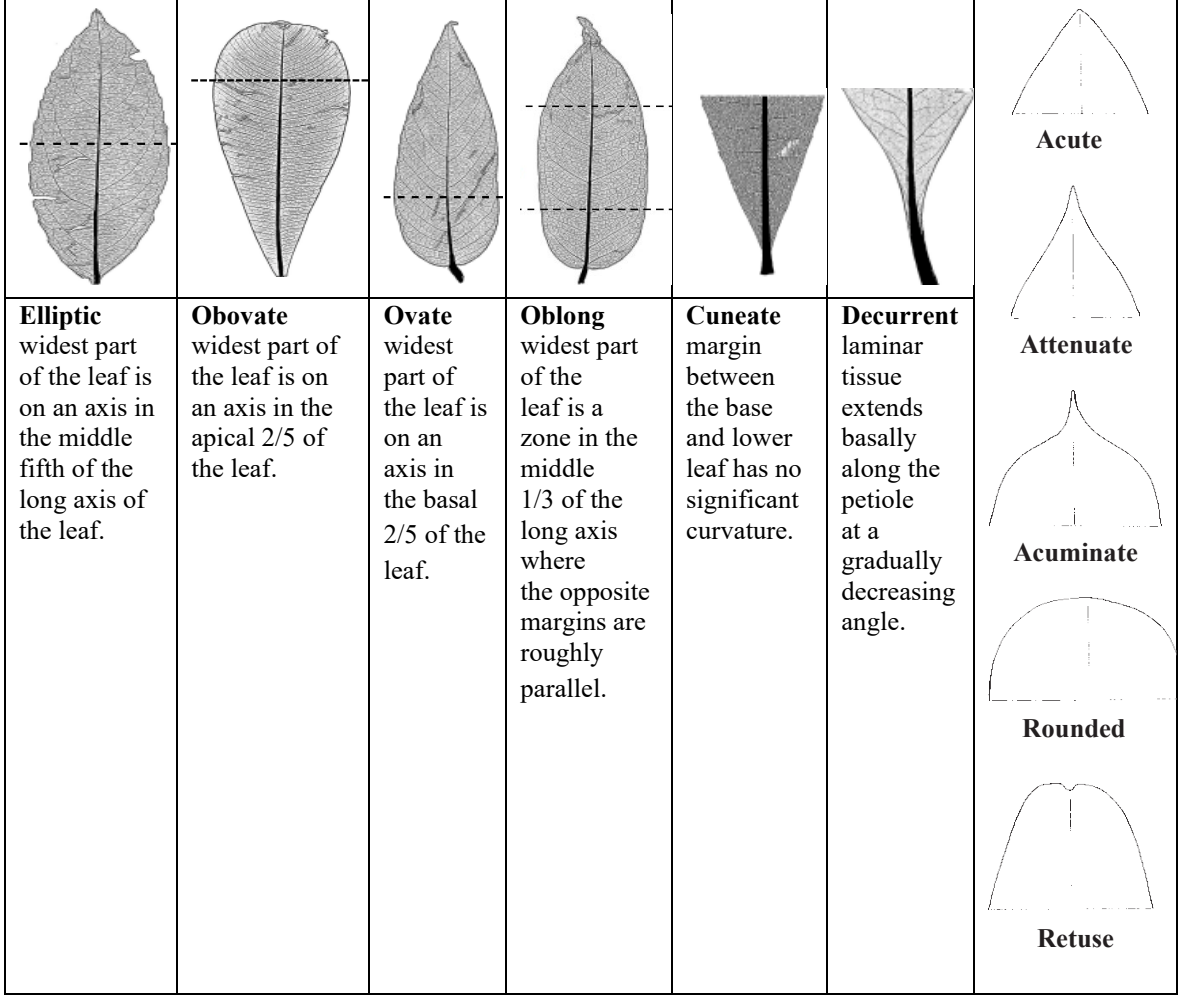



Figure 11: Definitions of leaf blade shape and leaf base reproduced from Leaf Architecture Working Group (1999), leaf apex from Beentje (2016).

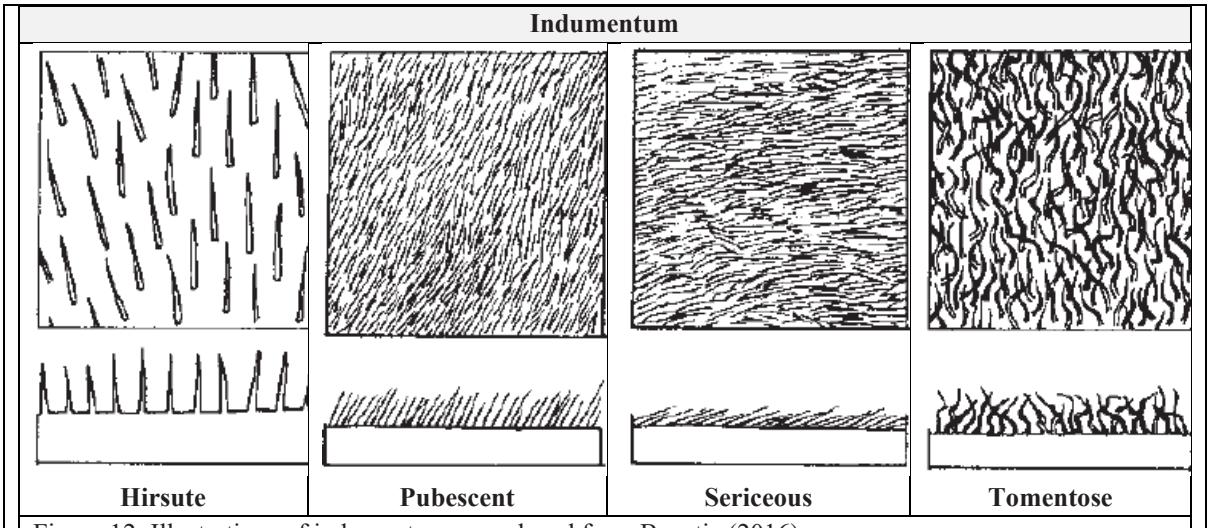
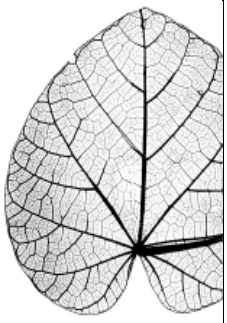
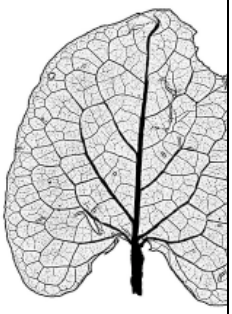
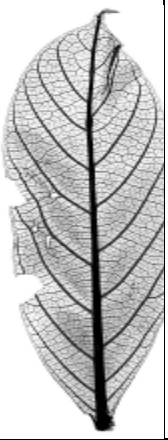
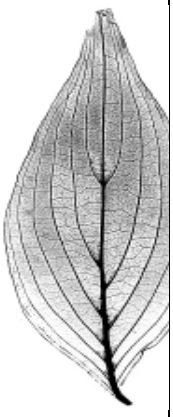
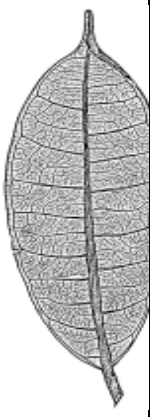
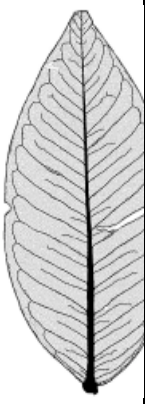



Figure 12: Illustrations of indumentum reproduced from Beentje (2016).

| Secondary veins (2°) | | | | | Inter-secondaries |
|---|---|---|---|---|---|
|  |  |  |  |  |  |
| **Brochidodromous** secondaries joined together in a series of prominent arches. | **Festooned brochidodromous** having one or more additional sets of loops outside of the main brochidodromous loop. | **Weak brochidodro-mous** secondaries joined together in a series of arches. | **Eucampto-dromous** secondaries upturned and gradually diminishing apically inside the margin, connected to the superadjacent secondaries by a series of 3° cross veins without forming any 2° marginal loops. | **Intra-marginal vein** secondaries end in a strong vein closely paralleling the leaf margin. | **Strong inter secondaries** width and course similar to the 2°s, but they are usually thinner than the costal 2°s and do not reach the margin. |

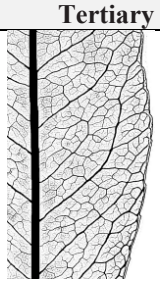
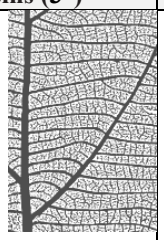
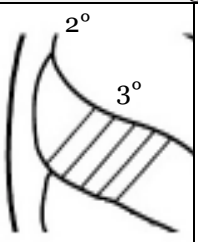
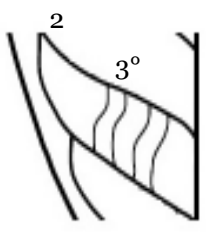
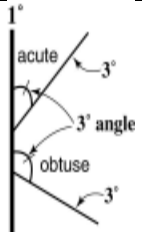
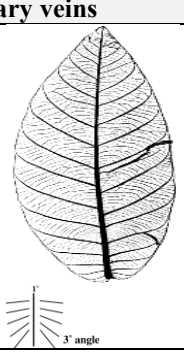
| Tertiary veins (3°) | | Relating only to opposite percurrent tertiary veins | | | |
|---|---|---|---|---|---|
|  |  |  |  |  |  |
| **Random reticulate** tertiaries anastomose (rejoin) with other 3° veins or 2° veins at random angles. | **Opposite percurrent** tertiaries cross between adjacent secondaries in parallel paths without branching. | **Straight** passing across the intercostal area without a noticeable change in course. | **Sinuous** Changing direction of curvature. | 3° vein angle to primary vein (1°) | **Increasing basally** tertiary angles become more obtuse toward the base of the lamina. |

Figure 13: Classifications of secondary and tertiary vein patterns reproduced from the Leaf Architecture Working Group (1999)

Major Flora accounts were consulted to understand the characters previously used to identify and delineate the genus and relevant species (including Lam, 1925; Assem, 1953; Royen, 1960; Ng, 1972; Pennington, 1991; Yii & Chai, 2002; Chantanarothai, 2014). Stearn's (1992) Botanical Latin was consulted when studying the protologues.

All characters seen were tabulated, compared and cross-referenced with the protologues and types. Characters and sizes of dried vegetative and fertile material visible on specimens were compared with descriptions in key taxonomic monographs or treatments that included collections from Peninsular Malaysia and Singapore (primarily King & Gamble, 1906; Lam, 1925; Assem, 1953, Royen, 1960, Ng, 1972). Other observations in this study, including ecology, growth habit or colour recorded on collector labels, were checked against previously published research. If these observations were out of range or unobserved in past treatments, then they were newly described. After collating all characters for collections from Singapore, cross-checks were then made with specimens collected from Johor and recent treatments of Sapotaceae including the *Tree Flora of Sabah and Sarawak* (Yii & Chai, 2002) and *Flora of Thailand* (Chantaranothai, 2014) to ensure overall consistency of species variation and to assess whether there were any atypical characters that would have given cause to re-determine species or create new infraspecific taxa.

### *2.4 Taxonomic Treatment*

A comprehensive search of all names published under the *Madhuca* species found in Singapore was undertaken, using online sources (see section 2.1.1) to locate the protologues of the respective species recognised. In addition to the protologues, relevant publications were compiled accordingly as references for each applicable name. Author abbreviations follow the list established by Brummitt & Powell (1992) and periodicals cited in nomenclatural text are abbreviated according to Botanico Periodicum Huntianum (BPH online at huntbotanical.org).

The format for taxonomic treatment conforms to the guidelines for the *Flora of Singapore*, where the following details are to be presented at genus-level: description of genera, key to species in each genus, detailed nomenclatural information for each species including synonyms and types, a description of each species, distribution of species globally and within Singapore (with up to five specimens from Singapore cited to enable species concept verification), species

ecology, IUCN conservation assessment of each species at global and national level, uses when relevant, vernacular names where known and notes to explain taxonomic or other issues (Middleton, 2019). Flowering and fruiting periods were taken from dates of relevant collections from Singapore and Johor.

### *2.5 National Red List Assessments*

While Red List categories and criteria have been put in place by the International Union for Conservation of Nature for almost 30 years (IUCN Species Survival Commission, 2001), the quantitative IUCN criteria have been difficult to apply in small countries like Singapore, as any Extent of Occurrence (EOO) will be very small and there is minimal information on population size, area of occupancy and rates of decline. Consequently it is challenging to apply the criteria at 'regional' or 'national level (Keller et al., 2005; Miller et al., 2007; Davison, 2008) and therefore, to place Singapore plants into categories of threat, the practical classification scheme adopted by Chong et al. (2009), which was adapted from Pyšek et al. (2004) and Davison (2008) is applied here (Tab. 3).

Table 3: Definitions and categories of threat applied to national red list assessments in Singapore (extracted from Chong et al., 2009, adapted from Pyšek et al., 2004 and Davison, 2008)

| **Key Definitions and Categories** | **Criteria** |
|---|---|
| Native Species | Originated in a given area without human involvement or have arrived there without intentional or unintentional intervention of humans from an area in which they are native. |
| Globally Extinct (EX) | Species endemic to Singapore and not seen in or collected from the wild in the last 30 years |
| Presumed Nationally Extinct (NE) | Non-endemic species which have not been seen in or collected from the wild in the last 30 years. |
| Critically Endangered (CR) | Fewer than 50 mature individuals, OR if more than 50 mature individuals but les than 250, with some evidence of decline or fragmentation. |
| Endangered (EN) | Fewer than 250 mature individuals, and no other evidence of decline or fragmentation. |
| Vulnerable (VU) | Fewer than 1000 mature individuals but more than 250 and there may or may not be any other evidence of decline, small range size, or fragmentation. |
| Near Threatened (NT) | Approaching but not yet reaching the threshold for the above criteria. |
| Least Concern (LC) | Not approaching the above criteria. |

| Key Definitions and Categories | Criteria |
|---|---|
| Data Deficient (DD) | Information is not adequate to make an informed assessment. |

Middleton (2019) notes that for assessments in the *Flora of Singapore*, the number of mature individuals in Singapore for most species will not have been counted accurately, and thus estimated. Other than known surveys documenting plant diversity, for example in Bukit Timah Nature Reserve (Ho et al., 2019) and Nee Soon freshwater swamp forest (Corner, 1978; Turner et al., 1996; Chong et al., 2018), the approach taken here is the same as Chong et al. (2012), where sighting information is supported by actual herbarium specimens (at SING and SINU) to provide the best documented evidence of species occurrences. This is consistent with the last national conservation assessment, where a species not recorded or collected in the past 30 years was considered extinct (Davison, 2008).

Global conservation assessments (applying the standard IUCN Red List categories and criteria, searchable by species on www.iucnredlist.org) already published for *Madhuca* species occurring in Singapore, are also included in this thesis as a point of reference.

# 3. RESULTS

## *3.1 Taxonomy*

A search of the literature (Chong et al., 2009; Turner, 1995) recorded six species of *Madhuca* as occurring in Singapore. From examination of herbarium material and online images, this study has also confirmed those same six species as native to Singapore, these are: *M. decipiens* J. Sinclair, *M. kingiana*, *M. malaccensis*, *M. motleyana, M. sericea* and *M. sessilis* (King & Gamble) Baehni.

Specimens identified as *Madhuca korthalsii* and *M. longifolia* in the material examined are not considered to occur in Singapore (see discussion).

Five species of *Madhuca* were found to occur in both Singapore and Johor: *M. decipiens*, *M. kingiana*, *M. malaccensis*, *M. motleyana*, and *M. sericea*. *Madhuca sessilis*, was found to have only been collected once in Singapore and not in Johor or anywhere else in Peninsular Malaysia. Specimens cultivated and collected only from the Singapore Botanic Gardens were excluded in the taxonomic account.

Seven additional species were found to occur in Johor but not Singapore: *M. erythrophylla* (King & Gamble) H.J.Lam, *M. hirtiflora* (Ridl.) H.J.Lam, *M. laurifolia* (King & Gamble) H.J Lam, *M. tomentosa* H.J.Lam, *M. tubulosa* H.J.Lam, *M. utilis* (Ridl.) H.J.Lam and *M. sessiliflora* P.Royen. As the focus of this project is on the species occurring in Singapore, the species in Johor were not studied in depth but rather used to confirm that they were not conspecific with species found in Singapore.

SINU database entries of *Madhuca* (Appendix 1), including *M. laurifolia* and *M. tomentosa* (both species have never been recorded in any checklists of Singapore's flora prior to and including Chong et al., 2009), as well as collections of *M. kingiana* and *Madhuca "*sp"., could not be verified against herbarium specimens at this stage and are hence currently excluded from this account. Personal communications with staff at the National University of Singapore indicate that their determinations of *M. tomentosa* may be erroneous, pending further checks.

An assessment of the validity of the name *Madhuca decipiens*, which had been reduced to a synonym of *Payena maingayi* Clarke in the World Checklist and Bibliography of Sapotaceae (Govaerts et al., 2001) recognises it as a good species (see notes under species and discussion).

Within the available herbarium material examined (in-herbarium and virtual) there were only a few fertile specimens in SING that were of a quality useful for taxonomic study, these are:

*Madhuca decipiens*: three specimens from Singapore were found to have flowers from which to make measurements (*Sinclair 10761*, *Lua et al. SING 2019-385* and *Ng SING 2019-245*). While whole fruit samples were available from *Ridley 11371* (a specimen growing in the Singapore Botanic Gardens) and *Ridley 6497*, immature seeds from a fruit section could only be seen from one Johor specimen (*Nur & Kiah 7785*).

*Madhuca malaccensis*: two Singapore collections (*Mat 6043* and *Mat 6133*) were found to have flowers, and for purposes of comparison, a flower from *Cockburn FRI 8043* collected near the Johor border was also dissected.

*Madhuca motleyana*: measurements of one flower of *M. motleyana* were taken from an earlier dissection of the only flowering specimen collected from Singapore (*Ridley 5645*), and compared with *Holtum 24921* and *Ridley 6496* from Johor.

*Madhuca kingiana*: flower measurements were taken from *Leong et al. SING 2005-59* and *Ngo SING 2019-207*. Seeds were found on only one specimen from the whole of Peninsular Malaysia in SING (*Everett FRI 13942*), which was collected in Perak.

*Madhuca sericea*: flowering material was described from a single dissection (*Cantley 2902*) in Singapore. No flowering specimens had been collected from Johor. No specimens with seeds were found from specimens from Singapore or the whole of Peninsular Malaysia at SING.

*Madhuca sessilis*: no flowering material was available in SING, whether in Singapore or Peninsular Malaysia. Images of the only potential flowering collection (*WKM 638* (BRUN, L), collected in Brunei, were insufficient to describe any finer details. Only seed fragments were found in a single SING specimen and measurements were instead obtained from the high-quality image of the same collection held at K (*Ridley 5076*).

### *3.1.1 Digital Specimen Images*

A total of 219 specimen images from various herbaria and databases were examined: 95 collected from Singapore and 124 from Johor (Tab. 4). Out of the 95 from Singapore, 11 specimens initially had no images and were available only after physical access to the SING herbarium.

All online catalogues allowed for straightforward searches by name and location, however only JSTOR and PADME allowed for more defined searches by minor locality. For E, K and L, location searches were limited to country, hence specimens within all of Malaysia (often greater than 50 per species for L) had to be sifted through in order to locate Johor occurrences. Images could be saved or downloaded from all databases, however only E allowed for image download in a range of seven sizes (from lower resolution around 100 dpi to high resolution of more than 5000, the latter requiring longer download times). At the start of this investigation, PADME images were not downloadable, but due to this project this useful feature is now available. The K and SING databases provided limited specimen information: the former consists mainly of type specimens, and the latter is a work-in-progress, where downloadable images are not yet attached to occurrence records, and the advanced search interface not yet fully functional, though minor localities appear as an option.

The images in this study varied widely in quality. All images of specimens collected in Singapore and held at SING had been professionally scanned (but not available publicly) for the *Flora of Singapore* project, and macro-measurements could thus be taken using the appended scale bars. Other sources of professionally-scanned Sapotaceae images were those downloadable directly from JSTOR, L and E online catalogues. Around half (116 out of 219) of all specimen images seen were professional scans, allowing detailed views of macro-morphological characters when expanded in zoom. The rest of the images across multiple herbaria (including all SAN, SAR, SING and KEP specimens collected in Johor) were downloaded from the PADME database (attached to the Sapotaceae Resource Centre): these had been personally uploaded by multiple botanists for collection record-keeping and for quick reference rather than for detailed taxonomic study, hence the quality was more uneven, with most images not having a scale bar or colour chart. These images were taken using a standard digital camera rather than special high-resolution scanning equipment, and in many cases the capsule had not been opened to reveal its contents (Fig. 14).

