



# Taxonomic recircumscriptions in the *Aglai* *elaeanoidea* complex (*Meliaceae*)

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## Key words

*Aglai* *elaeanoidea* complex  
coastal boodyarra  
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Priyangu  
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SNP

**Abstract** *Aglai* is the most widespread and species-rich genus in *Meliaceae*, comprising 124 species. *Aglai* *elaeanoidea* has presented a longstanding dilemma for taxonomists; it is highly morphologically and ecologically variable, and has a range extending across India, Southeast Asia, Australia and islands of the western Pacific Ocean. Previous work has examined molecular variation in the eastern part of the species' range; however, molecular variation in the western half of its distribution remained uncharacterised, precluding taxonomic resolution of the complex. In this study, we used DArT-seq analysis to investigate genetic structure in *A. elaeagnoidea* from India, Sri Lanka, Bangladesh, Thailand, Java and Bali. We find a strong genetic disjunction between Sri Lanka and Bangladesh, suggesting that western *A. elaeagnoidea* comprises two taxa. On the basis of these results, in combination with morphology and previous molecular work on eastern *A. elaeagnoidea*, we resolve *A. elaeagnoidea* into three species, retaining *A. elaeagnoidea* for the eastern (type) species, and reinstating *A. wallichii* for a species in Bangladesh, Thailand, Java and Bali, and *A. roxburghiana* for a species occurring in India and Sri Lanka. We provide descriptions for each taxon and a key to the species, thereby resolving a previously difficult species group in a notoriously complex genus.

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## INTRODUCTION

*Aglai* Lour., the most widespread and species-rich genus in *Meliaceae*, currently comprises 124 species (Pannell, pers. comm.) of dioecious shrubs and trees found in tropical rainforests in India, China, southeast Asia, Australia and the islands of the western Pacific Ocean (Pannell 1992, 2018). The genus is most readily distinguished by the presence of peltate scales, stellate hairs or stellate scales in the indumentum that sparsely to densely cover the stems, fertile organs and leaflets, as well as imparipinnate leaves (although a few species have simple leaves). *Aglai* has inflorescences of small, subglobose flowers (usually 1–2 mm diam) with a cup-shaped or subglobose staminal tube in both staminate and pistillate flowers, and the fruits can be dehiscent or indehiscent, usually with a non-fleshy peri-

carp that contains one to three seeds covered with an aril. Many species are locally important for their fruit, timber and traditional medicine, and hundreds of secondary metabolites unique to the genus have been researched for their cytotoxic (particularly anticarcinogenic), pesticidal, anti-inflammatory, antifungal and antiviral properties (Muellner et al. 2005, Mabberley 2011, Harneti & Supratman 2021, Greger 2021). Despite the ecological, cultural and biochemical importance of *Aglai*, many taxonomic issues remain in the genus at the species and sectional level, largely owing to complex patterns of morphological variation. Previous phylogenetic analyses suggest that the three sections currently recognised within the genus (sections *Aglai* Lour., *Amoora* (Roxb.) Pannell and *Neoaglai* Harms) are likely to be non-monophyletic (Muellner et al. 2008, Grudinski et al. 2014). In her seminal monograph of the genus, Pannell (1992) designated seven *Aglai* species as 'complex species', i.e., species with 'extensive, complicated and reticulated pattern(s) of variation' that may represent multiple taxa. In many cases, these complex species incorporated a myriad of previously published taxa with overlapping geographical, ecological and morphological variation. To encompass this overlapping variation in previous taxa, Pannell (1992) sank them into broadly-circumscribed complex species, explicitly stating that further, in-depth investigation was needed to identify and recircumscribe any taxon boundaries within them.