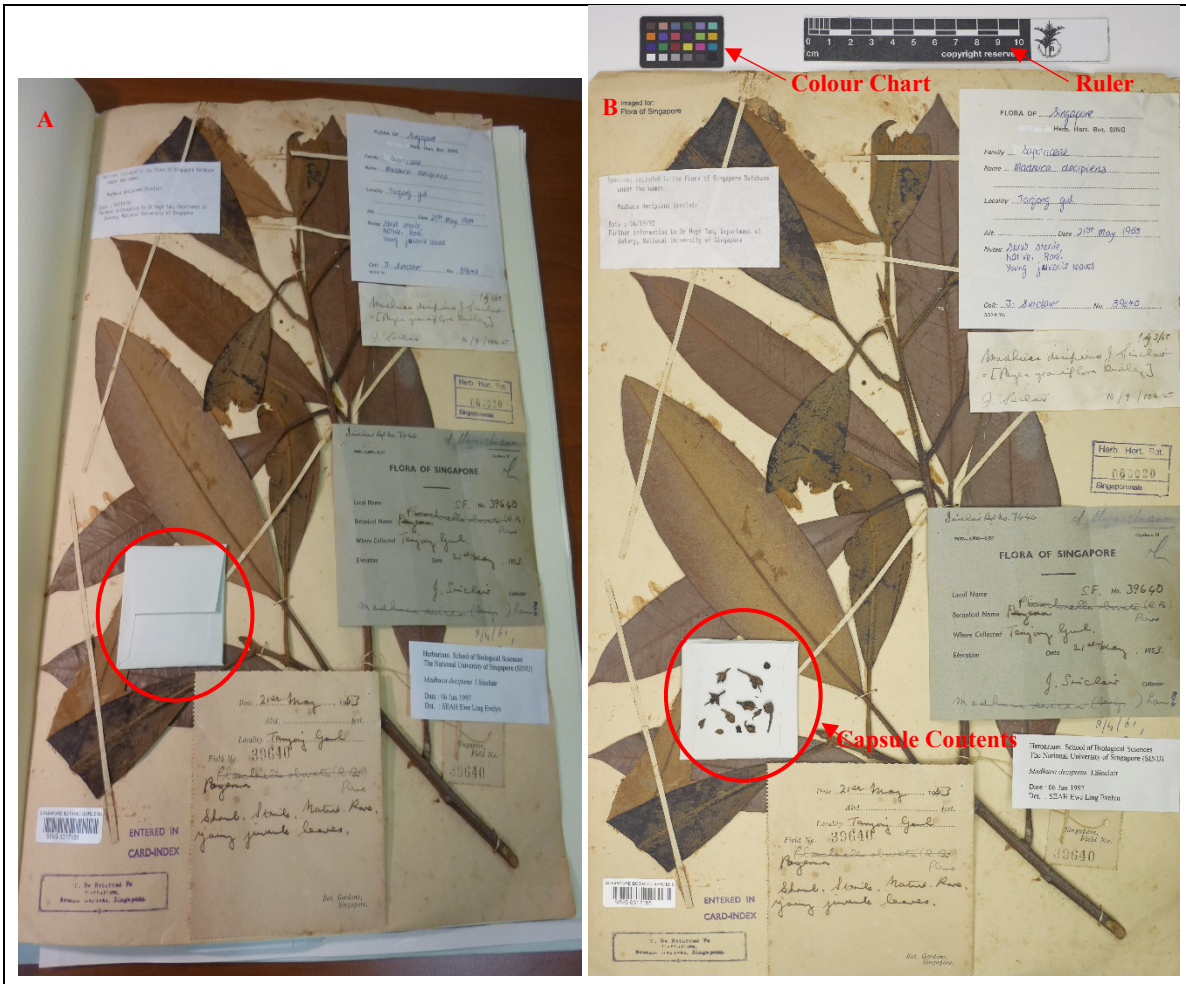



Figure 14: Specimen Images of the same collection (*Sinclair 10761,* SING) obtained from:
**A.** PADME database **B.** Professional scanning equipment at SING

Due to the limitations of observing specimens only from images, the characters initially prioritised as diagnostic were inevitably macro-morphological: petioles, leaves, shapes of leaf blades, midribs and venation details. While inflorescence sizes and some larger fertile material could be seen and measured, smaller attributes, including sepals, corollas, stamens, styles, margins, indumentum, fruit or seed details could not be described without the use of a microscope or close-ups of dissected material, even on images containing dissections.

Professionally-scanned images, which in all cases had scale bars, allowed measurements of macro-morphological characters and some limited smaller characters e.g. outer sepal and pedicel lengths, visible whole seeds or fruit. Measurements could not be accurately taken from the images downloaded from the PADME database as no scale bars were included, however the records were nevertheless useful for capturing information on ecology descriptions and collector notes, as well as confirming some identifications and qualitative characters such as leaf arrangement, blade shape, some venation patterns and inflorescence size. A summary of

the number of specimens examined, the number that were fertile, the number that had professionally-scanned images and those that had associated label information is shown in Table 4.

Table 4: Summary of number of specimen images studied, including those that were fertile, had associated label information and were professionally scanned.

| Species | Collected from | Total images | Herbarium Codes | | | | | | | No. of specimen images containing major aspects of taxonomic utility | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | SING | L | K | E | KEP | SAN | SAR | Flowering | Fruiting | Ecology description | Collector notes present | Professionally scanned |
| ***M. decipiens*** | Singapore | 17 | 10 | 1 | 4 | 2 | - | - | - | 8 | 5 | 7 | 11 | 14 |
| | Johor | 15 | 4 | 2 | 1 | - | 7 | - | 1 | 5 | 3 | 9 | 10 | 2 |
| ***M. kingiana*** | Singapore | 49 | 46 | 1 | - | 2 | - | - | - | 5 | 1 | 1 | 30 | 49 |
| | Johor | 61 | 13 | 12 | 9 | 1 | 19 | 1 | 6 | 25 | 20 | 53 | 60 | 13 |
| ***M. malaccensis*** | Singapore | 8 | 8 | - | - | - | - | - | - | 4 | 3 | 0 | 3 | 8 |
| | Johor | 13 | 4 | 4 | 1 | - | 3 | 1 | - | 12 | 0 | 10 | 12 | 4 |
| ***M. motleyana*** | Singapore | 3 | 3 | - | - | - | - | - | - | 1 | 2 | 0 | 1 | 3 |
| | Johor | 20 | 8 | 2 | 2 | 1 | 7 | - | - | 10 | 1 | 9 | 13 | 3 |
| ***M. sericea*** | Singapore | 9 | 7 | - | 1 | - | 1 | - | - | 4 | 0 | 0 | 5 | 7 |
| | Johor | 15 | 3 | 3 | 2 | 1 | 6 | - | - | 0 | 5 | 11 | 14 | 4 |
| ***M. sessilis*** | Singapore | 2 | 1 | - | 1 | - | - | - | - | 0 | 2 | 0 | 0 | 2 |
| | Johor | 0 | - | - | - | - | - | - | - | 0 | 0 | 0 | 0 | 0 |
| ***Incertae sedis*** | Singapore | 7 | 7 | - | - | - | - | - | - | 2 | 0 | 1 | 5 | 7 |

The taxonomic utility of each specimen examined is presented in Appendices 2 and 3. According to the assessment, professionally-scanned images received a high rating mainly due to the ability to measure macro-morphological characters with the appended ruler, whereas those from PADME ranged from low to medium, dependent on the degree of detail in the collector notes and quality of the particular image to discern venation. Collector notes from Johor specimens were generally more detailed than those collected from Singapore, with most containing information on tree dimensions, bole, buttresses, bark, slash, and sap.

Prior to physical access to the SING herbarium, species descriptions could only incorporate macro-morphological characters (mostly vegetative) and information gleaned from specimen images, collector notes and existing literature on distribution and ecology.

### *3.1.2 In-herbarium Analysis*

The herbarium-based analysis allowed the inspection of micro-morphological characters, especially flowers, fruit and seed details, and the completion of descriptions for the six species of *Madhuca* occurring in Singapore. This is presented in section 3.4.

Three recent flowering collections of *M. decipiens* (*Ng SING 2019-245* and *Lua et al. SING 2019-385*, April 2019) and *M. kingiana* (*Ngo SING 2019-207*, March 2019) were found in the SING herbarium that had not been in the initial set of digitised images but had been freshly mounted. These were particularly useful for studying internal flower morphology (Fig. 15).

Figure 15: Fresh dissection of *M. kingiana* flower from *Ngo SING 2019-207* (SING), allowing clear views of internal morphology and indumentum details.

For *Madhuca malaccensis* and *M. motleyana*, flower measurement ranges from Johor were consistent with Singapore collections. The only viable flower dissection for *M. sericea* was from a late 19$^{th}$ century collection of *Cantley 2902* in SING from Singapore, which like other *Cantley* collections, was possibly of dubious origin and not native (Ridley, 1900). Still, it has been cited in other accounts (Ng, 1972) and the flowering material coincides with the type description (Lam, 1925).

Fruit and seed measurements were challenging, with an even smaller number of fruiting specimens available for scrutiny. There was little useful fruit or seed material from Singapore,

and extending the range to Johor provided limited additional information. The sole Peninsular Malaysia collection of *M. kingiana* with seeds (*Everett FRI 13942* (SING)) was collected in Perak and provided a good view of the longitudinal and abaxial seed scars (Fig. 16).


Figure 16: Fruit section of *M. kingiana* from *Everett FRI 13942* (SING), allowing clear views of seed scars.

While fruit and seed descriptions could be made from the Singapore collections of *M. malaccensis* and *M. motleyana*, the seed scar could not be seen for the former. No seeds could be described for *M. sericea*, even extending the search to SING specimens collected in Peninsular Malaysia.

Fruit measurements were found, unsurprisingly, to differ between in situ and freshly-collected specimens that contain fleshier endosperm, as illustrated in Fig. 17. However, due to the lack of collector notes or field images, the species descriptions in this thesis contain only the length and breadth of dried fruit.


Figure 17: Collections of *M. malaccensis* from Singapore:
**A.** Fruiting specimen (*Ridley s.n.*, 1892 (SING))
**B.** Fresh collection (*Athen SING 2019- 573*) from Singapore Botanic Gardens' Jungle (image credit P. Leong)

With the help of a microscope, indumentum details could be seen and described for all species. Some specimens previously placed insertae sedis due to the inability to discern indumentum from images were positively identified to species in the SING herbarium, such as *Leong et al. MR 2014-049* for *M. sericea* (Fig. 18).

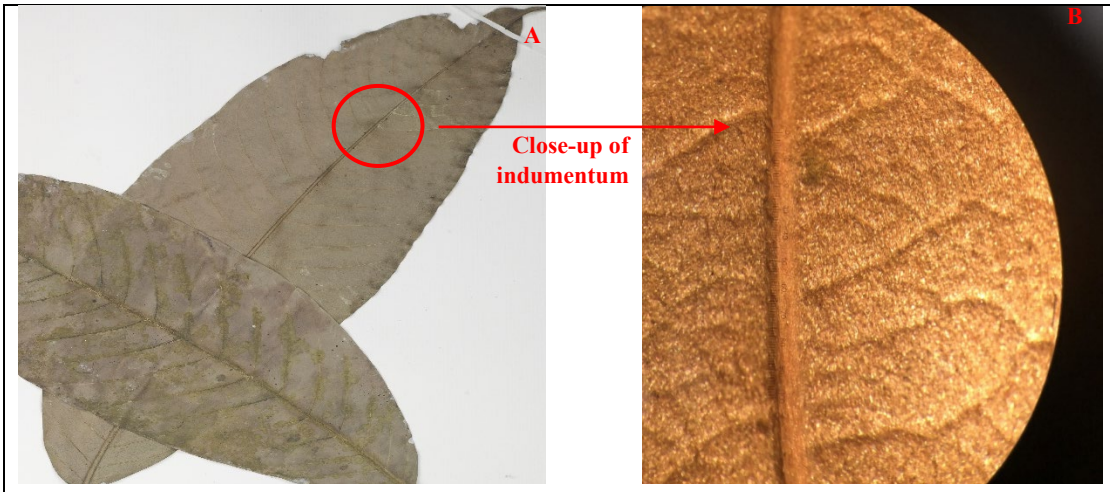



Figure 18: Images of the same collection of *M. sericea* in Singapore (*Leong et al. MR 2014-049,* (SING))
**A.** Crop from professionally-scanned image; leaf surfaces appear glabrous
**B.** Photo taken at SING herbarium of same leaf under microscope: visible sericeous indumentum

The use of light attachments in the herbarium was found to help illuminate venation details on specimens that could not be seen on digital images (Fig. 19).


Figure 19: Images of the same leaf from a collection of *M. motleyana* in Singapore (*Ridley 5645*, (SING))

**A.** Crop from professionally-scanned image Intersecondaries and tertiary veins unclear.

**B.** Photo taken at SING herbarium with light illumination. Intersecondaries, reticulate tertiary veins and looping intramarginal vein clear.

### *3.2 Morphological Character Assessment*

Vegetative characters that were found to be taxonomically informative included: blade shape, apex and base, petiole length, distinctive patterns and number of secondary veins, patterns of intersecondaries and tertiary veins, hairs or indumentum type. This allowed for clear species groupings, even of the mostly sterile specimens of *M. kingiana*. The extent of petiole grooves (varying between none, shallow or closed) was treated with caution, although it had been considered taxonomically significant by Ng (1972), as it was seen to vary considerably even within a single specimen (e.g. *Sinclair 39656*). There was also the tendency for leaves on saplings or treelets to be larger in size.

Fertile characters were found to provide further clarity, with taxonomically significant differentiations including sepal and corolla size, number of stamens, shape of anthers, and

placement of indumentum. However, fruit and seed material were insufficiently distinguishable across species groupings, and it was not possible to ascertain the number range of seeds per fruit, nor seed scar characteristics used by Baehni (1965).

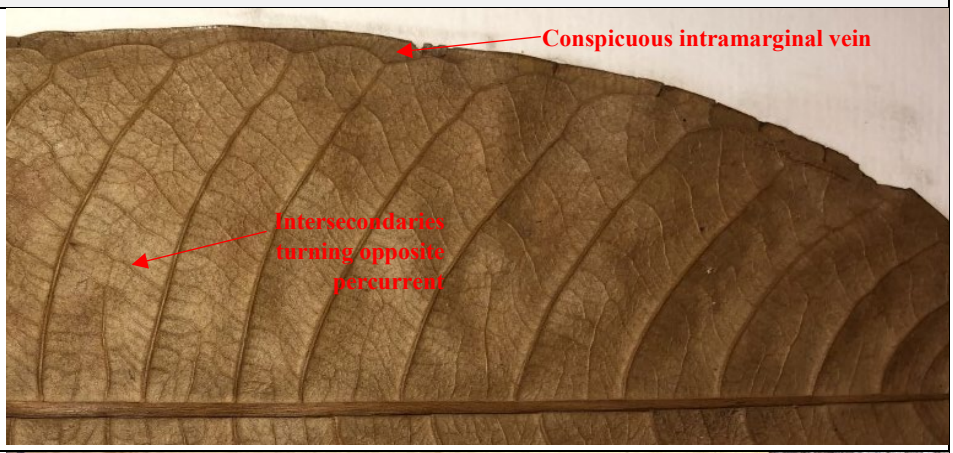
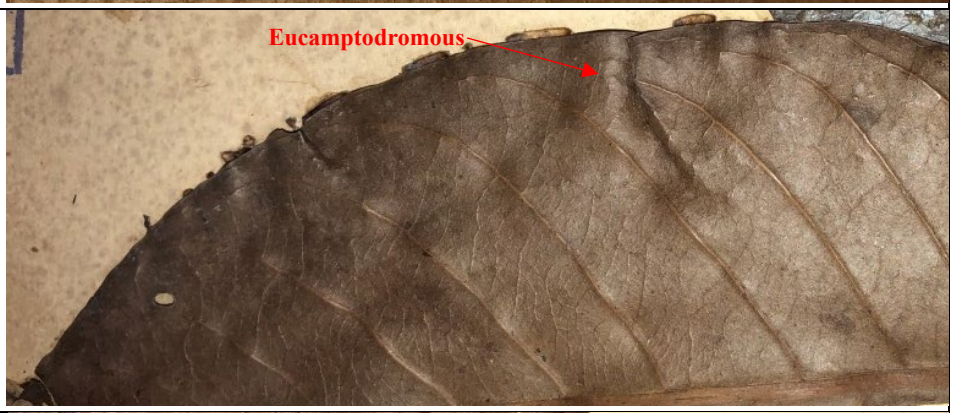
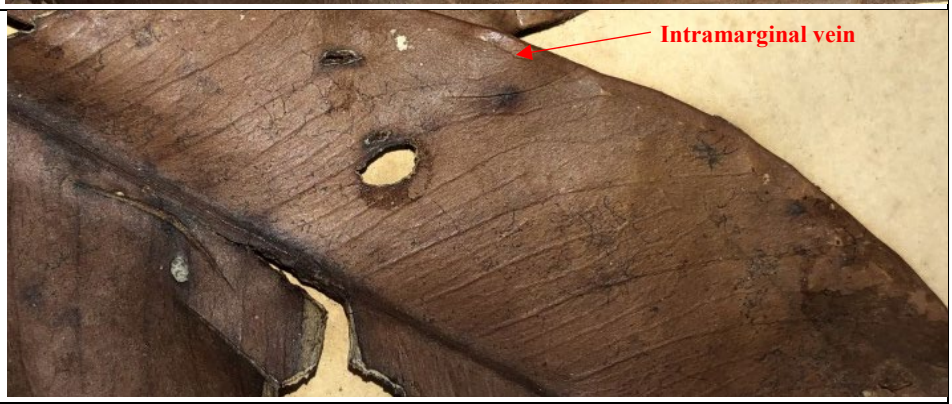
Flower colour in collector notes was found to frequently not distinguish whether the reference was to sepal or corolla. This is understandable given the general small size of flowers and enclosure of sepals around the corolla, but here it was considered that in most cases that the professional collector was referring to the corolla.

### *3.3 Useful Morphological Characters and Species Identification*

Analysis of both vegetative and fertile characters allowed for the positive identification and circumscription of the six *Madhuca* species found in Singapore. These are described in detail in section 3.4.

Distinctive leaf venation patterns (Fig. 20) and the absence or presence of golden or silvery sericeous indumentum (found on the blade undersides of only *M. decipiens* and *M. sericea*) are useful characters when in the field with access only to a 10x eyeglass.

| ***Species*** (SING collection) | **Distinctive venation patterns seen from blade undersides, with enhanced lighting** |
|---|---|
| ***M. decipiens*** (*Leong et al. SING 2016-051*) |   |

| ***Species*** (SING collection) | **Distinctive venation patterns seen from blade undersides, with enhanced lighting** |
|---|---|
| ***M. kingiana*** (*Samsuri et al. EP 31*) |   |
| ***M. malaccensis*** (*Mat 6500*) |   |
| ***M. motleyana*** (*Bayliss 5896*) |   |
| ***M. sericea*** (*Unknown 2808*) |   |

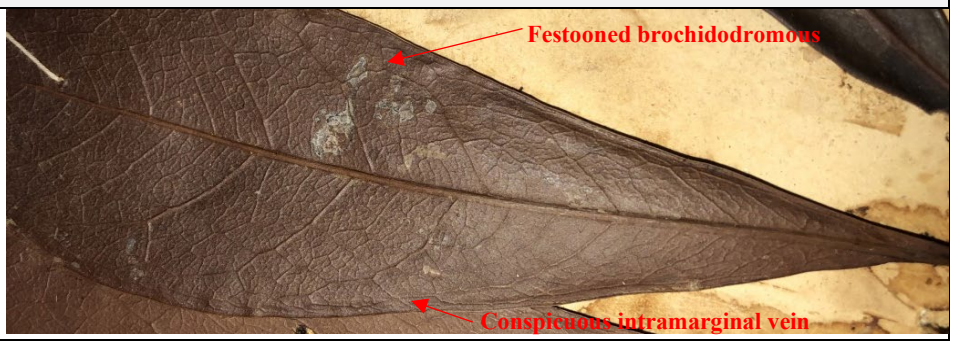
| ***Species*** (SING collection) | **Distinctive venation patterns seen from blade undersides, with enhanced lighting** |
|---|---|
| ***M. sessilis*** (*Ridley 5076*) |   |

Figure 20: Images capturing distinctive venation patterns of each *Madhuca* species found in Singapore

A number of SING collections were re-determined during this study:

*Khoo & Nik Faizu KMS 51*, previously determined as the only sterile collection of *M. korthalsii* in SING from Singapore, was determined as *M. sericea* after a close inspection of indumentum and vein characters. Moreover, *M. korthalsii* has never been recorded in Johor, and only collected further north in Peninsular Malaysia.

*Madhuca longifolia* (*Cantley 34*) is here considered exotic and excluded in this account for the *Flora of Singapore*. This follows Ng who noted that Royen (1960) does not cite this collection, and he himself excludes it in his family account (Ng, 1972), explaining that he has "..seen nothing like it in Malaya and [does] not believe it could have been collected in Singapore or Malaya". This scepticism ties in with the caution expressed by Ridley (1900) regarding the dubious origins of Cantley's collections in general.

Six collections from Singapore are placed incertae sedis, pending future closer investigation into other Johor or Peninsular Malaysia species not recorded in Singapore. However, these fall into three morphological groupings (Fig. 22) based on character affinities including blade shape, apex and base, number of pairs of secondary veins, patterns of venation as well as the absence or presence of indumentum on either surface. Group 1 contains two specimens both from Bukit Timah Nature Reserve, group 2 contains two specimens both from Nee Soon swamp forest and group 3 contains two specimens, one from Mandai and the other from Jurong. Other than *Leong et al. CTFS J2-1235* (group 1), which consisted only of loose leaves without branching detail, all other collections displayed the typical *Madhuca* spiral phyllotaxis.

*Madhuca* group 1 (Fig. 21A). (Fig. 21a) *Gwee SING 2009-507* had earlier been determined as *Madhuca "*sp. A", presumably corresponding to Ng's (1972) identification of three uncertain species of *Madhuca* found in Johor, which he denoted as *Madhuca "*sp. A"*, Madhuca "*sp. B" and *Madhuca "*sp. C". The collection, *Leong et al. CTFS J2-1235*, is most likely the same species, given the distinct reddish-brown tomentose indumentum found on the leaf undersides and midrib, as well as the ascending angle and number of pairs of secondary veins. While these characters, in part, correspond to Ng's *Madhuca "*sp. A"*,* (Ng, 1972) his description of eucamptodromous secondary veins contradicts the clear brochidodromous pattern in both collections, hence they are placed incertae sedis pending future closer investigation into the other Johor species not found in Singapore and outside the scope of this study.

*Madhuca* group 2 (Fig. 21B). The leaves of *Leong et al. SING 2009-244* initially determined as *M. malaccensis*, was found not to correspond with characters of that species (particularly the lack of both opposite percurrent tertiaries and prominent adaxial midrib), and was found instead to share similar characters with *Gwee SING 2010-496*, determined previously as *Madhuca "*sp". Checks with herbarium staff who had collected the former confirmed that the determination of *M. malaccensis* should indeed be reconsidered and needs further investigation.