One such complex species, *A. elaeagnoidea* (A.Juss.) Benth., has presented a longstanding dilemma for taxonomists (Pannell 1992). First described in the monotypic genus *Nemedra* (as *N. elaeagnoidea* A.Juss.) based on the conspicuous, peltate scales of an Australian specimen (De Jussieu 1830), it was transferred

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to *Aglaia* by Bentham in 1836. The species was initially considered to be restricted to New Caledonia and northern Australia. Meanwhile, *Milnea roxburghiana* Wight & Arn. from India was published in 1834 and transferred to *Aglaia* by Miquel in 1868 (*A. roxburghiana* (Wight & Arn.) Miq.). The initial publication of the two specific epithets, *elaeanoidea* and *roxburghiana*, was followed by the publication of a further 12 related species and nine varieties. *Aglaia lepidota* Miq. from Sumatra (Miquel 1861) was placed in synonymy under *A. roxburghiana* var. *paupercula* by Miquel (1868), who also recognised two new varieties of *A. roxburghiana* (var. *angustata* Miq. and var. *balica* Miq.). *Aglaia wallichii* Hiern from the eastern Himalayan Silhet region of Bangladesh was published in 1875 and *A. wallichii* var. *brachystachya* C.DC and *A. roxburghiana* var. *obtusata* C.DC were erected in 1878 (De Candolle 1878). *Aglaia hoanensis* Pierre from southern Vietnam was published in 1895, *A. canariifolia* Koord. from Sulawesi (Koorders 1898), *A. elaeagnoidea* var. *glabrescens* Valetton, of unknown origin, (cultivated in Bogor Botanic Garden), in 1905, and *A. poulocondorensis* Pellegr. from southern Vietnam (Pellegrin 1910). The variety *A. elaeagnoidea* var. *formosana* Hayata (1906) from Taiwan was subsequently elevated to species level as *A. formosana* (Hayata ex Matsum. & Hayata) Hayata (1913). *Aglaia roxburghiana* var. *beddomei* Gamble and *A. roxburghiana* var. *courtallensis* Gamble, both from the Eastern Ghats of India, were published in 1915 and transferred to *A. elaeagnoidea* by Nair (1981). In the Philippines, Merrill (1905) published *A. parvifolia* Merr. from Burias Island, *A. elaeagnoidea* var. *pallens* Merr. from Camiguin Island (Merrill 1908) (subsequently elevated to the species *A. pallens* (Merr.) Merr.; Merrill 1918) and *A. cupreolepidota* Merr. from Mindoro (Merrill 1922). Two more species from Vietnam were published by Pellegrin: *Aglaia poulocondorensis* Pellegr. (1910) and *A. poilanei* Pellegr. (Pellegrin 1944). *Aglaia talbotii* Sundararagh. from Mysore State in India (Sundara Raghavan 1969) and *A. abbreviata* C.Y.Wu from Yunnan, China (Wu 1977) were the last two species to be published. In 1896, Koorders & Valetton speculated that *A. roxburghiana* should be synonymised with *A. elaeagnoidea* and in 1912 Koorders (p. 445) stated that *A. roxburghiana* 'ist vielleicht nur eine form von *A. elaeagnoidea*' (is perhaps only a form of *A. elaeagnoidea*). Backer & Bakhuizen van den Brink (1965) synonymised *A. roxburghiana* under *A. elaeagnoidea* in the Flora of Java, which established a broad taxonomic circumscription of *A. elaeagnoidea* that included plants from India to the western Pacific. Pannell (1992) included all the species and varieties listed above, along with five names not validly published (*Walsura lanceolata* Wall., *Sapindus lepidotus* Wall., *Aglaia grata* Wall. ex Voigt, *A. midnaporensis* Carey ex Voigt, *A. spanoghei* Blume ex Miq.) in her synonymy of the accepted, broadly defined *A. elaeagnoidea*, which she placed in section *Aglaia* (Pannell 1992). Pannell (1992) therefore took a conservative view and maintained the concept of the species prevailing at the time, while providing the first complete synonymy and typification for *A. elaeagnoidea*, pending resolution of what she considered to be a morphologically intractable taxonomic problem, especially in Java and other parts of West Malesia.