*Madhuca* group 3 (Fig. 21C). A recent collection (*Lim & Wong SING 2018-209*) from Mandai in Singapore determined as *M. cf. motleyana* appeared to be similar to another collection (*Corner 26158*) also determined as *M. motleyana*, but determined by Ng in 1968 to be *Madhuca* "sp". Although the elliptic blade shape for both collections corresponded to *M. motleyana*, the leaf base and venation is out of range, notably the lack of an intramarginal vein. Furthermore, a dissection of one of the flowers attached to the *Lim & Wong* collection (though incomplete, as all flowers were missing corollas and stamens) showed that sepal and style characters, including dense sericeous indumentum, were not aligned to what had been described for *M. motleyana*. Some sterile characteristics (e.g. brochidodromous secondary veins, number of secondary vein pairs and leaf shape) correspond to *M. tubulosa* found in Johor; again, this needs further investigation.

| Preliminary groupings | SING specimen images |
|---|---|
| ***Madhuca* group 1**<br><br>*Gwee SING 2009-507* (left image)<br><br>*Leong et al. CTFS J2-1235* (right image)<br><br>Both collected in Bukit Timah Nature Reserve. |  A |
| ***Madhuca* group 2**<br><br>*Gwee SING 2010-496* (left image)<br><br>*Leong et al. SING 2009-244* (right image)<br><br>Both collected in Nee Soon swamp forest. |  B |
| ***Madhuca* group 3**<br><br>*Corner 26158* (left image), collected in Jurong<br><br>*Lim & Wong SING 2018-209* (right image), collected in Mandai |  C |

Figure 21: Incertae sedis specimens of Singapore collections (SING) currently determined as *Madhuca* "sp.". **A.** Group 1. **B.** Group 2. **C.** Group 3.

## 3.4 Taxonomic Treatment

### *3.4.1 Keys to Species*

Two separate keys are presented. The first is based solely on vegetative characters visible without magnification. This is aimed at field botanists without access to dissection kits and stereomicroscopes, and often only having access to sterile material. Key vegetative characters include the presence/absence of stipules, shape of leaves, length of petioles and secondary vein branching. The second key is based on floral characters and is more relevant to taxonomists working in herbaria who are able to dissect flowers and examine micro-morphological material under a microscope.

**Key using vegetative characters**

1. Secondary veins join into an intramarginal vein……..... 2
   Secondary veins without intramarginal vein ……... 3

2. Stipules absent or up to 0.4 cm long ……..…… 4
   Stipules persistent, conspicuous, 0.5–2 cm long …….***Madhuca kingiana***

3. Lower lamina silvery or golden sericeous …….……...5
   Lower lamina pale green, glabrous ……***Madhuca malaccensis***

4. Blade obovate, petiole up to 0.5 cm or sessile ……..... ***Madhuca sessilis***
   Blade elliptic, petiole 1.5–4 cm long ……...…….***Madhuca motleyana***

5. Secondary veins ascending at an angle of c.60° to the midrib ……...……. ***Madhuca sericea***
   Secondary veins ascending at an angle of 80–90° to the midrib ……. ***Madhuca decipiens***

**Key using fertile characters (excluding *M. sessilis* as flowers are unknown)**

1. Corolla greater than 0.5 cm long ……..……..... 2
   Corolla less than 0.5 cm long ……..……..... 3

2. Outer sepals 0.8 cm long or greater……..……..... 4
   Outer sepals less than 0.8 cm long ……***Madhuca malaccensis***

3. Stamens 16 in 1 row, anthers oblong to ovate ……..……... ***Madhuca motleyana***
   Stamens 14–15 in 2–3 rows, anthers sagittate ……***Madhuca sericea***

4. Anthers 0.3–0.4 cm long, filaments c.0.2 cm ……..... ***Madhuca kingiana***
   Anthers c.0.2 cm long, filaments less than 0.1 cm, almost sessile…… ***Madhuca decipiens***

### *3.4.2 Genus Description*

**MADHUCA** Buch.-Ham. ex J.F.Gmel.
(after an Indian plant name; *Madhukar* means honey-maker in Sanskrit)

Syst. Nat. ed. 13[bis]. 2(1) (1791) 779; Macbride, Contr. Gray Herb. N.s. 53 (1918) 16; Merrill, Enum. Phil. Fl. Pl. 3,3 (1923) 276; H.J. Lam, Bull. Jard. Bot. Buitenz., Sér. 3,7 (1925) 152 & 3,8 (1927) 443; P. Royen, Blume 10 (1960) 1; Baehni, Boissiera 11 (1965) 34, pro parte; Ng in Whitmore, Tree Fl. Malaya 1 (1972) 401; Pennington, Gen. Sapot. (1991) 154; Chantaranothai, Thai Forest Bull., Bot. 27 (1999) 142; Yii & Chai in Soepadmo, Saw & Chung, Tree Fl. Sabah & Sarawak 4 (2002) 221. **Type**: *Madhuca longifolia* J.F.Macbr. **Synonyms:** *Bassia* J.Koenig ex L., Mant. Pl. Altera [Linnaeus] (1771) 555 *nom. illeg.*; *Azaola* Blanco, Fl. Filip.[F.M.Blanco] (1837) 402; *Kakosmanthus* Hassk., Retzia 1 (1855) 97 et in Flora, xxxviii. (1855) 577; *Cacosmanthus* Miq., Fl. Ned. Ind. 2 (1859) 1040; *Dasyaulus* Thwaites, Enum. Pl. Zeyl. [Thwaites] (1860) 175; *Illipe* F.Muell., Extra-Trop. Pl. ed. Am. (1884) 181; *Aesandra* Pierre ex L.Planch., Etud. prod. Sapot. (1888) 26 nomen; et Notes Bot. Sapot. (1890) 2; *Vidoricum* Rumph. Herb. Amboin. i. (1741) 174-75, t. 67. iii. 184-186, t. 118, ex Kuntze, Rev. Gen. (1891) 407; *Ganua* Pierre ex Dubard, Rev. Gén. Bot. 20: 201, nomen; et in Bull. Mus.

Hist. Nat. Paris, xiv. (1908) 407, descr (1908; *Dasillipe* Dubard, Ann. Mus. Colon. Marseille, sér. 3, 1 (1913) 92

Small to large trees. **Leaves** in loose or close spirally-arranged clusters, always simple, entire, normally petiolate with swollen base, rarely sessile, stipules absent, small or large, blade chartaceous to coriaceous, obovate, elliptic, oblanceolate or lanceolate, apex rounded, retuse, acute, acuminate or obtuse, base acute, attenuate, or cuneate, often decurrent to border or forming groove on petiole, usually glabrous, sometimes sericeous below, midrib flat, impressed or prominent, secondary veins variable, ascending at an angle of 50–90°, festooned brochidodromous, brochidodromous, eucamptodromous or joing intramarginal vein, intersecondaries often conspicuous, joining opposite percurrent or reticulate tertiary veins. **Inflorescences** single to multi-flowered, flowers bisexual, fascicled in axils of leaves or leaf scars. **Sepals** 4, in 2 whorls, ovate, outer sepals valvate, inner sepals imbricate, usually sericeous to pubescent on outside, glabrous on inside, margin mostly fimbriate. **Corolla** lobes 8–16, imbricate, often hirsute between or at the base of stamens. **Stamens** 14–35, in 1–3 rows, inserted near the base of the tube, anthers oblong, ovoid or sagittate, with connective appendage, often hirsute, filaments free or absent. **Gynoecium** glabrous or pubescent, ovary 6–10-locular, style simple, filiform, often exserted, glabrous or pubescent at base. **Fruit** a berry, 1–4 seeded. **Seed** broadly ellipsoid or oblong, testa thin, crustaceous, shining, scar narrow, adaxial, nearly as long as the seed.

**Distribution**: About 100 species: Australia, Cambodia, India, Indonesia, Laos, Malaysia, Myanmar, New Guinea, Philippines, Sri Lanka, Thailand, Vietnam. Six species in Singapore.

**Uses**: ‘Nyatoh’ (Malay), referring to hardwood timber in common with other Sapotaceae.

### *3.4.3 Species Descriptions and Provisional Conservation Assessments*

**1. Madhuca decipiens** J.Sinclair

(Latin, *decipiens* = referring to the verb *decipere* (to ensnare), and therefore meaning deceiving, following from this species' initial misidentification as *Payena grandiflora*)

Gard. Bull. Singapore 22 (1967) 215; Ng in Whitmore, Tree Fl. Malaya 1 (1972) 405; Turner, Gard. Bull. Singapore 47 (1995) 463; Pennington, Gen. Sapot. (1991) 157; Chong et al., Checkl. Vasc. Pl. Fl. Singapore (2009) 58, 180, 194. **Basionym**: *Payena grandiflora* Ridl., J. Straits Branch Roy. Asiat. Soc. 61 (1912) 28, Ridley, Fl. Malay Penins. 2 (1923) 262 excl. *Goodenough 1268* = *Payena maingayi* Clarke. **Synonym**: *Diploknema grandiflora* (Ridl.) H.J.Lam, Bull. Jard. Bot. Buitenzorg, sér. 3, 7 (1925) 185. **Type**: *Ridley 11371* (lectotype SING [SING0046061]), cultivated in the Singapore Botanic Gardens with possible Sumatra source, designated by J. Sinclair, Gard. Bull. Singapore 22 (1967) 215; syntypes *Ridley 6497* (K [K000777882], SING[SING0054465]) and *Goodenough 1268* (SING). (Fig. 22**)**

Tree to 10m tall, 40 cm girth. **Leaves** in loose spirally-arranged clusters, stipules 0.2–0.5 cm, acute to obtuse, petiole 3–6 cm long, blade chartaceous to coriaceous, oblong to sometimes obovate, 6–34 x 3.5–11 cm, apex acute to acuminate, sometimes retuse, base decurrent to form closed or narrow groove along entire petiole, dark green to greyish, mostly glabrous, sometimes unevenly sericeous above, dull pale green to golden-yellow sericeous beneath, drying brown above and grey beneath when mature, midrib paler, flat to slightly raised above, raised and rounded below, secondary veins 12–30 pairs, ascending at 80–90° to the midrib before curving upwards near margin, brochidodromous to festooned brochidodromous, elevated beneath, often strong intersecondaries turning reticulate near margin, tertiary veins random reticulate. **Inflorescences** 1–7 flowered, fascicled in axils of leaves, pedicels 1.5–3 cm long, slightly pubescent. **Sepals** 4, outer sepals ovate, 1–1.2 x 0.8 cm, tomentous outside, glabrous on inside, inner sepals narrower, 1–1.1 x 0.5–0.7 cm, tomentose outside, keeled, also tomentose inside except for glabrous margin. **Corolla** white, 1.1–1.5 cm long, tube 0.4–0.6 cm long, lobes 8–12, lanceolate, 0.7–0.9 cm long, outside glabrous except sericeous central portion of lobes, inside glabrous except pubescent tube, especially at base of stamens, margin glabrous. **Stamens** 26–30 in 3 rows, anthers ovoid, c. 0.2 cm long, hirsute, connective appendage slender and tapered, filaments less than 0.1 cm, almost sessile. **Gynoecium** tomentose, 8–10 locular ovary,

style to 2 cm, exserted, sericeous at base. **Fruit** a berry, up to 2-seeded, ellipsoid, c. 1.5 x 1 cm, glabrous, supported by persistent sepals, 1–1.2 cm long, style c. 0.2–0.4 cm. **Seed** ellipsoid, immature 1.5–2 x 0.5 cm, testa shiny, scar c. 1 x 0.2 cm.

**Distribution.** Johor, possibly Sumatra. In Singapore, collected from Sungei Murai (*Ridley 6497*, 1894, SING [SING0054465]), Tanjong Gul (*Sinclair SFN 10761*, 3 Nov 1963, SING [SING0017155]), Western Catchment Pergam Marshes (*Lua et al. SING 2018-834*, 9 Oct 2018, SING [SING0274188]).

**Ecology.** Lowland forest to 300m. Found in primary forest patch or mature secondary forest, along edge of slopes or rocky wooded sea-cliffs. Flowering: April–May, November. Fruiting: April–June.

**Provisional conservation assessment.** Previously assessed as Nationally Extinct (NE) in Tan et al. (2008), which used SING records up to 21 Sep 2006: at that point the latest collection was in 1963, more than 30 years prior. However, it has since been re-discovered at the Western Catchment area in 2011, and collected again in 2017, 2018 and 2019. There are currently just six to seven individuals in a single locality, and hence assessed as Critically Endangered (CR) in Singapore. No global IUCN assessment is available.

**Specimens examined.** Sungei Murai (*Ridley 6497*, 1894, SING [SING0054465], K [K000777882]), Tanjong Gul (*Sinclair SFN 10761*, 3 Nov 1963, E [E00283994], E [E00013579], K, L [L.2655479], SING [SING0017155]; *Sinclair SFN 39640*, 21 May 1953, SING [SING0017156]), Western Catchment Live Firing Range, Pergam Marshes (*Lua et al. SING 2011-021*, 1 Feb 2011, SING [SING0153716], *Leong et al. SING 2016-051, 24 Feb 2016*, SING [SING0236441], *Lua SING 2017-219*, 20 Jun 2017, SING [SING0258575], *Lua et al. SING 2018-834*, 9 Oct 2018, SING [SING0274188]), *Ng SING 2019-245*, 2 Apr 2019, SING [SING0286162] and *Lua et al. SING 2019-385*, 12 April 2019, SING [SING0286358].)

**Notes.** Govaerts et al. (2001) erroneously reduced *M. decipiens* to synonymy with *Payena maingayi* Clarke. This has since been corrected in the current World Checklist of Selected Plant Families (WCSP), which recognises *M. decipiens* as a species distinct from *P. maingayi*.

Figure 22: Images of *M. decipiens* branchlet, leaves and flowers collected at Western Catchment, Singapore (credit P. Leong)

**2. Madhuca kingiana** (Brace ex King & Gamble) H.J.Lam

(Sir George King, 1840–1909, British botanist appointed as superintendent of the Royal Botanic Garden Calcutta from 1871–1898)

Bull. Jard. Bot. Buitenzorg ser. III, vii.(1925) 159; Bull. Jard. Bot. Buitenzorg, sér. III, viii. (1927) 444; Ridley, Fl. Malay Penins. 5 (1925) 319; Pennington, Gen. Sapot. (1991) 157; Turner, Gard. Bull. Singapore 47 (1995) 463; Yii & Chai in Soepadmo, Saw & Chung, Tree Fl. Sabah & Sarawak 4 (2002) 242; Chong et al., Checkl. Vasc. Pl. Fl. Singapore (2009) 58, 180, 216. **Basionym:** *Bassia kingiana* Brace ex King & Gamble, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 74(1): (1906) 178; Ridley, Fl. Malay Penins. 2 (1923) 267. **Synonym**: *Ganua kingiana* (Brace) Assem, Blumea vii. (1953) 373; Ng in Whitmore, Tree Fl. Malaya 1 (1972) 399; Keng, Concise Fl. Singapore, vol. 1, Gymn. Dicot. (1990) 134. **Type**: *King's Collector 3314* [Malaysia], Perak (lectotype KEP n.v.) designated by Assem, Blumea 7 (1953) 373, isolectotype K [K000777880]. **Heterotypic synonyms:** *Madhuca glaberrima* H.J.Lam, Bull. Jard. Bot. Buitenzorg ser. III, vii.. (1925) 263. *Ganua glaberrima* (H.J.Lam) H.J.Lam, Bull. Jard. Bot. Buitenzorg, ser. III, viii. (1927) 428. *Ganua kingiana* var. *euphlebia* Assem, Blumea 7 (1953) 374. (Fig. 23.)

Medium to large tree to 30.5 m tall, 1.8 m diameter, rhythmic branching, bark greyish. **Leaves** in close spirally-arranged clusters, stipules persistent, 0.5–2 cm long, c. 0.2–4 cm at base, acute to acuminate, conspicuous, petiole 1.5–6 cm long, swollen base, blade coriaceous, oblong to obovate, 8.5–34 x 2.5–9.5 cm, apex acuminate, base decurrent along upper part of petiole to form shallow or closed groove, dark green above, light green beneath, glabrous on both surfaces, midrib flat to slightly raised above, strongly prominent below, at least twice as thick as secondary veins, secondary veins 15–22 pairs, extending at c.85–90° to the midrib almost straight or gently curving toward margin to join smooth or looping intramarginal vein, conspicuously elevated beneath, intersecondaries anastomose into opposite percurrent tertiary veins midway toward margin, these tertiary veins straight to sinuous, angles to primary vein increasing basally. **Inflorescences** 1–3 flowered, fascicled in axils of leaf scars, pedicels 0.4–0.6 cm long, pubescent. **Sepals** 4, outer sepals ovate, 0.8–1 x 0.8–1 cm, densely tomentose outside, less on inside, inner sepals narrower, 0.6–1 x 0.6–0.7 cm, densely tomentose outside, less on inside, ciliate margin. **Corolla** white to cream, 0.7–1 cm long, tube 0.3–0.5 cm long, lobes 12–16, spathulate, 0.4–0.6 cm long, hirsute outside, pubescent to hirsute inside, denser

on top of lobes and base of stamens, margin ciliate. **Stamens** 28–35 in 2 rows, anthers oblong, 0.3–0.4 cm long, hirsute, connective appendage penicillate, appearing aristate in bud or when dry, filaments c. 0.2 cm. **Gynoecium** pubescent, 8–10 locular ovary, style 1–1.2 cm, exserted, pubescent at base. **Fruit** a berry, up to 4–seeded, ellipsoid, c. 2.5 x 2 cm, tomentose, supported by persistent sepals, 1 cm long, style c. 1 cm. **Seed** ellipsoid, c. 2–2.2 x 0.3–1 x 0.5–0.7 cm thick, testa shiny, scar c. 2 x 0.3–0.6 cm, covering about one third of seed surface.

**Distribution.** Peninsular Malaysia (Johor, Pahang, Perak, Selangor, Trengganu), Sumatra, Borneo. In Singapore only found in Bukit Timah Nature Reserve (*Ridley 6294*, 1894, SING [SING0058084], *Wilkie et al., PW 530*, 23 Jan 2007, SING [SING0092716]; *Gwee SING 2010-021*, 5 Jan 2010, SING [SING0138184]).

**Ecology.** Lowland, mixed dipterocarp forest, some hilltops, slopes and ridges up to 426 m. Flowering: March–May. Fruiting: March–July, Oct–Nov.

**Provisional conservation assessment.** Globally this species is Near Threatened (Olander & Wilkie, 2019a). This is the most intensely collected *Madhuca* species in Singapore, and is recorded as occurring in both primary forest and old secondary forest within Bukit Timah Nature Reserve (Ho et al., 2019). The last national assessment of Endangered (EN) is upheld (Tan et al., 2008), which estimates fewer than 250 mature individuals, but confined to the protected area within the Nature Reserve with no evidence of decline or fragmentation.

**Vernacular name.** Nyatoh king (Sabah)

**Specimens examined.** Bukit Timah Nature Reserve (*Mohd. Noor 1524*, 19 Feb 1973, SING [SING0025538]; *Mohd. Noor MN 1441*, 8 Dec 1970, SING [SING0025540]; *Mohd. Noor MN 402*, 1 Aug 1969, SING [SING0025541]; *Mohd. Noor MN 549*, 24 Sep 1969, SING [SING0025542]; *Mohd. Noor MN 756*, 19 Nov 1970, SING [SING002553]; *Mohd. Noor MN 1353*, 22 Sep 1970, SING [SING0025544]; *Mohd. Noor MN 1051*, 7 Apr 1970, SING [SING0025545]; *Mohd. Noor MN 705*, 23 Oct 1969, SING [SING0025546]; *Mohd. Noor MN 661*, 14 Oct 1969, SING [SING0025547]; *Mohd. Noor 1553*, 26 Feb 1973, SING [SING0025548]; *Mohd. Noor MN 1685*, 19 Mar 1973, SING [SING0025549]; *Mohd. Noor 1570*, 5 Mar 1973, SING [SING0025550]; *Mohd. Noor MN 689*, 23 Oct 1969, SING [SING0025551]; *Mohd. Noor MN 703*, 23 Oct 1969, SING [SING0025552]; *Mohd. Noor MN*

*350*, 17 July 1969, SING [SING0025553]; *Mohd. Noor MN 1323*, 1 Sep 1970, SING [SING0025554]; *Mohd. Noor MN 1376*, 6 Oct 1970, SING [SING0025555]; *Mohd. Noor MN 1222*, 26 May 1970, SING [SING0025556]; *Mohd. Noor MN 1210*, 26 May 1970, SING [SING0025557]; *Mohd. Noor MN 1233*, 9 Jun 1970, SING [SING0025558]; *Mohd. Noor MN 695*, 30 Oct 1969, SING [SING0025559]; *Mohd. Noor MN 611*, 30 Sep 1969, SING [SING0025560]; *Mohd. Noor MN 987*, 3 Mar 1970, SING [SING0025561]; *Mohd. Noor MN 839*, 30 Dec 1969, SING [SING0025562]; *Mohd. Noor MN 1148*, 12 May 1970, SING [SING0025563]; *Mohd. Noor MN 915*, 2 Feb 1970, SING [SING0025564]; *Mohd. Noor MN 582*, SING [SING0025565]; *Mohd. Noor MN 611*, 30 Sep 1969, SING [SING0025566]; *Hill H 426*, 10 Jun 1970, SING [SING0025567]; *Hill H432*, 11 May 1970, SING [SING0025568]; *Hill H.426*, 26 May 1970, SING [SING0025569]; *Hill H.*432, 6 May 1970, SING [SING0025570]; Corner *s.n.*, 6 Mar 1938, SING [SING0025571]; *Sinclair 40035*, 4 Oct 1953, L [L2652517], SING [SING0025572]; *Mohd. Shah & Samsuri MS 3908*, 12 Jul 1976, SING [SING0025573]; *Tang & Sidek 993*, 12 Oct 1995, SING [SING0037588]; *Samsuri et al. EP 31*, 9 Mar 2004, SING [SING0052809]; *Leong et al. SING 2005-59*, 23 Mar 2005, SING [SING0060007]; *Wilkie et al., PW 530*, 23 Jan 2007, E[E00304463], SING [SING0092716]; *Gwee SING 2010-021*, 5 Jan 2010, SING [SING0138184]; *Mat 6238*, April 1894, SING [SING0058083]; *Ridley 6294*, 1894, SING [SING0058084]; *Ridley* s.n., 1894, SING [FOS15390]; *Leong et al. CTFS 7424*, 13 Sep 2018, SING [SING0274124]; *Ngo SING 2019-207*, 28 Mar 2019, SING [SING0279209]).

**Notes.** The KEP specimen of *King's Collector 3314* that Assem (1953) designated as the lectotype is captured as a data entry in PADME, hence is here taken as a valid lectotypification even though no image of it has been seen for this study. An image of a duplicate held at K was seen on JSTOR. The duplicate described by Yii & Chai (2002) as the "hololectotype" and held at SING has not been found in any database nor in the SING herbarium.


Figure 23: Images of *M. kingiana* branchlet collected at Bukit Timah Nature Reserve, Singapore (credit P. Leong)

### 3. **Madhuca malaccensis** (C.B.Clarke) H.J.Lam

(of Malacca, a state in Peninsular Malaysia)

Bull. Jard. Bot. Buitenzorg, ser. III, vii. (1925) 167; Bull. Jard. Bot. Buitenzorg, sér. III, viii. (1927) 449; P. Royen, Blumea 10 (1960) 44; Ng in Whitmore, Tree Fl. Malaya 1 (1972) 407; Pennington, Gen. Sapot. (1991) 158; Keng, Concise Fl. Singapore, vol. 1, Gymn. Dicot. (1990) 134; Turner, Gard. Bull. Singapore 47 (1995) 464; Yii & Chai in Soepadmo, Saw & Chung, Tree Fl. Sabah & Sarawak 4 (2002) 245; Chong et al., Checkl. Vasc. Pl. Fl. Singapore (2009) 58, 180, 208; Chantaranothai, Fl. Thailand 11 (4) (2014) 620. **Basionym:** *Payena malaccensis* C.B. Clarke, Fl. Brit. India [J.D.Hooker] 3(9): (1882) 547**. Synonyms:** *Bassia malaccensis* (C.B.Clarke) King & Gamble, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 74(1) (1906) 180; Ridley, Fl. Malay Penins. 2 (1923) 268; *Isonandra malaccensis* (C.B.Clarke) Baehni, Boissiera xi. (1965) 84; *Dasyaulus malaccensis* Dubard, Rev. Gén. Bot. 20 (1980) 201. **Type:** *Griffith 3610*, [Malaysia], Malacca (lectotype K [K000777720], designated by P. Royen, Blumea 10 (1960) 45; isolectotype P [P00640400]). (Fig. 24.)

Tree to 18m tall, 0.6m girth. **Leaves** in close spirally-arranged clusters, stipules not seen, petiole 2.5–5 cm long, blade chartaceous, obovate to elliptic, 15–30 x 10–17 cm, apex acute to acuminate, base decurrent along upper borders of petiole, sometimes forming open groove,

green above, paler beneath, glabrous on both surfaces, midrib raised on both surfaces, more prominent below, at least twice as thick as secondary veins towards base, secondary veins 12–16 pairs, ascending straight at an angle of c.60° to the midrib then curving upwards, eucamptodromous, tending to become brochidodromous in apical part of leaf, elevated beneath, tertiary veins opposite percurrent, straight to sinuous, angles to primary vein increasing basally. **Inflorescences** 1–10 flowered, fascicled in axils of leaves or leaf scars, pedicels 1–1.5 cm long, pubescent. **Sepals** 4, outer sepals ovate, 0.4–0.6 x 0.3–0.4 cm, sericeous outside except for glabrous margin, glabrous inside, inner sepals longer, 0.5–0.6 x 0.3–0.4 cm, sericeous outside except for glabrous margin, sometimes slightly keeled, glabrous inside, fimbriate margin. **Corolla** white, c. 0.8 cm long, tube 0.2–0.3 cm long; lobes 8–10, elliptic, 0.5–0.6 x c. 0.1 cm, sericeous outside, glabrous inside except densely tomentose at base of stamens, margin glabrous. **Stamens** 21–22 in 2 rows, anthers ovate to sagittate, c. 0.3 cm long, hirsute, connective appendage acuminate; filaments c 0.2 cm. **Gynoecium** glabrous to tomentose, c. 10–locular ovary, style 0.6–0.9 cm long, slightly exserted, glabrous. **Fruit** a berry, obovate-oblong, c. 1–1.5 x 0.5–1 cm, with persistent sepals, 0.5 cm long, style c. 0.6–0.7 cm. **Seed** oblong, c. 2 x 0.9 x 0.7 cm thick, testa shiny, thin, scar not seen.

**Distribution.** Southern Thailand, Peninsular Malaysia, Sumatra, Riau Islands, Borneo. In Singapore known from Bukit Timah (*Ridley 6133*, April 1894, SING [SING0025529]), Changi (*Ridley 5643*, 1893, SING [FOS15417]), Choa Chu Kang (*Mat 6500*, 1894, SING [SING0025527]) Seletar (*Gwee et al. SING 2009-77*, 3 Feb 2009, SING [SING0120419]).

**Ecology.** In evergreen or lowland mixed dipterocarp forest, at altitudes 50–800 m. Flowering: January–April.

**Provisional conservation assessment.** Globally assessed as Least Concern (Olander & Wilkie, 2019b) as it is relatively widespread across Peninsular Malaysia and North Borneo, although subject to similar pressures as other forest species. The previous national assessment of Critically Endangered (CR) in Singapore (Tan et al., 2008) is upheld, as there has been only one documented wild collection this century (*Gwee et al. SING 2009-77* in 2009) and a single occurrence record from primary forest within Bukit Timah Nature Reserve (Ho et al., 2019). This suggests there are less than 50 mature individuals in Singapore, and thus fulfilling the CR criteria. A specimen growing in the Singapore Botanic Gardens rainforest is regularly monitored by herbarium staff for information on phenology.

**Vernacular name.** Basong, nyatoh kamayan (Sabah), sundek (Singapore)

**Specimens examined.** Bukit Timah (*Mat 6133*, April 1894, SING [SING0025529]), Changi (*Ridley 5643*, 1893, SING [FOS15417]; *Mat 6043*, SING [SING0025528]), Choa Chu Kang (*Mat 6500*, 1894, SING [SING0025527]) Seletar (*Ridley 6132*, 1894, SING [SING0025523]; *Mat 6498*, 1894, SING [SING0025530]; *Gwee et al.* SING 2009-77, 3 Feb 2009, SING [SING0120419]), Long bondis Gardens (*Ridley, s.n.*, SING [FOS15412])

**Notes.** The location on the original collector label of *Ridley s.n.* is not legible. It is possible that Ridley is referring to the long border of the Singapore Botanic Gardens, since the database entry of "Long bondis Gardens" is not a known historical place. Fruiting specimens seen were not dated to month, hence it was not possible to extract a putative fruiting period.


Figure 24: Image of *M. malaccensis* fallen leaves and flowers collected from Singapore Botanic Gardens (credit P. Leong)

**4. Madhuca motleyana** (de Vriese) J.F.Macbr.

(James Motley, 1822–1859, a British engineer and naturalist, who collected plants and birds in Borneo and lost his life in a local uprising during the beginning of the Bandjermasin War.)

Contr. Gray Herb., 53 (1918) 18; Baehni, Boissiera xi. (1965) 37; Pennington, Gen. Sapot. (1991) 158; Turner, Gard. Bull. Singapore 47 (1995) 464; Chong et al., Checkl. Vasc. Pl. Fl. Singapore (2009) 58, 180, 208; Yii & Chai in Soepadmo, Saw & Chung, Tree Fl. Sabah & Sarawak 4 (2002) 250; Chantaranothai, Fl. Thailand 11 (4) (2014) 620. **Basionym:** *Isonandra motleyana* de Vriese, Natuurk. Tijdschr. Ned.-Indië 21 (1860) 308. **Synonyms:** *Bassia motleyana* (de Vriese) Hook.f., Rep. Progr. Condition Roy. Gard. Kew 1881 (1882) 43; King & Gamble, J. As. Soc. Beng. 74, 2, Extra nr. 17 (1905) 187; Ridley, Fl. Malay Penins. 2 (1923) 271; *Illipe mottleyana* (de Vriese) Engl., Bot. Jahrb. Syst. 12(3-4) (1890) 509; *Vidoricum mottleyanum* (de Vriese) Kuntze, Revis. Gen. Pl. 2 (1891) 407; *Ganua motleyana* [‘mottleyana’] (de Vriese) Pierre ex Dubard, Rev. Gén. Bot. 20 (1908) 202; Lam, Bull. Jard. Bot. Buitenzorg, ser. III, vii. (1925) 122; Bull. Jard. Bot. Buitenzorg, sér. III, viii. (1927) 424; Assem, Blumea 7 (1953) 382; Ng in Whitmore, Tree Fl. Malaya 1 (1972) 399; Keng, Concise Fl. Singapore, vol. 1, Gymn. Dicot. (1990) 134. **Type:** *Motley II. 857*, [Indonesia], Borneo (lectotype L [L 0006147] provisionally designated here, also isolectotypes P [P00640447], K [K000777843], BO, KEP n.v.). **Heterotypic synonyms:** *Sideroxylon glabrescens* Miq., Fl. Ned. Ind., Eerste Bijv. 3 (1861) 580. *Payena longipetiolata* Kurz, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 40(1) (1871) 69. *Payena bankensis* Burck, Ann. Jard. Bot. Buitenzorg 5 (1885) 54. *Payena latifolia* Burck, Ann. Jard. Bot. Buitenzorg 5 (1885) 58. *Payena rubro-pedicellata* Burck, Ann. Jard. Bot. Buitenzorg 5 (1885) 55. *Bassia motleyana* var. *scortechinii* King & Gamble, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 74(2) (1906) 187. *Ganua scortechinii* H.J.Lam, Bull. Jard. Bot. Buitenzorg, ser. III, vii. (1925) 126. (Fig. 25).

Tree to 18m tall, 1.5m girth. **Leaves** in loose, scattered clusters, stipules not seen, petiole 1.5–4 cm long, blade chartaceous to coriaceous, elliptic, 5–16 x 2.5–8.5 cm, apex acuminate, base sometimes slightly asymmetrical, decurrent along upper borders of petiole, glossy green above, paler beneath, glabrous on both surfaces; midrib prominent, keeled above, secondary veins 8–12 pairs, ascending at an angle of c. 60° almost straight or gently curving toward margin to join smooth or looping intramarginal vein, inconspicuous to slightly raised beneath, often intersecondaries becoming reticulate midway between midrib and margin, tertiary veins random reticulate. **Inflorescences** 1–15 flowered, fascicled in axils of leaves, pedicels c.1.5 cm

long, glabrous. **Sepals** 4, outer sepals ovate, c. 0.3 x 0.3 cm, sericeous outside except for glabrous central portion, glabrous inside, inner sepals narrower, c. 0.3 x 0.2–0.25 cm, sericeous outside, glabrous inside, fimbriate margin. **Corolla** white, 0.3–0.4 cm long, tube c. 0.1 cm long, lobes 8, spathulate to oblong, 0.2–0.3 cm long, glabrous outside except hirsute at top of lobes, glabrous inside except hirsute at tops of lobes and between stamens, margin fimbriate. **Stamens** 16 in 1 row, anthers oblong to ovate, glabrous, c. 0.1 cm, connective appendage apiculate, filaments 0.1–0.2 cm. **Gynoecium** glabrous, 10-locular ovary, style 0.6–1 cm long, exserted, glabrous. **Fruit** a berry, up to 2-seeded, ellipsoid to obovoid, c. 0.5–2.5 x 0.3–2 cm, supported by persistent sepals, 0.4 cm long, style c.1 cm. **Seed** ellipsoid to oblong, c. 1.8 x 0.7–0.9 x 0.3–0.4 cm thick, testa shiny, thin, seed scar c. 1.5 x 0.3 cm, longitudinal along side of seed.

**Distribution.** Thailand, Peninsular Malaysia, Sumatra, Bangka Belitung Islands, Riau Islands, Borneo. In Singapore known from Bukit Mandai (*Bayliss 5896*, Jan 1894, SING[SING0025533]), Changi (*Ridley 5645*, 1893, SING [SING0025531]) and Sungei Jurong (*Ridley 6039*, 1894, SING [SING0025532]).

**Ecology.** Widely distributed in evergreen, freshwater or peat swamp or lowland mixed dipterocarp and sandstone forest, at altitudes 0–800 m. Flowering: March, July–August, October. Fruiting: January, May.

**Provisional conservation assessment.** Globally assessed as Near Threatened (Olander & Wilkie, 2019c). The last SING herbarium specimen is dated 1894, however in the last national conservation assessment using 2006 data (Tan et al., 2008), it was assessed as Critically Endangered (CR), and presumably took into account the records of four individuals in a 1992–93 forest survey that included Nee Soon swamp forest (Turner et al., 1996). There have been no records of *M. motleyana* since. As the last forest survey recording of *M. motleyana* occurred less than 30 years ago, in this thesis the assessment is maintained as Critically Endangered (CR) since the estimate of less than 50 individuals holds.

**Vernacular name.** Ketiau paya (Malay and Melanau in Sabah and Sarawak), nyatoh tanjong, surin, ketur, medang ketur, nyatoh ketiau, ketiau, bengku, pujang, mitis, nyatoh bekas (in Sumatra).

**Uses**. The seed is a source of cooking fat, the latex a low-quality gutta-percha, and the wood used for timber.

**Specimens examined.** Bukit Mandai (*Bayliss 5896*, Jan 1894, SING[SING0025533]), Changi (*Ridley 5645*, 1893, SING [SING0025531]) and Sungei Jurong (*Ridley 6039*, 1894, SING [SING0025532]).

**Notes.** In the protologue by de Vriese (1860), he only mentions the collector number (*Motl. II.857*) of the type specimen and not the herbarium. Assem (1953) identified the specimens of *Motley 857* at both P and L as types (effectively syntypes) of *Isonandra motleyana* de Vriese. Yii & Chai (2002) erroneously cited *Motley 857* at P as the holotype, with an isotype at L. On JSTOR, the collector for the type specimen at L is wrongly identified as de Vriese; though there is no mention of Motley, it is clear that the collector number on the tag is II.857, in the same handwriting as the duplicate of the *Motley II.857* collection at P, also de Vriese was not in Borneo during 1857 (the collection date stated on JSTOR). The quality of both specimens at P and L is similar, however as de Vriese was a Dutch botanist based in the Netherlands and would have without doubt seen the specimen deposited there, the duplicate at L is here provisionally designated as the lectotype. Tree dimensions are taken from Johor specimens as the collections from Singapore contain no habit details.

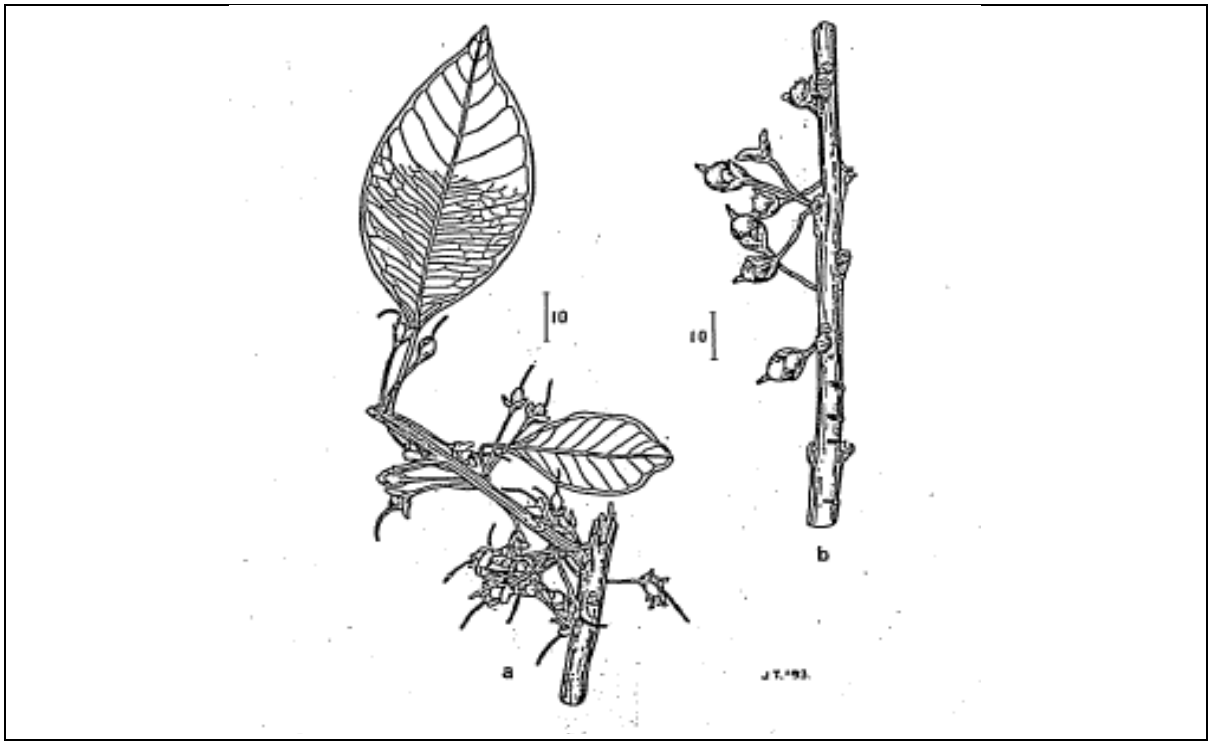



Figure 25: Illustration of *M. motleyana* in Assem (1953) – a. branchlet with inflorescences; b. with young fruits. Dimensions in mm.

**5. Madhuca sericea** (Miq.) H.J.Lam

(Latin, *sericeus* = silky, referring to the indumentum on the leaf undersurface)

Bull. Jard. Bot. Buitenzorg, sér. III, vii. (1925) 163; Bull. Jard. Bot. Buitenzorg, sér. III, viii. (1927) 446; P. Royen, Blumea 10 (1960) 70; Ng in Whitmore, Tree Fl. Malaya 1 (1972) 410; Pennington, Gen. Sapot. (1991) 159; Turner, Gard. Bull. Singapore 47 (1995) 465; Yii & Chai in Soepadmo, Saw & Chung, Tree Fl. Sabah & Sarawak 4 (2002) 263; Chong et al., Checkl. Vasc. Pl. Fl. Singapore (2009) 58, 180, 208; Keng, Concise Fl. Singapore, vol. 1, Gymn. Dicot. (1990) 134. **Basionym:** *Payena sericea* Miq., Fl. Ned. Ind. 2 (1859) 1039. **Synonyms**: *Bassia sericea* (Miq.) King ex S.Moore, J. Bot. 63(Suppl.) (1925) 61. **Type**: *Horsfield s.n.*, [Indonesia], Bangka (lectotype P [P00640460] provisionally designated here). **Heterotypic Synonyms:** *Bassia argentea auct. non* de Vriese, Pl. Ind. Bat. Orient. 62 (1856); C.B.Clarke in J.D.Hooker, Fl. Brit. India 3 (1882) 545; King & Gamble, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 74(2) (1906) 184; Ridley, Fl. Malay Penins. 2 (1923) 270. *Kakosmanthus argenteus* Pierre ex Dubard, Rev. Gén. Bot. 20 (1908) 198; *Madhuca sericea* var. *ridleyi* (Gand.) Ng in Whitmore, Tree Fl. Malaya 1 (1972) 410; *Payena ridleyi* Gandoger, Bull. Soc. Bot. France 65 (1918) 56. (Fig. 26.)

Large tree to 40m tall, 1.2m girth. **Leaves** in loose clusters, stipules c. 0.2 cm, obtuse, petiole c. 3 cm long, blade chartaceous to coriaceous, elliptic, oblong to obovate, 13–28 x 3–9.5 cm, apex acute to acuminate, base decurrent along upper part of petiole to form shallow or closed groove, green glabrous above, rarely sparsely hirsute on midrib, golden or silvery sericeous beneath, midrib flat to impressed above, prominent below, secondary veins 12–20 pairs, ascending straight at an angle of c. 60° to the midrib then curving upwards, eucamptodromous, elevated beneath, tertiary veins opposite percurrent, straight to sinuous, angles to primary vein increasing basally. **Inflorescences** 5–12 flowered, greenish-yellow in bud, fascicled in axils of leaves, pedicels c.1.5 cm long, sericeous. **Sepals** 4, outer sepals ovate, c. 0.3–0.5 x 0.2–0.5 cm, sericeous outside except for glabrous margin, glabrous inside, inner sepals rounder, c. 0.3–0.4 x 0.3–0.4 cm, sericeous outside except for glabrous margin, slightly keeled, glabrous inside, fimbriate margin. **Corolla** colour unknown, c. 0.4 cm long, tube c. 0.25 cm long, lobes oblong, 8–9, 0.4 cm long, glabrous outside and inside except hirsute between stamens, margin glabrous. **Stamens** 14–15 in 2–3 rows, anthers sagittate, c. 0.2–0.3 cm long, hirsute, connective appendage penicillate, filaments c. 0.1 cm or almost sessile. **Gynoecium** tomentose, c. 8-

locular ovary, style 0.6–0.7 cm long, exserted, sericeous halfway up. **Fruit** a berry, ellipsoid, c. 1.6–1.7 x 1.5 cm, supported by persistent sepals, 0.4 cm long, style not seen. **Seeds** not seen.

**Distribution.** Peninsular Malaysia (Johor, Malacca, Negri Sembilan, Pahang, Perak, Selangor), Borneo, Sumatra, Bangka Belitung Islands, Riau Islands, Brunei. In Singapore known from Choa Chu Kang (*Mat* 6698, 15 May 1894, SING [SING0069593]) and MacRitchie in the Central Catchment Nature Reserve (*Sinclair SFN 39656*, 30 May 1953, SING [SING0025537]).

**Ecology.** Scattered in primary lowland, marshy and hill mixed dipterocarp forests, at altitudes to 1000 m. Fruiting: July–August.

**Provisional conservation assessment.** This species is globally assessed as Vulnerable (Olander & Wilkie, 2019d). In Singapore, only three records have been documented this century: two herbarium specimens (see below for details) and one potential SING database entry (*Leong et al. CTFS H5-11746*, 27 Mar 2019, determined as *Madhuca cf. sericea* and collected from Bukit Timah Nature Reserve, voucher not seen). Given the lack of records for this species in recent forest surveys and in herbaria, it is estimated that there are fewer than 50 mature individuals left in Singapore, and hence the last national assessment (Tan et al., 2008) as Critically Endangered (CR) is maintained.

**Vernacular name.** Nyatoh balam, nyatoh percha, melawis, getah sondeh, natu daun lebar, njatu kelep, kayu gugading (Malacca). In Sumatra, ketiau, mayam percha balam merah, balam abang, kemodan, melikuran.