As currently circumscribed, *A. elaeagnoidea* is distinguished from other *Aglaia* species by the presence of large, peltate scales in its leaf, twig and inflorescence indumentum (Pannell 1992). It is distributed from Sri Lanka and the Western Ghats of India, through Bangladesh (where it is now considered extinct; Bangladesh National Herbarium pers. comm.) and much of Southeast Asia to northern Australia and the western Pacific Ocean islands as far east as the Samoan Islands (Pannell 1992). Morphologically, it varies considerably across this range particularly in the colour and density of peltate scales, the presence of stellate scales, fruit shape and colour, pericarp rigidity and indumentum, leaflet shape, and in the degree of

prominence of leaflet vein reticulation. It also varies in height and habitat, with individuals from coastal secondary forest often smaller than those occurring on dry, sandy soils and limestones in inland parts of India, Sri Lanka, Thailand, Borneo and the Philippines (Pannell 1992).

In a molecular phylogenetic study of *A. elaeagnoidea* using one nuclear marker (ITS) and 13 samples from the two extremes of its distribution, Muellner et al. (2009) found high genetic variance between Australian, Malaysian and Sri Lankan specimens and suggested that this may be correlated with morphological and ecological variation. They indicated that *A. elaeagnoidea* sensu Pannell (1992) may comprise more than one taxon, and that the name *A. roxburghiana* may warrant reinstatement, but as they only included samples from the extremes of its range, they could not determine whether genetic variation was continuous or discontinuous, precluding taxonomic delimitation. Similarly, Grudinski et al. (2014) included two samples of *A. elaeagnoidea* in a genus-wide phylogenetic analysis, recovering the species as non-monophyletic, but like Muellner et al. (2009) sampling was insufficient to infer correlation between genetic, geographic, morphological and ecological variation and thereby test species delimitations.

Joyce et al. (2021) conducted a molecular (DArT-seq) phylogeographic study of *A. elaeagnoidea* to infer tracks of colonisation between Southeast Asia and Australia. This study included 144 samples from across the entire range of the taxon, and recovered 176331 high-quality single nucleotide polymorphisms (SNPs) across 90456 loci. It confirmed high genetic differentiation within *A. elaeagnoidea* and recovered two major genetic groups (Fig. 1): 1) eastern *A. elaeagnoidea* (including individuals from Taiwan, the Philippines, Borneo, Bali, Sulawesi, Maluku, New Guinea, Timor, Australia and islands of the western Pacific); and 2) western *A. elaeagnoidea* (comprising samples from India, Sri Lanka, Bangladesh, Thailand, Java and Bali). These genetic groups were broadly correlated with morphological differences (Joyce et al. 2021). Furthermore, the results confirmed those of Muellner et al. (2009) and Grudinski et al. (2014) in recovering *A. elaeagnoidea* as non-monophyletic, with the western populations more closely related to *A. edulis* (Roxb.) Wall. and the eastern populations more closely related to *A. korthalsii* Miq. Joyce et al. (2021) reiterated the need for a complete revision of species boundaries in *A. elaeagnoidea* but focussed on the phylogeography of eastern *A. elaeagnoidea*, leaving taxonomic boundaries within *A. elaeagnoidea* s.lat. unresolved.

In this study, we present a DArT-seq analysis of western *A. elaeagnoidea* individuals to investigate genetic structure across India, Sri Lanka, Bangladesh, Thailand, Java and Bali. We discuss the results in the context of the dataset of Joyce et al. (2021) and circumscribe three species within *A. elaeagnoidea* s.lat. based on correlated morphological and genetic variation. Associated nomenclatural changes are made, and full synonymies and morphological descriptions for the segregate taxa are presented.