**Uses**. Possible adulterant for gutta-percha.

**Specimens examined.** Choa Chu Kang (*Mat* 6698, 15 May 1894, SING [SING0069593]), MacRitchie in Central Catchment Nature Reserve (*Sinclair SFN 39656*, 30 May 1953, SING [SING0025537]; *Leong et al. MR 2014-049*, 2 Sep 2014, SING [SING0211889]), Bukit Timah Nature Reserve (*Khoo & Nik Faizu KMS 51*, 20 Dec 2008, SING [SING0137289]) and unspecified location/date (*Unknown 2808*, SING [SING0025536], *Cantley 2902*, SING [SING0025534]; *Cantley 3003*, SING [SING0025535]).

**Notes.** The *Cantley* collections (*Cantley 2902* and *Cantley 3003*) have been cited in previous treatments of *Madhuca sericea* (Lam, 1925; Ng, 1972); however Ridley (1900) cautioned that many Cantley specimens "labelled from Singapore in the herbarium, are either cultivated plants or from some part of the [Malay] peninsula", and hence should be treated with circumspection.

Royen (1960) cites *Horsfield s.n* from BO as the type of *Madhuca sericea.* Yii & Chai (2002) also cite the same collection as the type but erroneously identified the status of the BO specimen as the holotype (NB. there is no mention of the herbarium in the protologue) and K specimen as isotype. During this study no such specimen could be located online in the BO or K herbaria. The only specimen of *Horsfield s.n.* from Bangka found online in JSTOR was from P, and is here provisionally designated the lectotype, although once access to the BO and K herbaria is possible again a thorough search for these specimens will need to be undertaken. Also found on JSTOR were two sheets of *Horsfield 37* held at K. These collections are of the same species and from Bangka, therefore may be the potential types referred to by Yii & Chai; however, as the collector numbers do not match, these are not considered types here.

Regarding the synonym *Bassia argentea*, de Vriese (1856) validly published the name and cited type material (*Teysmann s.n.* from Java). Having looked through images of the collections in BO, L and K, this specimen has not been located, and locating it is essential if we are to definitively place the name to a species. However, for now we have followed Lam (1925) who indicated that he had seen the specimen and that it was *Planchonella obovata* H.J.Lam. In this thesis *Bassia argentea* de Vriese is considered a synonym of *Planchonella obovata* until the type specimen can be found. King & Gamble (1906) and Ridley (1923) excluded the type specimen of *Bassia argentea* de Vriese from this name, which is not permissible under the International Code of Botanical Nomenclature; the material they misidentified is cited in this thesis as *Bassia argentea auct. non* de Vriese and is currently considered a synonym of *Madhuca sericea.*

The holotype of *Payena ridleyi* Gandoger, Bull. Soc. Bot. France 65 (1918) 56 is cited as *Ridley 6698* in the protologue, however to account for the proper name of the collector, that is corrected to *Mat 6698* in Ng (1972) and is reiterated here. Flowering specimens did not provide the month of collection.

Figure 26: Image of *M. sericea* branchlet collected at MacRitchie, Central Catchment Nature Reserve, Singapore (credit P. Leong)

### 6. Madhuca sessilis (King & Gamble) Baehni

(Latin, *sessilis* = attached without a distinct stalk; referring to the sessile or almost sessile leaves, without or with only a very short petiole)

Boissiera xi. (1965) 36; Turner, Gard. Bull. Singapore 47 (1995) 465; Yii & Chai in Soepadmo, Saw & Chung, Tree Fl. Sabah & Sarawak 4 (2002) 264; Chong et al., Checkl. Vasc. Pl. Fl. Singapore (2009) 58, 180, 194. **Basionym:** *Payena sessilis* King & Gamble, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 74(1) (1906) 174; Ridley, Fl. Mal. Pen. 2 (1923) 265. **Synonym:** *Ganua sessilis* (King & Gamble) H.J.Lam, Bull. Jard. Bot. Buitenzorg, sér. III, vii. (1925) 120; Bull. Jard. Bot. Buitenzorg, sér. III, viii. (1927) 424; Assem, Blumea 7 (1953) 387; Keng, Concise Fl. Singapore, vol. 1, Gymn. Dicot. (1990) 134. **Type:** *Ridley 5076*, [Singapore], lectotype SING [SING0058081] designated by Assem, Blumea 7 (1953), isolectotypes (K [K000777878], KEP [KEP109047] n.v.) (Fig. 27.)

Tree to 18m tall, 0.4m girth. **Leaves** in close, spirally-arranged clusters along branch, stipules 0.2–0.3cm, acute to obtuse, petiole up to 0.5 cm long or sessile, blade coriaceous, obovate, 5–9 x 2–4 cm, apex rounded to retuse, base cuneate to decurrent, colour unknown, glabrous above

and beneath, midrib prominent on both surfaces, secondary veins 7–9 pairs, ascending at an angle of 50–60° to the midrib, brochidodromous to festooned brochidodromous to join smooth or looping intramarginal vein, elevated beneath, often strong intersecondaries becoming reticulate toward margin, tertiary veins random reticulate. **Inflorescences** 1–3 flowered, fascicled in axils of leaves, pedicels c.1.3 cm long, slender. **Sepals** (seen on fruit) 4, outer sepals ovate, 0.4 x 0.2 cm, sparsely sericeous outside, glabrous inside, inner sepals rounder, 0.5 x 0.3 cm, glabrous outside, slightly keeled, glabrous inside, membranous margin. **Flowers** not seen. **Fruit** a berry, globose, black, c. 1.2 x 0.8 cm, glabrous, supported by 4 persistent sepals, 0.5 cm long, acute, glabrous; style slender, black, c. 1 cm. **Seed** oblong, c. 0.8 cm long, testa crustaceous, scar not seen.

**Distribution.** Sumatra, Borneo. In Singapore only known from Tuas (*Ridley 5076*, 30 Mar 1893, SING [SING0025531]).

**Ecology.** In mixed dipterocarp forest, low slopes. Fruiting: March.

**Provisional conservation assessment.** This species is assessed as Globally Endangered (Olander & Wilkie, 2019e): it has few known collections and the estimated extent of occurrence at 423,694 $km^2$ is within the EN range, with a continuing decline in habitat quality. In Singapore it is presumed Nationally Extinct (NE) as it has not been recorded since the type specimen was collected by Ridley in 1893.

**Vernacular name.** Nyatoh.

**Specimens examined.** Tuas (*Ridley 5076*, 30 Mar 1893, SING [SING0025531], K [K000777878]).

**Notes.** This species is very rare and has never been collected in Peninsular Malaysia and only once in Singapore (type). The two other known collections are from Borneo, one in Brunei, the other in Sarawak. Tree dimensions are taken from the *Tree Flora of Sabah and Sarawak* (Yii & Chai, 2002).

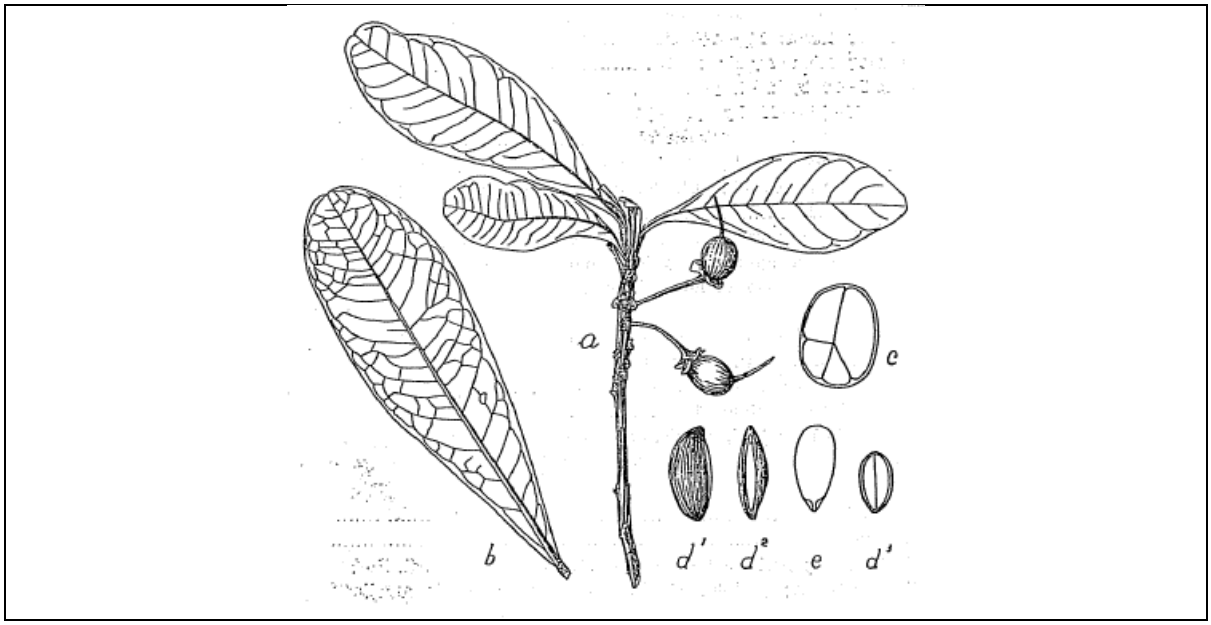



Figure 27: Illustration of *M. sessilis* in Lam (1925) – a. branchlet with leaves and fruits; b. leaf; c. fruit, cross-section through base, $d^1$. seed, lateral view; $d^2$. seed ventral view; $d^3$. seed cross-section; e. embryo, longitudinal section.

# 4. DISCUSSION

## *4.1 Benefits and Limitations of Virtual Taxonomy vs. In-herbarium Taxonomy*

Large amounts of resources are being invested by herbaria around the world to digitise their specimens and to make these available online. Borges et al. (2020) noted that accurate morphological data, particularly measurable values, can be obtained from professionally-scanned 2D specimen images. This is supported in this study where around half of the characters in the taxonomic treatment of *Madhuca* could be measured and described without access to physical specimens. This is a massive research benefit during a situation such as the COVID-19 pandemic with limited travel, restricted loan access and widespread institutional lockdowns. It has allowed examination of specimen images in an efficient and relatively inexpensive way, and access to taxonomic data. It is clear that for plant families possessing diagnostic characters that are mainly macro-morphological in scale, a comprehensive taxonomic account based on virtual specimen images is potentially possible. However, in families such as Sapotaceae where critical micro-morphological details such as fertile parts and indumentum need to be studied in detail and analysed this would be difficult, if not impossible, to deliver.

The RBGE database PADME that captures a wide range of specimen data, including geo-tagged references across multiple collection locations and from different herbaria, has played a significant role in the ability to undertake virtual taxonomy and conservation studies, e.g. by providing images to understand species variation and data points to assess extent of occurrence and area of occupancy used in standard IUCN criteria.

Duplicates of the same collection are normally stored in different herbaria and databases and given the difficulty in obtaining multiple loans as well as the uneven capture of publicly-available herbarium records, the only way of studying known duplicates has been through this taxonomically-focused centralised repository. This has, to some extent, been replaced by the advent of large institutional digitisation initiatives, but these do not usually provide the depth of information (e.g. suite of characters that can be seen or described from multiple specimens from a single collection, as one specimen may have fertile material while another is sterile) needed for taxonomic studies and not all herbaria are currently digitising their collections, especially important smaller regional herbaria. The PADME database interface for specimen

record capture has supported this study in allowing the upload of multiple images tagged to a specific record. This can include useful field images to supplement herbarium specimens, such as fresh material and dissections of flower or fruit unlike traditional herbarium databases where a single record is normally tied to only a single image of a dried specimen.

Despite the indisputable utility of virtual information (both high quality and more general images), it was found to be ultimately insufficient to complete a full taxonomic treatment of the genus *Madhuca* in Sapotaceae. Micro-morphological characters including indumentum, internal flower and fruit structures, as well as venation patterns could only been observed using illuminated external light sources and dissections. As these were diagnostic for species delimitation in *Madhuca*, the information missing from a purely virtual taxonomic account would have been substantial enough to affect specimen identification and species delimitation. This is consistent with findings of image use where specimen measurement accuracy is highly reduced for smaller traits, and images cannot be manipulated to observe organs that are concealed such as petals overlapping stamens and gynoecium (Alcantara et al., 2013; Borges et al., 2020). Access to physical herbarium material for analysis therefore remains critical, although the taxonomic process could be accelerated if a thorough virtual analysis could be undertaken and specimens pre-identified from images for dissections and closer study. This would lower the number of characters needed to be verified than if the study had freshly begun in the herbarium. In this project, seven full days in the herbarium were sufficient to complete the taxonomic descriptions of each *Madhuca* species as the macro-morphological characters had been analysed using images and the micro-morphological characters had already been shortlisted beforehand, enabling a focused study when in the herbarium.

### *4.2 Minimum Requirements for Taxonomic Treatment*

If herbarium access had not been possible during this study, the following strategies would have been needed to produce a useful taxonomic account:

1) All relevant specimens to have been professionally scanned (Hauser et al. (2005) sets out best practices for digitally imaging biological specimens), with available images to the "gold standard" type requirements laid out in the JSTOR-Plants-Handbook (including 600 dpi image resolution and 24-bit colour depth), and with capsules opened. (Fig. 28, showing the HerbScan setup in the SING herbarium).

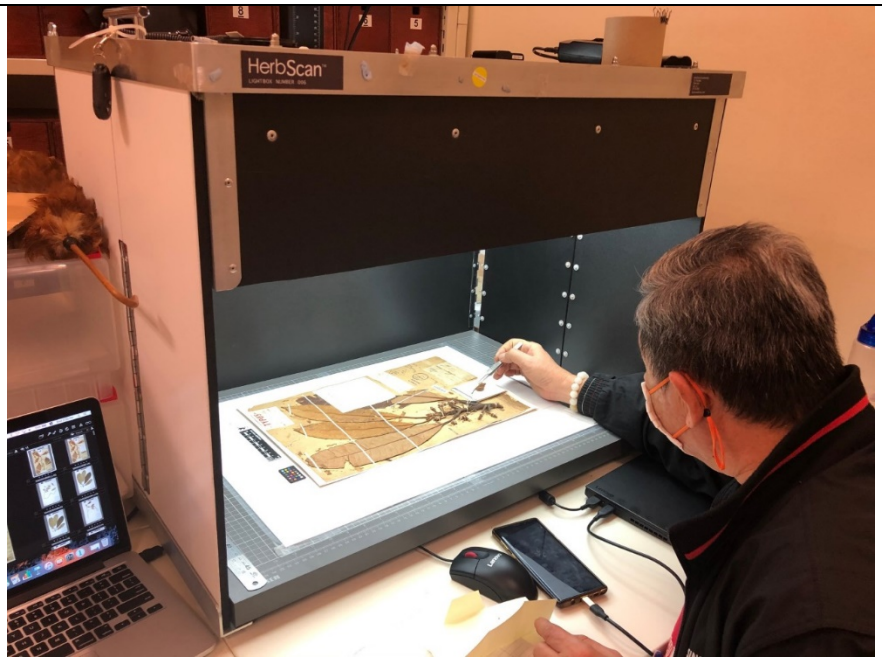



Figure 28: HerbScan setup at SING herbarium, with staff laying out capsule contents with tweezers prior to image capture

2) A range of images available for each specimen that were taken under a range of light conditions such as camera flash or external light attachment, in order to light up venation details and provide sharper contrast to assess level of indentation or protrusion.
3) Available microscope-level images of relevant specimens for essential micro-morphological characters, to be narrowed down by taxonomists familiar with the particular family. For Sapotaceae, these would include images of indumentum on twigs, both leaf surfaces and midrib, all fertile parts.
4) Where microscopic images are not available and dissections required, an available network of willing herbarium collaborators to outsource dissections and descriptions of micro-morphological characters and make them available virtually.

The importance of enhancing digital collections to mitigate missing data on specimen images has been noted by Borges et al. (2020), who suggest to capture more images with varying magnifications and exposing hidden structures, though this complexity requires an active feedback channel between researchers and herbaria. Human input through crowdsourcing (Zhou et al., 2018) may also provide some avenues to address missing observations.

### *4.3 Species Delimitation and Identification*

This study covers six species of *Madhuca* and 41 names. Of these there were delimitation or nomenclatural issues with one species (*M. decipiens*), which are resolved within this study.

*Madhuca decipiens* and *Payena maingayi*

The nomenclatural confusion between *M. decipiens* and *Payena maingayi*, regarding the assignment of the former as a synonym of the latter, in Govaerts et al. (2001) was resolved, with both determined as separate species. *Madhuca decipiens* was first published by Sinclair (1967) upon a re-assessment of *Payena grandiflora* Ridley. After close examination of the three syntypes (*Ridley 11371*, *Ridley 6497* and *Goodenough 1268*) cited in Ridley's (1912) original description of *Payena grandiflora*, Sinclair (1967) found *Ridley 11371* and *Ridley 6497* to be *M. decipiens* sp. nov. and *Goodenough 1268* to be *Payena maingayi* Clarke, a decision affirmed by Ng (1972) and verified here. Due to this differential treatment of the three syntypes, particularly relating to *Goodenough 1268* being identified as *P. maingayi* and the erroneous label on the type specimen at SING (Fig. 29), associating *M. decipiens* with *P. maingayi*, it appears that Govaerts et al. (2001) made an understandable error in reducing *M. decipiens* to synonymy. That mistake has since been corrected in the current World Checklist of Selected Plant Families (WCSP), which recognises *M. decipiens* as a species distinct from *P. maingayi*. Indeed, descriptions of *P. maingayi* from the literature (recently Chantanarothai, 2014) and examination of types and specimens of those species do not align with characters identified as *M. decipiens* in this account, particularly indumentum and floral parts (e.g. pale green to golden indumentum on blade underside, larger sepals and densely hirsute stamens for *M. decipiens*; yellow to reddish-brown indumentum on blade underside, glabrous stamens for *P. maingayi*).

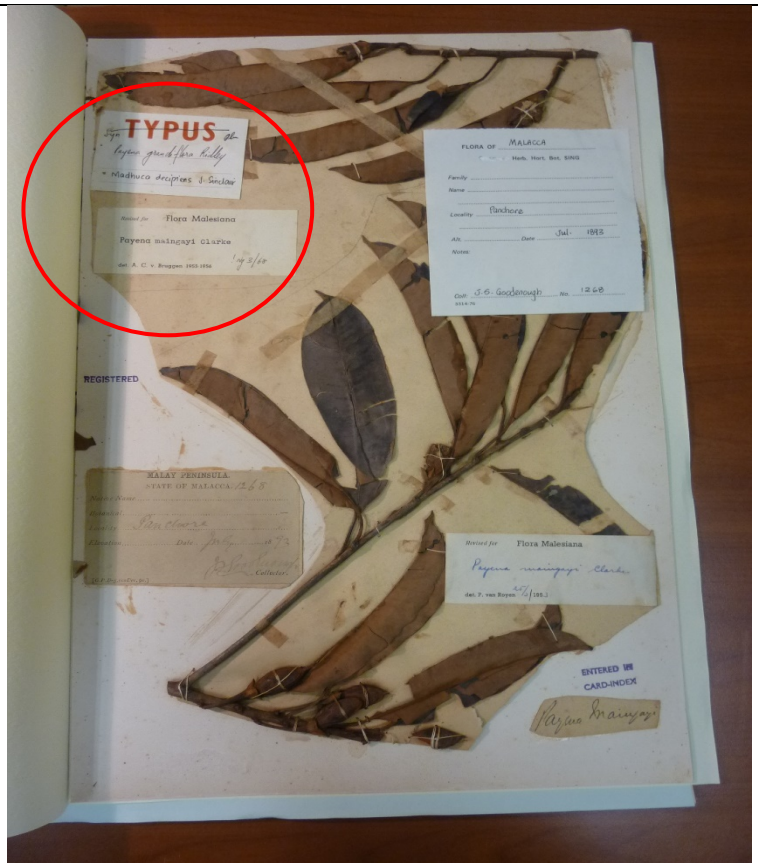



Figure 29: Specimen image of *Goodenough 1268* (SING) wrongly labelled as *M. decipiens*

*Ganua* and *Madhuca*

Another taxonomic focus of this study was the historical separation between *Ganua* and *Madhuca*. This was verified to be tenuous: while the presence of an intramarginal vein in species previously in *Ganua* (i.e. *M. kingiana, M. motleyana* and *M. sessilis*) was a factor distinguishing it from the rest of the Singapore *Madhuca* species and useful for identification in keys, other characters including indumentum and fertile parts were generally overlapping. The hirsute stamens, sericeous surfaces of outer sepals and glabrous ones of inner sepals, shiny testa were found across all species, whether previously placed in *Ganua* or *Madhuca. Madhuca malaccensis* leaves were also found to be completely glabrous on both surfaces, despite this being a character associated with *Ganua*. The findings in this study agree with Pennington's (1991) decision to reduce *Ganua* to synonymy with *Madhuca* and Ng's (1972) observation that the two genera are closely related, with the differences cited by Assem (1953) inconsistent and very challenging to apply in practice (see section 1.3 Taxonomic History of *Madhuca*). Indeed, many of Assem's distinguishing factors for *Ganua*, including stipules, sepals with hair tufts,

ovary contracted into the style and linear seed scar, were also seen in the *Madhuca* species found in Singapore.

*M. sericea* var. *ridleyi*

Ng (1972) had been compelled to assign a new variety *M. sericea* var. *ridleyi* due to a few characters he considered distinct: the petiole having a closed groove above, the midrib being generally more slender above, and secondary veins from 11–22 pairs (as opposed to *M. sericea* var. *sericea* having 12–17 pairs). This was however not found to be a convincing differentiation in relation to the Singapore collections, as these characters were frequently overlapping. The grooves for many collections in Singapore varied even within the same specimen (e.g. closed to open grooves could be seen in both *Sinclair 39656* and *Unknown 2808,* with the former having been determined by Ng as var. *sericea*), and the vein pairs do not appear sufficiently diagnostic since the numbers for both var. *sericea* and var. *ridleyi* overlap significantly. The indumentum for all collections of *M. sericea* was identical to that for the type specimen var. *ridleyi* (*Mat 6698*) that Ng had designated. There is also no observable pattern of geographic differentiation for Ng's rank definition that might have contained an underlying biological species concept, since var. *sericea* and var. *ridleyi* are found across Peninsular Malaysia and Borneo. Hence the separation of varieties is not supported in this study and is consistent with the World Checklist and Bibliography of Sapotaceae (Govaerts et al., 2001) that reduces var. *ridleyi* to synonymy with *M. sericea*.

*Singapore and Johor*

As the state of Johor is more than 25 times larger than Singapore (19,166 $km^2$ vs 725 $km^2$), it is not surprising that there are more *Madhuca* species found in the former. As noted by Corner (1960) and Keng (1970), Singapore's flora is overwhelmingly a subset of what is found in Peninsular Malaysia and related to that of Borneo and Sumatra, since it was part of the emerged Sunda shelf during the Last Glacial Minimum, and linked by land to the south of Peninsular Malaysia as recently as 10,000 years ago (Wong & Ganesan, 2019). Moreover, the narrow Johor Strait separating Singapore and Peninsular Malaysia arose fairly recently during the early Holocene (Bird et al., 2005). Conceivably, Singapore's small land area and limited physiographic diversification (with the highest point at 163m, Bukit Timah summit) contain

less biodiversity than bigger landmasses (Hawksworth & Kalin-Arroyo, 1995; Mutke & Barthlott, 2005).

As such, it is likely that the taxa placed incertae sedis in this account would eventually be identified as existing species that occur in Peninsular Malaysia, probably Johor due to proximity, but also possibly Borneo and Sumatra. After all, *M. sessilis* was found to occur only in Singapore and Borneo, but not in Peninsular Malaysia. Hence if no species matches occur in Peninsular Malaysia, it is important to look toward Borneo occurrences as well. Unfortunately this was not possible within the time limits of this study.

### *4.4 Conservation Considerations*

Out of the six *Madhuca* species identified as native to Singapore, this study has assessed one as presumed Nationally Extinct (*M. sessilis*), four as Critically Endangered (*M. decipiens*, *M. malaccensis*, *M. motleyana* and *M. sericea*), and one as Endangered (*M. kingiana*). These categories are generally the same as the last national conservation assessment in Singapore's Red Data Book (Tan et al., 2008), except for *M. decipiens* (formerly Nationally Extinct) which has since been rediscovered.

*Madhuca decipiens* is a fine example of a species rediscovery during the last decade, when taxonomic botany in Singapore increased in pace. As of 2019 around 140 rediscoveries have been made of vascular plant species earlier presumed to be nationally extinct (Wong & Ganesan, 2019). Although *M. decipiens* was first re-collected in 2011 according to SING herbarium records, it has not been registered in official checklists of species rediscoveries in the past nine years (Chong et al., 2012; Lim et al., 2018). As part of this study, discussions with herbarium and conservation staff at the Singapore Botanic Gardens and National Parks Board have confirmed that flowering material collected in 2019 (collections from 2011–2018 had been sterile) is indeed *M. decipiens*. Unfortunately there are issues regarding publication of this rediscovery due to security reasons, as all the contemporary collections of *M. decipiens* are from the Western Catchment region under the management of the Ministry of Defence.

The confirmation of the identity and conservation status of *M. decipiens* in this research now means that conservation actions such as propagation and habitat protection can be undertaken under the national Nature Conservation Masterplan (National Parks Board, 2009; Lim et al.,

2019), especially since the present occurrences are not recorded within a Nature Reserve and only afforded limited protection within military training grounds.

The conservation status of *Madhuca motleyana*, provisionally determined as Critically Endangered (CR) in this study, is tenuous given that there have been no SING or SINU herbarium records of *M. motleyana* since 1894. The assumed basis for the previous assessment (Tan et al., 2008) of CR instead of Nationally Extinct is the occurrence records of 4 individuals documented in the 1992–1993 tree surveys of Singapore's nature reserves including Nee Soon swamp forest (Turner et al., 1996). *Madhuca motleyana* has a clear ecological preference for freshwater and peat swamps and this is particularly relevant as many of these areas in Singapore have been destroyed. Corner in a survey carried out in 1933 found the Jurong area to contain 57 individuals but sadly today this has been totally felled (Corner, 1978). Also in 1933 Corner found four individuals in Mandai (again most of the area has been lost to development). Currently, the Nee Soon freshwater swamp forest is the final remaining portion of the larger Mandai swamp forest but in the latest survey carried out between 2011 and 2016 and related checklist (Wong et al., 2013; Chong et al, 2018), *M. motleyana* is not recorded. Latest SINU records of vouchers collected at Nee Soon (Appendix 1) also do not contain this species. It is highly probable that the *M. motleyana* records in Turner et al. (1996) were erroneous. Corner (1978) himself notes that he "..may have confused more than one species… *SFN 26158* (Jurong, Singapore), which (he) took to be *Ganua motleyana*, is named *Madhuca sp.* by F.S.P. Ng in the Singapore Herbarium. If there is a complex of two or three species, it is not clear how they differ ecologically".

As part of this project, an effort was made to explore the Mandai swamp forest area near Nee Soon where *Lim & Wong 2018-209* (SING 0286267) was collected (determined then as *M. cf. motleyana*, placed incertae sedis here though sharing several sterile characteristics with *M. tubulosa*, see results above in section 3.3). This collection was from a "fallen branch" near one of the areas (plot 27) that Turner et al. (1996) had last recorded an occurrence of *M. motleyana*. The tree was eventually located during this study with the assistance of SING herbarium staff (Fig. 30), and though it was too tall to collect a fresh branch (greater than 25m), it was confirmed as the same species as the *Lim & Wong 2018-209* collection from fallen leaves. Saplings were seen around the main tree, and a DNA sample collected for potential barcoding. With the location of the tree now known, the phenology of this *Madhuca* species can be better studied in future.


Figure 30: Images from field study of source tree for collection *Lim & Wong 2018-209* at Mandai near Nee Soon swamp forest. **A.** Straight bole; **B.** Spiral leaf arrangement; **C.** copious white sap oozing out of bark slash. (credit A-B: P. Athen; C: A Phang)

With regard to *M. motleyana*, it is hoped that continuing discoveries in Nee Soon swamp forest and its vicinity (Chong et al., 2018) will allow individuals to be found in the next few years, as the 30-year cut off to determine national extinction is approaching (the last recorded occurrences are 1992–93).

From an examination of historical collection dates on the few flowering or fruiting specimens, there appears to be an indicative flowering period for *Madhuca* in Singapore and Johor of between March to May, and then again later in October. Ng (1988) reports a community-level flowering peak in lowland forest around April, presumably triggered by climatic contrasts between the beginning of the northeast monsoon in November/December and drier period towards February/March, and Corner (1988) suggests a second weaker period later in the year triggered by less predictable dry periods (Corlett, 1992). These may provide some helpful broad guidance for conservation staff intending to collect fertile specimens of *Madhuca* for documentation or propagation.

*Madhuca kingiana, M. malaccensis,* and *M. sericea* have been recorded in two out of four of the legally protected nature reserves in Singapore (Bukit Timah Nature Reserve and the Central Catchment Nature Reserve), and a specimen of *M. malaccensis* growing in the Singapore Botanic Gardens Rain Forest also enjoys protection under Singapore's Parks and Trees Act (Davison, 2019). Such protection allows high levels of plant diversity to be found in the four Nature Reserves, the Singapore Botanic Gardens' Rain Forest and other National Parks (Fig. 31). The last remnant of swamp forest in Nee Soon, which fortunately falls within the Central Catchment Nature Reserve, contains the highest overall recorded native biodiversity in Singapore, and is a valuable botanical area that warrants high conservation priority (Turner et al., 1996; Chong et al., 2018; Clews et al., 2018).

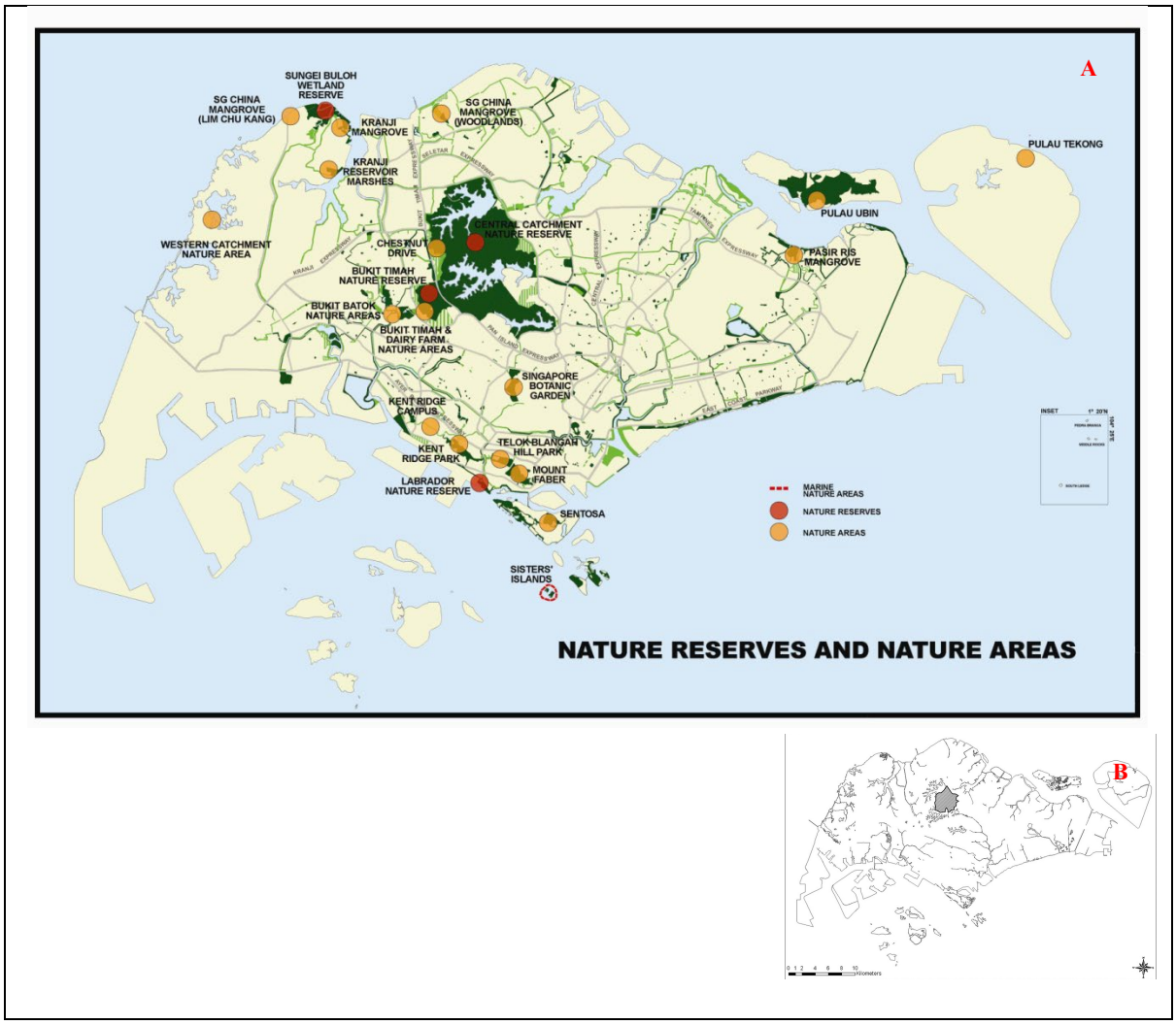



Figure 31: **A.** Map of Singapore containing information on protected nature reserves and nature areas (Singapore's 4th CBD report, 2010). **B.** Grey shaded area indicates the boundaries of Nee Swee swamp forest within the Central Catchment Nature Reserve (Li et al., 2014)

## 5. CONCLUSIONS AND FUTURE RESEARCH

This study has resulted in a floristic account of the genus *Madhuca* for the *Flora of Singapore*, which includes identification keys, full descriptions and specimen citations. Six species (*M. decipiens, M. kingiana, M. malaccensis, M. motleyana, M. sericea* and *M. sessilis*) are recognised, based on a phenetic species concept and usual herbarium taxonomy methods. The account of *Madhuca* is a contribution to the revision of Sapotaceae being prepared for a wider project on the flora of the Malesian region (Wilkie, 2011), which will be a necessary contribution to update the too-few inventories of tropical taxa (Goodwin et al., 2015) so urgently needed not only for accurate identification but importantly, for conservation decisions.

Amid the continued threat of global coronavirus spread, the traditional methods of botanical experts visiting herbaria to conduct taxonomic research cannot be relied upon, and digitized specimens available remotely will be essential. However, progress to digitize specimens has been positive but patchy: one of the most significant efforts is the JSTOR Global Plants Initiative that sought to digitize all plant types globally. However the largest herbaria in Asia (China, India and Indonesia) were not part of the consortium (Staples & Lee, 2013). Certain herbaria in Europe, namely Naturalis (Netherlands – all 4 million plant specimens in Leiden have been digitized), Digitarium (Finland – around 5 million records), and the Muséum National d'Histoire Naturelle (Paris – 5.4 million specimens) have shown that major herbaria can successfully digitize their collections within a few years (Borsch et al., 2020). Initiatives in the United States such as iDigBio (Integrated Digitized Biocollections; www.idigbio.org), have made nearly 20 million global specimen records available (Soltis et al., 2018) and is taxonomically useful in so far as institutions share high-quality data and image links, which currently are still lacking for most records in the Malesian region, including *Madhuca*. The RBGE has imaged nearly 500,000 out of a total of three million specimens, and is also actively exploring ways to complete specimen data entry, including Optical Character Recognition (OCR) and citizen science platforms to accurately transcribe specimen label data (King et al., 2019).

There appears to be a disjunct in the process of capturing specimen images and the specimen data linked to them. While some research has cited the capture of information on specimen labels as the rate-limiting factor in digitization (King et al., 2019), other papers identify the

imaging of herbarium specimens as the first important step (Takano et al., 2019). About 20% (around 2 million) of specimen data in Japan is deposited in the Global Biodiversity Information Facility (GBIF.org) without images, and Takano et al. (2019) have proposed workarounds to reduce the resources needed for smaller herbaria to produce usable digital images, such as using a digital camera with a light-bank system, rather than a flat-bed scanner. As more institutions move toward digitization of their collections, it would be helpful for international-agreed standard protocols to spell out the minimum requirements necessary for different kinds of research, including taxonomic studies to complete species-level revisions remotely in the context of the COVID-19 pandemic. This will need to take into account each institution's level of resources to speedily capture (i) images of high-enough quality and (ii) data associated with the specimen, including on labels. Also importantly, a willingness to share specimen information either publicly or through expert researcher networks.

In order to address the gaps in this study, further work needs to be conducted in the following areas:

(i) **Complete the description for flowering material of *M. sessilis*** by requesting access to the specimen of *WKM 638* collected in Brunei, and held at BRUN or L.

(ii) **Establish the species affinities and groupings of the incertae sedis taxa** by comparing characters across all *Madhuca* species occurring in Johor, and further afield to the rest of Peninsular Malaysia, Borneo and Sumatra if there are no matches.

(iii) **Examine the collections at SINU** when reopened to visitors, and incorporate relevant species occurrences into the *Flora of Singapore* account for *Madhuca*.

(iv) **Undertake DNA sampling** for *Madhuca* species not already included in the existing wider phylogeny for the Isonandreae tribe, expanding sampling for all other species previously under *Ganua* not found in Singapore (such as *G. hirtiflora*), so as to obtain stronger phylogenetic resolution that can shed light on evolutionary relationships within the genus.

(v) **Enhance records and collections of *Madhuca* in Singapore**, particularly flowering or fruiting specimens of known trees, and to revisit occurrences of species that have not been collected or recorded for a long time, such as *M. motleyana*.

(vi) **Help develop conservation actions in Singapore**, using the information produced from this study relating to national conservation assessments of *Madhuca* species.

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Appendix 1: SINU data entries of *Madhuca* collections in Singapore, as of 4 August 2020

| SINU accession number | Collecting No. | Date of collection | Species | Locality | Collector(s) |
|---|---|---|---|---|---|
| 2007010661 | BT 009 | 26 Sep 96 | Madhuca kingiana | Bukit Timah Nature Reserve | Seah, E.E.L. |
| 2007010662 | | 13 Sep 1957 | Madhuca laurifolia | - | Abdul Panji |
| 2007010663 | | 13 Sep 1957 | Madhuca laurifolia | - | Abdul Panji |
| 2007023540 | NSSF2-Q112U90 | 08 Jan 2014 | Madhuca sp. | Q112 (Nee Soon Swamp Forest) | Chong, K.Y., Neo, L., Tan, S.Y., Koh, C.Y., Loh, J.W., Lim, R.C.J. |
| 2007023541 | NSSF2-Q203aU90 | 23 Mar 2014 | Madhuca sp. | Q203a (Nee Soon Swamp Forest) | Chong, K.Y., Neo, L., Tan, S.Y., Koh, C.Y., Loh, J.W., Lim, R.C.J. |
| 2007023542 | NSSF2-Q6T30 (1) | 13 Apr 2013 | Madhuca sp. | Q6 (Nee Soon Swamp Forest) | Chong, K.Y., Neo, L., Tan, S.Y., Koh, C.Y. |
| 2007023543 | NSSF2-Q6T30 (2) | 13 Apr 2013 | Madhuca sp. | Q6 (Nee Soon Swamp Forest) | Chong, K.Y., Neo, L., Tan, S.Y., Koh, C.Y. |
| 2007024124 | NSSF1-Q400-429 | Aug 2011 | Madhuca sp. | Q 4 (Nee Soon Swamp Forest) | Heyzer, A., Koh, C.Y., Li, T.J., Siow, M.P.H.J., Tan, S.Y., Wong, H.F. |
| 2007024123 | NSSF1-Q1000-2177 | Jan 2012 | Madhuca tomentosa | Q 10 (Nee Soon Swamp Forest) | Heyzer, A., Koh, C.Y., Li, T.J., Siow, M.P.H.J., Tan, S.Y., Wong, H.F. |
| 2007023544 | NSSF2-Q4T06 | 26 Apr 2013 | Madhuca tomentosa | Q4 (Nee Soon Swamp Forest) | Chong, K.Y., Neo, L., Tan, S.Y., Koh, C.Y. |

Appendix 2**:** Details of specimen images; collections of *Madhuca* in Singapore, det. A Phang (NB. 'Y' denotes Yes)

| Collector | Collector No. | Date | Species | Location | Habitat | Collector Observations | Herbarium code | Barcode | Image Source | Notes | Usefulness Rating |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Ridley, H. N. | 6497 | 1894 | Madhuca decipiens | Sungai Murai | | | SING | SING0054465 | SING | Fruiting | High |
| Ridley, H. N. | 6497 | 1894 | Madhuca decipiens | Sungai Murai | | | K | K000777882 | JSTOR | Fruiting | High |
| Ridley, H. N. | 11371 | June 1902 | Madhuca decipiens | C.H.B.S. (SBG) | | Y | SING | SING0046061 | SING | Fruiting | High |
| Ridley, H. N. | 11371 | June 1902 | Madhuca decipiens | C.H.B.S. | | | K | | PADME (Image 1) | Fruiting | Low |
| Ridley, H. N. | 11371 | June 1902 | Madhuca decipiens | C.H.B.S. | | | K | | PADME (Image 2) | Fruiting | Low |
| Sinclair, J. | 10761 | 3 Nov 1963 | Madhuca decipiens | Tanjong Gul | Y | Y | SING | SING0017155 | SING | Flowering | High |
| Sinclair, J. | 10761 | 3 Nov 1963 | Madhuca decipiens | Tanjong Gul | Y | Y | K | K | PADME | Flowering | Medium |
| Sinclair, J. | 10761 | 3 Nov 1963 | Madhuca decipiens | Tanjong Gul | Y | Y | E | E00013579 | E | Flowering | High |
| Sinclair, J. | 10761 | 3 Nov 1963 | Madhuca decipiens | Tanjong Gul | Y | Y | E | E00283994 | E | Flowering | High |
| Sinclair, J. | 10761 | 3 Nov 1963 | Madhuca decipiens | Tanjong Gul | | | L | L.2655479 | L | Flowering | High |
| Sinclair, J. | 39640 | 21 May 1953 | Madhuca decipiens | Tanjong Gul | | Y | SING | SING0017156 | SING | Flowering | High |

| Collector | Collector No. | Date | Species | Location | Habitat | Collector Observations | Herbarium code | Barcode | Image Source | Notes | Usefulness Rating |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Lua, H.K., Hassan, I., Geoffrey, D. | SING 2011-021 | 1 Feb 2011 | Madhuca decipiens | Western Catchment Live Firing Range | | | SING | SING0153716 | SING | Sterile | High |
| Leong, P., Ali, I; Lua, H.K., Hassan, I et al | SING 2016-051 | 24 Feb 2016 | Madhuca decipiens | Western Catchment, Peram Marsh | | Y | SING | SING0236441 | SING | Sterile | High |
| Lua, H.K. | SING 2017-219 | 20 Jun 2017 | Madhuca decipiens | Western Catchment, Pergam Marshes | Y | Y | SING | SING0258575 | SING | Sterile | High |
| Lua, H.K. et al | SING 2018-834 | 9 Oct 2018 | Madhuca decipiens | Western Catchment, Pergam Marshes | | Y | SING | SING0274188 | SING | Sterile | High |
| Ng, X.Y. | SING 2019-245 | 2 Apr 2019 | Madhuca decipiens | Western Catchment | Y | Y | SING | SING0286162 | SING | Flowering | High |
| Lua, H.K., Ng, X.Y.; Teo, J.; Yeo, C.K. | SING 2019-385 | 12 Apr 2019 | Madhuca decipiens | Western Catchment, Pergam Marshes, along the banks of an old tributary of Sungei Murai, Western Catchment Live-firing Area. | Y | Y | SING | SING0286358 | SING | Flowering | High |

| Collector | Collector No. | Date | Species | Location | Habitat | Collector Observations | Herbarium code | Barcode | Image Source | Notes | Usefulness Rating |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Ridley, H. N. | s.n. | 1894 | Madhuca kingiana | Bukit Timah | | | SING | FOS15390 | SING | Flowering | High |
| Mohd. Noor | 1524 | 19 Feb 1973 | Madhuca kingiana | Fern Valley, Bukit Timah Nature Reserve | | Y | SING | SING0025538 | SING | Sterile | High |
| Mohd. Noor | 1364/MN 1441 | 8 Dec 1970 | Madhuca kingiana | Bukit Timah Nature Reserve | | | SING | SING0025540 | SING | Sterile | High |
| Mohd. Noor | 325/MN 402 | 1 Aug 1969 | Madhuca kingiana | Jalan Kutu, Bukit Timah Nature Reserve | | | SING | SING0025541 | SING | Sterile | High |
| Mohd. Noor | 472/MN 549 | 24 Sep 1969 | Madhuca kingiana | Boundary path pipeline & Ngadiman Bridge to Main Road, Bukit Timah Nature Reserve | | | SING | SING0025542 | SING | Sterile | High |
| Mohd. Noor | 1276/MN1353 | 22 Sep 1970 | Madhuca kingiana | Hampstade Path, Bukit Timah | | Y | SING | SING0025544 | SING | Sterile | High |