## MATERIAL AND METHODS

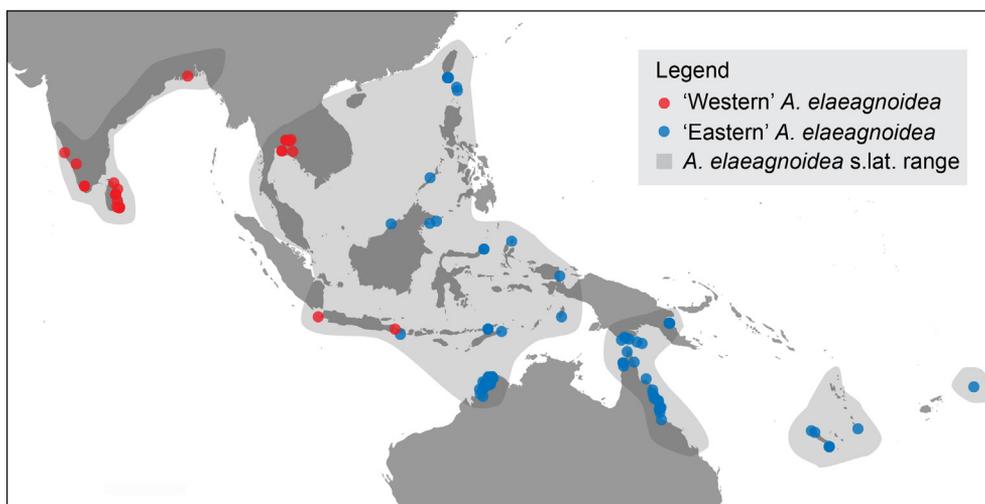
### Sampling, DNA extraction, sequencing

Thirty samples from India, Sri Lanka, Bangladesh, Thailand, Java and Bali in the Lesser Sunda Islands of the western *A. elaeagnoidea* group of Joyce et al. (2021) were included in this study (Fig. 1). Two samples of *A. edulis* were included as an outgroup, as *A. edulis* was found to be the most genetically similar taxon to the western *A. elaeagnoidea* group by Joyce et al. (2021). All samples were obtained from herbarium specimens from five herbaria (Table 1).

**Table 1** *Aglaia* herbarium specimens sequenced for this study including western *A. elaeagnoides* s.lat. and outgroup species *A. edulis*.

Original species	DNA no.	Herbarium code*	Collector	Collection number	Collection date	Locality	New species assignment
<i>A. elaeagnoides</i> s.lat.	G08356	FHO	H. Greger	HG753	11/25/2000	Bangladesh	<i>A. wallichii</i>
<i>A. elaeagnoides</i> s.lat.	G08357	FHO	H. Greger	HG502	2/15/1998	Thailand	<i>A. wallichii</i>
<i>A. elaeagnoides</i> s.lat.	G08363	A	K.M. Matthew	RHT27482	4/11/1980	Western Ghats, India	<i>A. roxburghiana</i>
<i>A. elaeagnoides</i> s.lat.	G08438	NY	R. Wight	140	April 1835	Western Ghats, India	<i>A. roxburghiana</i>
<i>A. elaeagnoides</i> s.lat.	G08441	NY	R. Wight	418	–	Western Ghats, India	<i>A. roxburghiana</i>
<i>A. elaeagnoides</i> s.lat.	G08495	GH/A	P.L. Comanor	1165	3/28/1968	Sri Lanka	<i>A. roxburghiana</i>
<i>A. elaeagnoides</i> s.lat.	G08496	GH/A	D.D. Soejarto, T. Smitinand, K. Taylor & N. Nantasan	6026	4/22/1987	Thailand	<i>A. wallichii</i>
<i>A. elaeagnoides</i> s.lat.	G08498	GH/A	A. Kostermans	24392	6/2/1971	Sri Lanka	<i>A. roxburghiana</i>
<i>A. elaeagnoides</i> s.lat.	G08504	GH/A	G. Murata, C. Phengklai, S. Mitsuta, H. Nagamasu & N. Nantasan	37072	10/2/1984	Thailand	<i>A. wallichii</i>
<i>A. elaeagnoides</i> s.lat.	G08518	GH/A	J.F. Maxwell	01-359	9/3/2001	Thailand	<i>A. wallichii</i>
<i>A. elaeagnoides</i> s.lat.	G08519	GH/A	O. Petrmir	516	5/22/2002	Thailand	<i>A. wallichii</i>
<i>A. elaeagnoides</i> s.lat.	G08527	US	D. Mueller-Dombois & R.G. Cooray	67120614	12/6/1967	Sri Lanka	<i>A. roxburghiana</i>
<i>A. elaeagnoides</i> s.lat.	G08528	US	D. Mueller-Dombois & R.G. Cooray	68013012A	1/30/1968	Sri Lanka	<i>A. roxburghiana</i>
<i>A. elaeagnoides</i> s.lat.	G08530	US	S. Ripley	469	11/22/1971	Sri Lanka	<i>A. roxburghiana</i>
<i>A. elaeagnoides</i> s.lat.	G08532	US	J.W. Nowicke & M. Jayasuriya	392	7/18/1973	Sri Lanka	<i>A. roxburghiana</i>
<i>A. elaeagnoides</i> s.lat.	G08536	US	F.R. Fosberg	39687	12/18/1958	Pulau Peutjung, Java	<i>A. wallichii</i>
<i>A. elaeagnoides</i> s.lat.	G08540	US	R.G. Cooray	69111624R	11/16/1969	Sri Lanka	<i>A. roxburghiana</i>
<i>A. elaeagnoides</i> s.lat.	G08541	US	A. Kostermans	26000	6/5/1976	Western Ghats, India	<i>A. roxburghiana</i>
<i>A. elaeagnoides</i> s.lat.	G08542	US	W. Meijer	188	6/28/1970	Sri Lanka	<i>A. roxburghiana</i>
<i>A. elaeagnoides</i> s.lat.	G08544	US	S. Ripley	151	4/14/1969	Sri Lanka	<i>A. roxburghiana</i>
<i>A. elaeagnoides</i> s.lat.	G08545	US	S. Ripley	259	1/31/1969	Sri Lanka	<i>A. roxburghiana</i>
<i>A. elaeagnoides</i> s.lat.	G08550	US	W. Dittus	WD71090303	9/3/1971	Sri Lanka	<i>A. roxburghiana</i>
<i>A. elaeagnoides</i> s.lat.	G08551	US	W. Meijer	766	7/8/1971	Sri Lanka	<i>A. roxburghiana</i>
<i>A. elaeagnoides</i> s.lat.	G08560	US	D.J. Collins	1132	3/11/1926	Thailand	<i>A. wallichii</i>
<i>A. elaeagnoides</i> s.lat.	G08561	US	D.J. Collins	802	April 1922	Thailand	<i>A. wallichii</i>
<i>A. elaeagnoides</i> s.lat.	G08562	US	S. Ripley	232	9/24/1968	Sri Lanka	<i>A. roxburghiana</i>
<i>A. elaeagnoides</i> s.lat.	G08563	US	P.L. Comanor	674	12/10/1967	Sri Lanka	<i>A. roxburghiana</i>
<i>A. elaeagnoides</i> s.lat.	G08609	NY	C.G.G.J. van Steenis	7573	1/4/1936	Bali, Lesser Sunda Islands	<i>A. wallichii</i>
<i>A. elaeagnoides</i> s.lat.	G08638	GH/A	A. Kostermans	24308	5/30/1971	Sri Lanka	<i>A. roxburghiana</i>
<i>A. elaeagnoides</i> s.lat.	G08648	GH/A	A. Boonkongchart	206	5/12/2003	Thailand	<i>A. wallichii</i>
<i>A. edulis</i>	G08555	US	S.K. Lau	58	6/10/1932	Hainan	
<i>A. edulis</i>	G08556	US	N.K. Chun & C.L. Tso	44404	Dec. 1932–1933	Hainan	

\* Herbarium codes: FHO = Daubeny Herbarium; GH/A = Harvard University Herbaria; NY = New York Botanic Garden; US = United States National Herbarium. New species assignment indicates the species that the sample is designated to following the results of this paper (see Discussion).