| Collector | Collector No. | Date | Species | Location | Habitat | Collector Observations | Herbarium code | Barcode | Image Source | Notes | Usefulness Rating |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Nature Reserve | | | | | | | |
| Mohd. Noor | 974/MN 1051 | 7 Apr 1970 | Madhuca kingiana | North View Path, Bukit Timah Nature Reserve | | Y | SING | SING0025545 | SING | Sterile | High |
| Mohd. Noor | 628/MN 705 | 23 Oct 1969 | Madhuca kingiana | Rock Path from Catchment Contour Path, Bukit Timah Nature Reserve | | | SING | SING0025546 | SING | Sterile | High |
| Mohd. Noor | 584/MN 661 | 14 Oct 1969 | Madhuca kingiana | Catchment Contour Path Bukit Timah Nature Reserve | | Y | SING | SING0025547 | SING | Sterile | High |
| Mohd. Noor | 1553 | 26 Feb 1973 | Madhuca kingiana | Fern Valley, Bukit Timah Nature Reserve | | Y | SING | SING0025548 | SING | Sterile | High |
| Mohd. Noor | 1608/MN 1685 | 19 Mar 1973 | Madhuca kingiana | Fern Valley Contour Path, Bukit Timah | | Y | SING | SING0025549 | SING | Sterile | High |

| Collector | Collector No. | Date | Species | Location | Habitat | Collector Observations | Herbarium code | Barcode | Image Source | Notes | Usefulness Rating |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Nature Reserve | | | | | | | |
| Mohd. Noor | 1570 | 5 Mar 1973 | Madhuca kingiana | Fern Valley, Bukit Timah Nature Reserve | | Y | SING | SING0025550 | SING | Sterile | High |
| Mohd. Noor | 612/MN 689 | 23 Oct 1969 | Madhuca kingiana | Rock Path from Catchment Contour Path, Bukit Timah Nature Reserve | | | SING | SING0025551 | SING | Sterile | High |
| Mohd. Noor | 626/MN 703 | 23 Oct 1969 | Madhuca kingiana | Rock Path from Catchment Contour Path, Bukit Timah Nature Reserve | | | SING | SING0025552 | SING | Sterile | High |
| Mohd. Noor | 273/MN 350 | 17 July 1969 | Madhuca kingiana | Boundary path near Upper Quarry, Bukit Timah Nature Reserve | | | SING | SING0025553 | SING | Sterile | High |

| Collector | Collector No. | Date | Species | Location | Habitat | Collector Observations | Herbarium code | Barcode | Image Source | Notes | Usefulness Rating |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Mohd. Noor | 1246/MN 1323 | 1 Sep 1970 | Madhuca kingiana | Hampstade Path, Bukit Timah Nature Reserve | | Y | SING | SING0025554 | SING | Sterile | High |
| Mohd. Noor | 1299/MN 1376 | 6 Oct 1970 | Madhuca kingiana | Hampstade Path, Bukit Timah Nature Reserve | | Y | SING | SING0025555 | SING | Sterile | High |
| Mohd. Noor | 1145/MN 1222 | 26 May 1970 | Madhuca kingiana | North View Path, Bukit Timah Nature Reserve | | Y | SING | SING0025556 | SING | Sterile | High |
| Mohd. Noor | 1133/MN 1210 | 26 May 1970 | Madhuca kingiana | North View Path, Bukit Timah Nature Reserve | | Y | SING | SING0025557 | SING | Sterile | High |
| Mohd. Noor | 1156/MN 1233 | 9 Jun 1970 | Madhuca kingiana | North View Path, Bukit Timah Nature Reserve | | Y | SING | SING0025558 | SING | Sterile | High |
| Mohd. Noor | 618/MN 695 | 30 Oct 1969 | Madhuca kingiana | Rock Path from Catchment Contour Path, Bukit | | | SING | SING0025559 | SING | Sterile | High |

| Collector | Collector No. | Date | Species | Location | Habitat | Collector Observations | Herbarium code | Barcode | Image Source | Notes | Usefulness Rating |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Timah Nature Reserve | | | | | | | |
| Mohd. Noor | 534/MN 611 | 30 Sep 1969 | Madhuca kingiana | Jalan Tiup Tiup. Bukit Timah Nature Reserve | | Y | SING | SING0025560 | SING | Sterile | High |
| Mohd. Noor | 910/MN 987 | 3 Mar 1970 | Madhuca kingiana | North View Path, Bukit Timah Nature Reserve | | Y | SING | SING0025561 | SING | Sterile | High |
| Mohd. Noor | 762/MN 839 | 30 Dec 1969 | Madhuca kingiana | Jungle Fall Path, Bukit Timah Nature Reserve | | Y | SING | SING0025562 | SING | Sterile | High |
| Mohd. Noor | 1071/MN 1148 | 12 May 1970 | Madhuca kingiana | North View Path, Bukit Timah Nature Reserve | | Y | SING | SING0025563 | SING | Sterile | High |
| Mohd. Noor | 838/MN 915 | 2 Feb 1970 | Madhuca kingiana | Jungle Fall Path, Bukit Timah Nature Reserve | | Y | SING | SING0025564 | SING | Sterile | High |
| Mohd. Noor & Selamat | 505/MN 582 | | Madhuca kingiana | Tangga Rengas from North | | Y | SING | SING0025565 | SING | Sterile | High |

| Collector | Collector No. | Date | Species | Location | Habitat | Collector Observations | Herbarium code | Barcode | Image Source | Notes | Usefulness Rating |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | View Path. Bukit Timah Nature Reserve | | | | | | | |
| Mohd. Noor & Hj. Baharuddin | 534/MN 611 | 30 Sep 1969 | Madhuca kingiana | Jalan Tiup Tiup. Bukit Timah Nature Reserve | | Y | SING | SING0025566 | SING | Sterile | High |
| Hill, R. D. (Dr) | H426 | 10 Jun 1970 | Madhuca kingiana | Jungle Fall Path, Bukit Timah Nature Reserve | | | SING | SING0025567 | SING | Sterile | High |
| Hill, R. D. (Dr) | H432 | 11 May 1970 | Madhuca kingiana | Bukit Timah Nature Reserve | | | SING | SING0025568 | SING | Sterile | High |
| Hill, R. D. (Dr) | H426 | 26 May 1970 | Madhuca kingiana | Bukit Timah Nature Reserve | | | SING | SING0025569 | SING | Sterile | High |
| Hill, R. D. (Dr) | H.432 | 6 May 1970 | Madhuca kingiana | Jungle Fall Path, Bukit Timah Nature Reserve | | | SING | SING0025570 | SING | Sterile | High |
| Corner, E.J.H. | s.n. | 6 Mar 1938 | Madhuca kingiana | Bukit Timah | | | SING | SING0025571 | SING | Sterile | High |
| Sinclair, J. | 40035 | 4 Oct 1953 | Madhuca kingiana | Taban Circle, | | Y | L | L2652517 | L | Sterile | High |

| Collector | Collector No. | Date | Species | Location | Habitat | Collector Observations | Herbarium code | Barcode | Image Source | Notes | Usefulness Rating |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Bukit Timah Nature Reserve | | | | | | | |
| Sinclair, J. | 40035 | 4 Oct 1953 | Madhuca kingiana | Taban Circle, Bukit Timah Nature Reserve | | Y | SING | SING0025572 | SING | Sterile | High |
| Mohd. Shah & Samsuri | MS 3908 | 12 Jul 1976 | Madhuca kingiana | Fern Valley Contour Path, Bukit Timah Nature Reserve | | Y | SING | SING0025573 | SING | Fruiting | High |
| Tang, Eugene & Sidek, Hj | 993 | 12 Oct 1995 | Madhuca kingiana | Bukit Timah Nature Reserve Catchment Path | | Y | SING | SING0037588 | SING | Sterile | High |
| Samsuri, A., Lee, S, Mohd Noor, Leong, P., Gwee, A.T., Ganesan, S.K. | EP 31 | 9 Mar 2004 | Madhuca kingiana | Bukit Timah Nature Reserve, Rengas Path, right side down | | Y | SING | SING0052809 | SING | Sterile | High |
| Leong, P., Skornickova, | SING 2005-59 | 23 Mar 2005 | Madhuca kingiana | Bukit Timah Nature | | Y | SING | SING0060007 | SING | Flowering | High |

| Collector | Collector No. | Date | Species | Location | Habitat | Collector Observations | Herbarium code | Barcode | Image Source | Notes | Usefulness Rating |
|---|---|---|---|---|---|---|---|---|---|---|---|
| J., Teo, S. et al | | | | Reserve, Taban Valley. Near pathway. | | | | | | | |
| Wilkie, P., Khoo, M.S., Leong, P., Ali Ibrahim | PW 530 | 23 Jan 2007 | Madhuca kingiana | Bukit Timah Nature Reserve, South view path | | Y | SING | SING0092716 | SING | Sterile | High |
| Wilkie, P., Khoo, M.S., Leong, P., Ali Ibrahim | PW 530 | 23 Jan 2007 | Madhuca kingiana | Bukit Timah Nature Reserve, South view path | | Y | E | E00304463 | E | Sterile | High |
| Gwee, A.T. | SING 2010-021 | 5 Jan 2010 | Madhuca kingiana | Bukit Timah 2 | | | SING | SING0138184 | SING | Sterile | High |
| Mohd. Noor | MN 756 | 19 Nov 1969 | Madhuca kingiana | Bukit Timah forest reserve. Rock path | | | SING | SING0025543 | SING | Sterile | High |
| Sinclair, J. | 7791 | 6 Oct 1953 | Madhuca kingiana | Bukit Timah Forest Reserve | | | E | E00330643 | E | Sterile | High |
| Mat | 6238 | April 1894 | Madhuca kingiana | Bukit Timah | | | SING | SING0058083 | SING | Flowering | High |

| Collector | Collector No. | Date | Species | Location | Habitat | Collector Observations | Herbarium code | Barcode | Image Source | Notes | Usefulness Rating |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Ridley, H. N. | 6294 | 1894 | Madhuca kingiana | Bukit Timah | | | SING | SING0058084 | SING | Flowering | High |
| Leong, P., Nissalo, M.A.; Sylvia, T.K.B.; Ngo, K.M.; Lim, W.H. et al | CTFS 7424 | 13 Sep 2018 | Madhuca kingiana | Bukit Timah NR. Catchment Path, Plot A2 | Y | Y | SING | SING0274124 | SING | Sterile | High |
| Ngo, Kang Min | SING 2019-207 | 28 Mar 2019 | Madhuca kingiana | Bukit Timah NR | | Y | SING | SING0279209 | SING | Flowering | High |
| Mohd. Noor | MN 756 | 19 Nov 1969 | Madhuca kingiana | Bukit Timah forest reserve. Rock path | | Y | SING | SING0025543 | SING | Sterile | High |
| Ridley, H. N. | s.n. | 1892 | Madhuca malaccensis | Long bondis. Gardens. | | | SING | FOS15412 | SING | Fruiting | High |
| Ridley, H. N. | 6132 | 1894 | Madhuca malaccensis | Seletar | | | SING | SING0025523 | SING | Flowering | High |
| Mat | 6500 | 1894 | Madhuca malaccensis | Chua Chu Kang | | | SING | SING0025527 | SING | Fruiting | High |
| Mat | 6043 | 189? | Madhuca malaccensis | Changi | | Y | SING | SING0025528 | SING | Flowering | High |
| Mat | 6133 | Apr 1894 | Madhuca malaccensis | Bukit Timah | | Y | SING | SING0025529 | SING | Flowering | High |
| Mat | 6498 | 1894 | Madhuca malaccensis | Seletar | | | SING | SING0025530 | SING | Flowering | High |

| Collector | Collector No. | Date | Species | Location | Habitat | Collector Observations | Herbarium code | Barcode | Image Source | Notes | Usefulness Rating |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Gwee, A.T., Chew, P.T. et al | SING 2009-77 | 3 Feb 2009 | Madhuca malaccensis | Seletar Firing Range, NS3: north of Plot 24, south of Seletar Firing Range, FT 4 | | Y | SING | SING0120419 | SING | Sterile | High |
| Ridley, H. N. | 5643 | 1893 | Madhuca malaccensis | Changi | | | SING | | SING | Fruiting | High |
| Bayliss | 5896 | Jan 1894 | Madhuca motleyana | Bukit Mandai | | | SING | SING0025533 | SING | Fruiting | High |
| Ridley, H. N. | 5645 | 1893 | Madhuca motleyana | Changi | | Y | SING | SING0025531 | SING | Flowering | High |
| Ridley, H. N. | 6039 | 1894 | Madhuca motleyana | Sungai Jurong | | | SING | SING0025532 | SING | Fruiting | High |
| Mat | 6698 | 15 May 1894 | Madhuca sericea | Chua Chu Kang | | Y | SING | SING0069593 | SING | Flowering | High |
| Cantley, N. | 2902 | 188? | Madhuca sericea | | | | SING | SING0025534 | SING | Flowering | High |
| Cantley, N. | 3003 | 188? | Madhuca sericea | | | | SING | SING0025535 | SING | Flowering | High |
| Unknown | 2808 | | Madhuca sericea | | | | SING | SING0025536 | SING | Flowering | High |
| Sinclair, J. | 39656 | 30 May 1953 | Madhuca sericea | North East end MacRitchie Reservoir | | Y | SING | SING0025537 | SING | Sterile | High |
| Sinclair, J. | 39656 | 30 May 1953 | Madhuca sericea | North East end | | Y | KEP | | PADME | Sterile | Low |

| Collector | Collector No. | Date | Species | Location | Habitat | Collector Observations | Herbarium code | Barcode | Image Source | Notes | Usefulness Rating |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | MacRitchie Reservoir | | | | | | | |
| Leong, P., Ali, I., Lua, H.K. | MR 2014-049 | 2 Sep 2014 | Madhuca sericea | MacRitchie FR, Transsect 2, Plot 6 | | Y | SING | SING0211889 | SING | Sterile | High |
| Sinclair, J. | 39655 | 30 May 1953 | Madhuca sericea | MacRitchie Nature Reserve | | | K | | PADME | Sterile | Low |
| Khoo, M.S., Nik Faizu, N.H. | KMS 51 | 20 Dec 2008 | Madhuca sericea | Fern Valley, Bukit Timah Nature Reserve | | Y | SING | SING0137289 | SING | Sterile | High |
| Ridley, H. N. | 5076 | 30 Mar 1893 | Madhuca sessilis | Tuas | | | K | K000777878 | JSTOR | Fruiting | High |
| Ridley, H. N. | 5076 | 30 Mar 1893 | Madhuca sessilis | Tuas | | | SING | SING0058081 | SING | Fruiting | High |
| Corner, E.J.H. | 26158 | 25 Dec 1932 | Madhuca sp. | Jurong | | | SING | FOS15444 | SING | Sterile | High |
| Lim, R.C.J., Wong, S.L. | 2018-209 | 6 Mar 2018 | Madhuca sp. | Mandai Track 7 | | Y | SING | SING0286267 | SING | Flowering | High |
| Leong, P., Chew, P.T., Ali Ibrahim, Staples, G et al. | SING 2009-244 | 17 Feb 2009 | Madhuca sp. | Nee Soon freshwater swamp forest | | Y | SING | SING0124443 | SING | Sterile | High |

| Collector | Collector No. | Date | Species | Location | Habitat | Collector Observations | Herbarium code | Barcode | Image Source | Notes | Usefulness Rating |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Gwee, A.T. | SING 2010-496 | 3 Mar 2010 | Madhuca sp. | Nee Soon swamp forest | | Y | SING | SING0144536 | SING | Sterile | High |
| Leong, P., Koh, S.L.; Niissalo, M.A.; Choo, L.M.; et al. | CTFSJ2-1235 | 25 Jan 2019 | Madhuca sp. | Bukit Timah NR, Catchment Path, Plot J2 | | Y | SING | SING0286125 | SING | Sterile | High |
| Gwee, A.T. | SING 2009-507 | 24 Nov 2009 | Madhuca sp. | Bukit Timah | Y | Y | SING | SING0144235 | SING | Sterile | High |
| Cantley, N. | 34 | Aug 1881 | Madhuca longiflora | | | | SING | FOS15409 | SING | Flowering | High |

Appendix 3 Details of specimen images; collections of *Madhuca* in Johor

| Collector | Collector No. | Date | Species (det) | Location | Habitat | Collector Observations | Herbarium code | Barcode | Image Source | Notes | Usefulness rating |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Ng, F.S.P. | FRI 1725 | 17 Nov 66 | Madhuca decipiens | Panti F.R., Water Catchment Area, Johore | Y | Y | L | L 2655477 | L | Sterile | High |
| Ng, F.S.P. | FRI 1725 | 30 Mar 68 | Madhuca decipiens | Panti F.R., Kota Tinggi | Y | Y | KEP | | PADME | Sterile | Medium |
| Ng, F.S.P. | FRI 1725 | 30 Mar 68 | Madhuca decipiens | Panti F.R. Kota Tinggi | Y | Y | SING | | PADME | Sterile | Medium |
| Ng, F.S.P. | FRI 1726 | 30 Mar 68 | Madhuca decipiens | Kota Tinggi | | Y | KEP | | PADME | Sterile | Low |
| Whitmore, T.C. | FRI 8655 | 10 May 68 | Madhuca decipiens | N.E. Johore Lenggor FR. | Y | Y | L | L 2655478 | L | Flowering | High |
| Whitmore, T.C. | FRI 8655 | 10 May 68 | Madhuca decipiens | N.E. Johore Lenggor FR. | Y | Y | SAR | | PADME | Flowering | Medium |
| Whitmore, T.C. | FRI 8655 | 10 May 68 | Madhuca decipiens | N.E. Johore Lenggor FR. | Y | Y | SING | | PADME | Flowering | Medium |
| Whitmore, T.C. | FRI 8655 | 10 May 68 | Madhuca decipiens | N.E. Johore Lenggor FR. | Y | Y | KEP | | PADME | Flowering | Medium |
| Whitmore, T.C. | FRI 8655 | 10 May 68 | Madhuca decipiens | N.E. Johore Lenggor FR. | Y | Y | K | | PADME | Flowering | Medium |
| Cockburn, P.F. | FRI 7544 | Apr 68 | Madhuca decipiens | Kluang Forest Reserve | Y | Y | KEP | | PADME | Fruiting | Medium |

| Collector | Collector No. | Date | Species (det) | Location | Habitat | Collector Observations | Herbarium code | Barcode | Image Source | Notes | Usefulness rating |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Holtum, R.E. | SFN 10884 | 1 Jun 1923 | Madhuca decipiens | Ulu Kahang, Kluang, Johor | | | KEP | | PADME | Fruiting | Low |
| Holtum, R.E. | SFN 10884 | 1 Jun 1923 | Madhuca decipiens | Ulu Kahang, Kluang, Johor | | | SING | | PADME | Sterile | Low |
| Motan | KEP 53938 | 30 Mar 68 | Madhuca decipiens | Panti Forest Reserve: Kota Tinggi, Johor | | Y | KEP | | PADME | Sterile | Low |
| Nur, M & Kiah | SFN 7785 | 24 Apr 1922 | Madhuca decipiens | Gunung Pulai Forest Reserve | | | SING | | PADME | Sterile | Low |
| Teo, L.E. & Tarelli, O. | KL 4598 | 13 Jun 1996 | Madhuca decipiens | Lenggor Forest Reserve | | | KEP | 1228 | PADME | Fruiting | Low |
| Cockburn, P.F. | FRI 8012 | 30 Mar 68 | Madhuca kingiana | Ulu Endau Johore. Labis FR. Compt 280 | Y | Y | K | | PADME | Flowering | Medium |
| Cockburn, P.F. | FRI 8012 | 30 Mar 68 | Madhuca kingiana | Ulu Endau Johore. Labis FR. Compt 280 | Y | Y | SING | | PADME | Flowering | Medium |
| Cockburn, P.F. | FRI 8012 | 30 Mar 68 | Madhuca kingiana | Ulu Endau Johore. Labis | Y | Y | KEP | 106233 | PADME | Flowering | Medium |

| Collector | Collector No. | Date | Species (det) | Location | Habitat | Collector Observations | Herbarium code | Barcode | Image Source | Notes | Usefulness rating |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | FR. Compt 280 | | | | | | | |
| Cockburn, P.F. | FRI 8012 | 30 Mar 68 | Madhuca kingiana | Ulu Endau Johore. Labis FR. Compt 280 | Y | Y | KEP | 106248 | PADME | Flowering | Medium |
| Cockburn, P.F. | FRI 8012 | 30 Mar 68 | Madhuca kingiana | Ulu Endau Johore. Labis FR. Compt 280 | Y | Y | L | L 2652511 | L | Flowering | High |
| Cockburn, P.F. | FRI 7876 | 22 Mar 68 | Madhuca kingiana | Ulu Endau Johore. Labis FR. Compt 277 | Y | Y | K | | PADME | Flowering | Low |
| Cockburn, P.F. | FRI 7876 | 22 Mar 68 | Madhuca kingiana | Ulu Endau Johore. Labis FR. Compt 277 | Y | Y | SING | | PADME | Flowering | Low |
| Cockburn, P.F. | FRI 7876 | 22 Mar 68 | Madhuca kingiana | Ulu Endau Johore. Labis FR. Compt 277 | Y | Y | KEP | 106224 | PADME | Flowering | Medium |
| Cockburn, P.F. | FRI 7876 | 22 Mar 68 | Madhuca kingiana | Ulu Endau Johore. Labis FR. Compt 277 | Y | Y | SAR | | PADME | Flowering | Medium |

| Collector | Collector No. | Date | Species (det) | Location | Habitat | Collector Observations | Herbarium code | Barcode | Image Source | Notes | Usefulness rating |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Cockburn, P.F. | FRI 7876 | 22 Mar 68 | Madhuca kingiana | Ulu Endau Johore. Labis FR. Compt 277 | Y | Y | L | L 2652507 | L | Flowering | High |
| Ogata, K. | KEP 105011 | 30 Mar 68 | Madhuca kingiana | compt 280, Labis FR, Ulu Endau, Johore | Y | Y | KEP | 106239 | PADME | Fruiting | Medium |
| Ogata, K. | KEP 105011 | 30 Mar 68 | Madhuca kingiana | compt 280, Labis FR, Ulu Endau, Johore | Y | Y | SING | | PADME | Fruiting | Medium |
| Ogata, K. | KEP 105011 | 30 Mar 68 | Madhuca kingiana | compt 280, Labis FR, Ulu Endau, Johore | Y | Y | L | L 2652510 | L | Fruiting | High |
| Chew W-L | CWL 719 | 8 Sep 63 | Madhuca kingiana | Johore, G. Panti. | | Y | L | L 2652506 | L | Fruiting | High |
| Chew W-L | CWL 719 | 8 Sep 63 | Madhuca kingiana | Johore, G. Panti. | | Y | SAR | | PADME | Fruiting | Medium |
| Chew W-L | CWL 719 | 8 Sep 63 | Madhuca kingiana | Johore, G. Panti. | | Y | SING | | PADME | Fruiting | Medium |
| Hassan, M. | KEP 92238 | 12 Jul 59 | Madhuca kingiana | Kluang Forest Reserve, | Y | Y | KEP | 106244 | PADME | Sterile | Low |

| Collector | Collector No. | Date | Species (det) | Location | Habitat | Collector Observations | Herbarium code | Barcode | Image Source | Notes | Usefulness rating |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Compartment 66 | | | | | | | |
| Ng, F.S.P. | FRI 1675 | 17 Nov 66 | Madhuca kingiana | Compt. 1, Panti F.R., Johore (slope of Gunong Panti) | Y | Y | SING | | PADME | Sterile | Low |
| Ng, F.S.P. | FRI 1675 | 17 Nov 66 | Madhuca kingiana | Compt. 1, Panti F.R., Johore (slope of Gunong Panti) | Y | Y | KEP | 106234 | PADME | Sterile | Low |
| Ng, F.S.P. | FRI 1675 | 17 Nov 66 | Madhuca kingiana | Compt. 1, Panti F.R., Johore (slope of Gunong Panti) | Y | Y | L | L 2652505 | L | Sterile | High |
| Ng, F.S.P. | FRI 1682 | 17 Nov 66 | Madhuca kingiana | Compt. 1, Panti F.R., Johore | Y | Y | SING | | PADME | Sterile | Low |
| Ng, F.S.P. | FRI 1682 | 17 Nov 66 | Madhuca kingiana | Compt. 1, Panti F.R., Johore | Y | Y | KEP | 106240 | PADME | Sterile | Low |
| Ng, F.S.P. | FRI 5247 | 28 Apr 67 | Madhuca kingiana | Compt. 26 Gunung Arong FR Etension, | Y | Y | KEP | 106232 | PADME | Sterile | Low |

| Collector | Collector No. | Date | Species (det) | Location | Habitat | Collector Observations | Herbarium code | Barcode | Image Source | Notes | Usefulness rating |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Hersing, Johore. | | | | | | | |
| Ng, F.S.P. | FRI 5247 | 28 Apr 67 | Madhuca kingiana | Compt. 26 Gunung Arong FR Etension, Hersing, Johore. | Y | Y | SING | | PADME | Sterile | Low |
| Ng, F.S.P. | FRI 5247 | 28 Apr 67 | Madhuca kingiana | Compt. 26 Arong FR Etension, Hersing, Johore. | Y | Y | L | L 2652504 | L | Sterile | High |
| Ng, F.S.P. | FRI 5284 | 29 Apr 67 | Madhuca kingiana | 24th Mile Kota Tinggi-Jemaluang Road, Mersing Johor | Y | Y | KEP | 106231 | PADME | Sterile | Low |
| Cockburn, P.F. | FRI 7924 | 26 Mar 68 | Madhuca kingiana | Ulu Endau Labis FR, compt 285 | Y | Y | SING | | PADME | Flowering | Medium |
| Cockburn, P.F. | FRI 7924 | 26 Mar 68 | Madhuca kingiana | Ulu Endau Labis FR, compt 285 | Y | Y | SAR | | PADME | Flowering | Medium |

| Collector | Collector No. | Date | Species (det) | Location | Habitat | Collector Observations | Herbarium code | Barcode | Image Source | Notes | Usefulness rating |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Cockburn, P.F. | FRI 7924 | 26 Mar 68 | Madhuca kingiana | Ulu Endau Labis FR, compt 285 | Y | Y | KEP | 106247 | PADME | Flowering | Medium |
| Cockburn, P.F. | FRI 7924 | 26 Mar 68 | Madhuca kingiana | Ulu Endau Labis FR, compt 285 | Y | Y | L | L 2652513 | L | Flowering | High |
| Cockburn, P.F. | FRI 7825 | 5 Mar 68 | Madhuca kingiana | Gunong Panti FR. Compt 1, Johore | Y | Y | L | L 2652514 | L | Flowering | High |
| Cockburn, P.F. | FRI 7825 | 5 Mar 68 | Madhuca kingiana | Gunong Panti FR. Compt 1, Johore | Y | Y | KEP | | PADME | Flowering | Medium |
| Cockburn, P.F. | FRI 7825 | 5 Mar 68 | Madhuca kingiana | Gunong Panti FR. Compt 1, Johore | Y | Y | K | | PADME | Flowering | Medium |
| Cockburn, P.F. | FRI 7825 | 5 Mar 68 | Madhuca kingiana | Gunong Panti FR. Compt 1, Johore | Y | Y | SAR | | PADME | Flowering | Medium |
| Cockburn | FRI 7852 | 6 Mar 68 | Madhuca kingiana | Gunung Pulai Forest Reserve | Y | Y | SING | | PADME | Flowering | Medium |

| Collector | Collector No. | Date | Species (det) | Location | Habitat | Collector Observations | Herbarium code | Barcode | Image Source | Notes | Usefulness rating |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Cockburn, P.F. | FRI 7913 | 23 Mar 68 | Madhuca kingiana | Labis FR. Compt. 285, Ulu Endau Johore. | Y | Y | K | | PADME | Flowering | Medium |
| Cockburn, P.F. | FRI 7916 | 25 Mar 68 | Madhuca kingiana | Labis FR. Compt. 285, Ulu Endau Johore. | Y | Y | SING | | PADME | Fruiting | Medium |
| Cockburn, P.F. | FRI 7916 | 25 Mar 68 | Madhuca kingiana | Labis FR. Compt. 285, Ulu Endau Johore. | Y | Y | K | | PADME | Fruiting | Medium |
| Cockburn, P.F. | FRI 7916 | 25 Mar 68 | Madhuca kingiana | Labis FR. Compt. 285, Ulu Endau Johore. | Y | Y | KEP | | PADME | Fruiting | Medium |
| Cockburn, P.F. | FRI 7916 | 25 Mar 68 | Madhuca kingiana | Labis FR. Compt. 285, Ulu Endau Johore. | Y | Y | L | L 2652515 | L | Fruiting | High |
| Kochummen, K.M. | FRI 2280 | 13 Apr 67 | Madhuca kingiana | Labis Forest Reserve, Compartment M4: Mersing Johor | Y | Y | KEP | 106237 | PADME | Sterile | Low |

| Collector | Collector No. | Date | Species (det) | Location | Habitat | Collector Observations | Herbarium code | Barcode | Image Source | Notes | Usefulness rating |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Kochummen, K.M. | FRI 2280 | 13 Apr 67 | Madhuca kingiana | Labis Forest Reserve, Compartment M4: Mersing Johor | Y | Y | KEP | 106236 | PADME | Sterile | Low |
| Saw, L.G. | FRI 34204 | 25 Oct 85 | Madhuca kingiana | Gunung Janing Barat, H.S. Labis: Mersing, Johor. Endau Rompin Expedition | | Y | K | | PADME | Fruiting | Low |
| Saw, L.G. | FRI 34204 | 25 Oct 85 | Madhuca kingiana | Gunung Janing Barat, H.S. Labis: Mersing, Johor. Endau Rompin Expedition | | Y | SAN | | PADME | Fruiting | Low |
| Saw, L.G. | FRI 34204 | 25 Oct 85 | Madhuca kingiana | Gunung Janing Barat, H.S. Labis: Mersing, Johor. Endau Rompin Expedition | | Y | SAR | | PADME | Fruiting | Low |

| Collector | Collector No. | Date | Species (det) | Location | Habitat | Collector Observations | Herbarium code | Barcode | Image Source | Notes | Usefulness rating |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Saw, L.G. | FRI 34204 | 25 Oct 85 | Madhuca kingiana | Gunung Janing Barat, H.S. Labis: Mersing, Johor. Endau Rompin Expedition | | Y | KEP | 72070 | PADME | Fruiting | Low |
| Whitmore, T.C. | FRI 8653 | 10 May 68 | Madhuca kingiana | N.E. Johore Lenggor FR. | Y | Y | K | | PADME | Flowering | Medium |
| Whitmore, T.C. | FRI 8653 | 10 May 68 | Madhuca kingiana | N.E. Johore Lenggor FR. | Y | Y | SING | | PADME | Flowering | Medium |
| Whitmore, T.C. | FRI 8653 | 10 May 68 | Madhuca kingiana | N.E. Johore Lenggor FR. | Y | Y | KEP | 106235 | PADME | Fruiting | Low |
| Whitmore, T.C. | FRI 8653 | 10 May 68 | Madhuca kingiana | N.E. Johore Lenggor FR. | Y | Y | L | L 2652518 | L | Sterile | High |
| Whitmore, T.C. | FRI 8754 | 15 May 68 | Madhuca kingiana | N. Johore NW Gunong Blumut Upper Camp | Y | Y | K | | PADME | Flowering | Medium |
| Whitmore, T.C. | FRI 8754 | 15 May 68 | Madhuca kingiana | N. Johore NW Gunong Blumut Upper Camp | Y | Y | SAR | | PADME | Fruiting | Low |
| Whitmore, T.C. | FRI 8754 | 15 May 68 | Madhuca kingiana | N. Johore NW Gunong | Y | Y | KEP | 106249 | PADME | Fruiting | Medium |

| Collector | Collector No. | Date | Species (det) | Location | Habitat | Collector Observations | Herbarium code | Barcode | Image Source | Notes | Usefulness rating |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Blumut Upper Camp | | | | | | | |
| Whitmore, T.C. | FRI 8754 | 15 May 68 | Madhuca kingiana | N. Johore NW Gunong Blumut Upper Camp | Y | Y | SING | | PADME | Fruiting | Medium |
| Cockburn, P.F. & Whitmore, T.C. | FRI 8754 | 15 May 68 | Madhuca kingiana | N. Johore NW Gunong Blumut Upper Camp | Y | Y | L | L 2652508 | L | Fruiting | High |
| Whitmore, T.C. | FRI 8803 | 15 May 68 | Madhuca kingiana | N. Johore NW Gunong Blumut Upper Camp | Y | Y | KEP | 106227 | PADME | Flowering | Medium |
| Whitmore, T.C. | FRI 8803 | 15 May 68 | Madhuca kingiana | N. Johore NW Gunong Blumut Upper Camp | Y | Y | K | | PADME | Flowering | Medium |
| Whitmore, T.C. | FRI 8803 | 15 May 68 | Madhuca kingiana | N. Johore NW Gunong Blumut Upper Camp | Y | Y | L | L 2652512 | L | Sterile | High |
| Yao, T.L., Pannell, C., Imin, K. & Nazre, A. | FRI 65623 | 23 Nov 11 | Madhuca kingiana | Endau-Rompin State Park, Sungai Kemamuk, Johor | Y | Y | E | E00613746 | E | Fruiting | High |

| Collector | Collector No. | Date | Species (det) | Location | Habitat | Collector Observations | Herbarium code | Barcode | Image Source | Notes | Usefulness rating |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Corner, E.J.H. | s.n. | 6 Aug 39 | Madhuca kingiana | Bukit Tinjau Laut: Johor | | | SING | | PADME | Sterile | Low |
| Embong | KEP 92273 | 17 Jul 57 | Madhuca kingiana | Mersing, Johor, Sungai Sarah | Y | Y | KEP | 106245 | PADME | Sterile | Low |
| T & P | 584 | 24 Feb 76 | Madhuca malaccensis | Batu 35, Hutan simpanan Mersing Johore. | | Y | L | L 2652234 | L | Flowering | High |
| Everett, B. | FRI 14091 | 18 Mar 70 | Madhuca malaccensis | Lowlands below G. Besar massif 2 miles E of Kg. Tepoh, Labis FR Johore. | Y | Y | L | L 2652263 | L | Flowering | High |
| Everett, B. | FRI 14091 | 18 Mar 70 | Madhuca malaccensis | Lowlands below G. Besar massif 2 miles E of Kg. Tepoh, Labis FR Johore. | Y | Y | K | | PADME | Flowering | Medium |
| Everett, B. | FRI 14091 | 18 Mar 70 | Madhuca malaccensis | Lowlands below G. Besar massif 2 miles E of | Y | Y | SING | | PADME | Flowering | Medium |

| Collector | Collector No. | Date | Species (det) | Location | Habitat | Collector Observations | Herbarium code | Barcode | Image Source | Notes | Usefulness rating |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Kg. Tepoh, Labis FR Johore. | | | | | | | |
| Everett, B. | FRI 14091 | 18 Mar 70 | Madhuca malaccensis | Lowlands below G. Besar massif 2 miles E of Kg. Tepoh, Labis FR Johore. | Y | Y | SAN | | PADME | Flowering | Medium |
| Everett, B. | FRI 14091 | 18 Mar 70 | Madhuca malaccensis | Lowlands below G. Besar massif 2 miles E of Kg. Tepoh, Labis FR Johore. | Y | Y | KEP | | PADME | Flowering | Medium |
| Cockburn, P.F. | FRI 7918 | 25 Mar 68 | Madhuca malacccensis | Lubis FR. Compt. 285, Ulu Endau Johore | Y | Y | KEP | | PADME | Flowering | Medium |
| Cockburn, P.F. | FRI 7918 | 25 Mar 68 | Madhuca malacccensis | Lubis FR. Compt. 285, Ulu Endau Johore | Y | Y | L | L 2652277 | L | Flowering | High |
| Cockburn, P.F. | FRI 7895 | 23 Mar 68 | Madhuca malaccensis | Ulu Endau Labis FR, compt 280 | Y | Y | SING | | PADME | Flowering | Medium |

| Collector | Collector No. | Date | Species (det) | Location | Habitat | Collector Observations | Herbarium code | Barcode | Image Source | Notes | Usefulness rating |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Cockburn, P.F. | FRI 7895 | 23 Mar 68 | Madhuca malaccensis | Ulu Endau Labis FR, compt 280 | Y | Y | KEP | | PADME | Flowering | Medium |
| Cockburn, P.F. | FRI 7895 | 23 Mar 68 | Madhuca malaccensis | Ulu Endau Labis FR, compt 280 | Y | Y | L | L 2652281 | L | Flowering | High |
| Goodenough, J.S. | 1830 | Apr 1890 | Madhuca malaccensis | Panchor: Johor | | | SING | | PADME | Flowering | Low |
| Wray Jnr., L | 1229 | | Madhuca malaccensis | Lower camp, Batu Pahat, Johor | | Y | SING | | PADME | Flowering | Medium |
| Cockburn, P.F. | FRI 7924 | 26 Mar 68 | Madhuca motleyana | Ulu Endau Labis FR, compt 285 | Y | Y | K | | PADME | Flowering | Medium |
| Abdgaata | KEP 74105 | 4 Jun 52 | Madhuca motleyana | Muar, Y.Land 14 Miles Muar - Pt: Yulong Rd | Y | Y | KEP | 106288 | PADME | Sterile | Low |
| Kadim & M.Noor | KN 288 | 14 Jul 59 | Madhuca motleyana | Kampong Hubong, Endau, Johore | Y | Y | SING | | PADME | Flowering | Low |
| Kadim & M.Noor | KN 288 | 14 Jul 59 | Madhuca motleyana | Kampong Hubong, | Y | Y | L | L 2652121 | L | Flowering | Medium |

| Collector | Collector No. | Date | Species (det) | Location | Habitat | Collector Observations | Herbarium code | Barcode | Image Source | Notes | Usefulness rating |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Endau, Johore | | | | | | | |
| Cockburn, P.F. | FRI 7609 | 22 Feb 68 | Madhuca motleyana | Tg. Penawar East Johore Coast | Y | Y | K | | PADME | Sterile | Low |
| Cockburn, P.F. | FRI 7609 | 22 Feb 68 | Madhuca motleyana | Tg. Penawar East Johore Coast | Y | Y | KEP | 106256 | PADME | Sterile | Low |
| Cockburn, P.F. | FRI 7609 | 22 Feb 68 | Madhuca motleyana | Tg. Penawar East Johore Coast | Y | Y | L | L 2652118 | L | Sterile | Medium |
| Corner, E.J.H. | 28442 | 21 May 34 | Madhuca motleyana | Mawai, Johore | | | SING | | PADME | Fruiting | Low |
| Corner, E.J.H. | 28442 | 21 May 34 | Madhuca motleyana | Mawai, Johore | | | KEP | 106275 | PADME | Sterile | Low |
| Corner, E.J.H. | 28442 | 21 May 34 | Madhuca motleyana | Mawai, Johore | | | E | E00330648 | E | Sterile | Medium |
| Corner, E.J.H. | SFN 32253 | 14 Feb 37 | Madhuca motleyana | Sungai Pendas, S. Johor | | | SING | | PADME | Flowering | Low |
| Corner, E.J.H. | SFN 32253 | 14 Feb 37 | Madhuca motleyana | Sungai Pendas, S. Johor | | | KEP | 109103 | PADME | Flowering | Low |

| Collector | Collector No. | Date | Species (det) | Location | Habitat | Collector Observations | Herbarium code | Barcode | Image Source | Notes | Usefulness rating |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Holtum, R.E. | SFN 24921 | 6 Jul 31 | Madhuca motleyana | Sungai Terap, Johore | | Y | SING | | PADME | Flowering | Low |
| Kiah, M.S. | SFN 32154 | 23 Oct 36 | Madhuca motleyana | Sungai Kayu, S. Johor | Y | Y | SING | | PADME | Flowering | Low |
| Kiah, M.S. | SFN 32154 | 23 Oct 36 | Madhuca motleyana | Sungai Kayu, S. Johor | | | KEP | 106253 | PADME | Sterile | Low |
| Ridley, H.N. | 6496 | 1894 | Madhuca motleyana | Sungei Ban | | | SING | | PADME | Flowering | Low |
| Ridley, H.N. | 13489 | Aug 08 | Madhuca motleyana | Johor (River?) | | Y | SING | | PADME | Flowering | Low |
| Sinclair | 40328 | Jul 54 | Madhuca motleyana | Sungei Tiram | | Y | SING | | PADME | Flowering | Medium |
| Sahak, K | KEP 84620 | 7 Mar 67 | Madhuca motleyana | Gunung Arong FR | Y | Y | KEP | 106265 | PADME | Sterile | Low |
| Zakaria | KEP 72904 | 20 Jan 52 | Madhuca motleyana | | | Y | KEP | 106292 | PADME | Sterile | Low |
| Kochummen, K.M. | FRI 16100 | 25 Jul 70 | Madhuca sericea | Compt. 5 Maokil F.R., Johore | Y | Y | SING | | PADME | Fruiting | Low |
| Kochummen, K.M. | FRI 16100 | 25 Jul 70 | Madhuca sericea | Compt. 5 Maokil F.R., Johore | Y | Y | K | | PADME | Fruiting | Low |
| Kochummen, K.M. | FRI 16100 | 25 Jul 70 | Madhuca sericea | Compt. 5 Maokil F.R., Johore | Y | Y | KEP | | PADME | Fruiting | Low |

| Collector | Collector No. | Date | Species (det) | Location | Habitat | Collector Observations | Herbarium code | Barcode | Image Source | Notes | Usefulness rating |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Kochummen, K.M. | FRI 16100 | 25 Jul 70 | Madhuca sericea | Compt. 5 Maokil F.R., Johore | Y | Y | L | L 2652927 | L | Fruiting | High |
| Ng, F.S.P. | FRI 1027 | 16 Apr 66 | Madhuca sericea | State Land 3 miles south of Labis F.R., Johore. | Y | Y | KEP | | PADME | Sterile | Low |
| Ng, F.S.P. | FRI 1027 | 16 Apr 66 | Madhuca sericea | State Land 3 miles south of Labis F.R., Johore. | Y | Y | L | L 2649527 | L | Sterile | High |
| Ng, F.S.P. | FRI 5205 | 25 Apr 67 | Madhuca sericea | Compt. 90 Arong FR, Meraing. | Y | Y | SING | | PADME | Sterile | Low |
| Ng, F.S.P. | FRI 5205 | 25 Apr 67 | Madhuca sericea | Compt. 90 Arong FR, Meraing. | Y | Y | K | | PADME | Sterile | Low |
| Ng, F.S.P. | FRI 5205 | 25 Apr 67 | Madhuca sericea | Compt. 90 Arong FR, Meraing. | Y | Y | KEP | | PADME | Sterile | Low |
| Ng, F.S.P. | FRI 5244 | 27 Apr 67 | Madhuca sericea | Compt. Boundary 24/25 Arong FR Extension, Mersing, Johore | Y | Y | KEP | | PADME | Sterile | Low |

| Collector | Collector No. | Date | Species (det) | Location | Habitat | Collector Observations | Herbarium code | Barcode | Image Source | Notes | Usefulness rating |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Ng, F.S.P. | FRI 5244 | 27 Apr 67 | Madhuca sericea | Compt. Boundary 24/25 Arong FR Extension, Mersing, Johore | Y | Y | L | L 2649528 | PADME | Sterile | High |
| Wilkie, P., Chan, Y.C., Mohd. Hairul, M.A. & Norazmi, A | FRI7213 7 | 23 Feb 11 | Madhuca sericea | Kota Tinggi: Panti Forest Reserve Compartmen t 63 | | Y | E | E00898828 | E | Sterile | High |
| Teo, L.E. & Din | KL 5045 | 14 Aug 03 | Madhuca sericea | Hutan Simpan Labis Segamat, Johor | | Y | KEP | 124397 | PADME | Fruiting | Medium |
| Unknown | KEP 70141 | 23 Jul 50 | Madhuca sericea | Mersing, T.43 bali 23 jalan Mersing Luang | | Y | KEP | | PADME | Sterile | Low |