**Fig. 1** Map of localities of the genetically distinct eastern and western *A. elaeagnoidea* following Joyce et al. (2021). Red points indicate localities of western *A. elaeagnoidea* samples used in this study to investigate genetic variation and taxonomic boundaries within western *A. elaeagnoidea*. Blue points represent samples used in Joyce et al. (2021) to investigate genetic structure and phylogeography of eastern *A. elaeagnoidea*. Shading represents the range of *A. elaeagnoidea* s.lat. according to Pannell (1992).

Leaflet material (15 mg per sample) was ground using a Tissue-Lyser (Qiagen; Hilden, Germany) and DNA extracted with a modified Dneasy Plant Mini Kit (Qiagen; Hilden, Germany) protocol (see Joyce et al. 2021 for details). Library preparation and DArTseq sequencing was undertaken by Diversity Arrays Technology Pty Ltd (DArT; [www.diversityarrays.com](http://www.diversityarrays.com)). DArTseq is a proprietary restriction-based reduced-representation genome sequencing method that recovers thousands of single or low copy markers and SNPs within or proximal to genes throughout the plant genome (Garavito et al. 2016, Rossetto et al. 2019). DArT analysis pipelines were used to clean raw data (remove poor-quality sequences, correct low-quality bases and BLAST-search data to eliminate possible microbial contaminant sequences), call SNPs and generate genotype data for each sample. DArTseq SNP data has been deposited to the James Cook University Research Data data repository and is available at <https://doi.org/10.25903/D3AZ-YB02>.

Genotype data were cleaned in R using the workflow of Rossetto et al. (2019). Poor quality SNP loci were removed to retain loci with > 0.96 reproducibility and < 20 % missing genotypes. Data were then randomly sampled to retain one SNP per locus. Poor quality samples (> 20 % missing loci) were identified and removed.

#### **Analysis of genetic structure in western *A. elaeagnoidea***

Addressing questions at the species-population interface is challenging, as the data produced in such investigations may not meet all the assumptions of methods tuned for either population-level or species-level questions. In population genetics, a population is the unit of study, and is usually defined as a group of conspecific individuals that have a high probability of interacting with each other genetically (e.g., Hastings 2013); in phylogenetics, single representatives of independently evolving lineages (such as separate species) are often used as the unit of study. Deciding on an appropriate unit to conduct a study to tease apart a species complex is difficult, and must be weighed against the logistics of sampling. At the spatial scale of this study, we believe it is sensible to assume that genetic interactions between individuals occupying the same island have been more frequent than those between islands; hence, 'population' is used here to refer to individuals from the same island, or geographically separated region. We recognise that this is not the traditional definition of population, and have therefore taken care in the interpretation of analyses designed for

conventional population genetic studies, as the assumptions of some of these analyses may not be met (see Holsinger & Weir 2009). This is especially the case for islands (e.g., Java) where genetic material of only a single representative was available for analysis, as one individual is unlikely to sample adequately the genetic diversity of the island as a whole.

Genetic structure within western *A. elaeagnoidea* compared to the outgroup taxon *A. edulis* was initially visualised using Principal Components Analysis (PCA) and UPGMA clustering using the R packages *adegenet* v. 2.1.0 (Jombart 2008) and 'ape' (Paradis & Schliep 2019), respectively.

Once it was established that *A. edulis* was well-separated from *A. elaeagnoidea* in the PCA and UPGMA clustering analyses, a distance-based phylogenetic network focussing on western *A. elaeagnoidea* samples was generated using NeighbourNet analysis in SplitsTree v.4.15.1 (Bryant & Moulton 2004, Huson & Bryant 2006).

Admixture analysis was conducted using sparse non-negative matrix factorisation as implemented in the 'snmf' function in the R package 'LEA' on western *A. elaeagnoidea* samples (Frichot & François 2015). The optimal number of ancestral populations ( $k$ ) was determined as two by using the entropy criterion (Alexander & Lange 2011, Frichot & François 2015). Ancestry coefficients were visualised by plotting the Q-values of each individual in a bar plot.

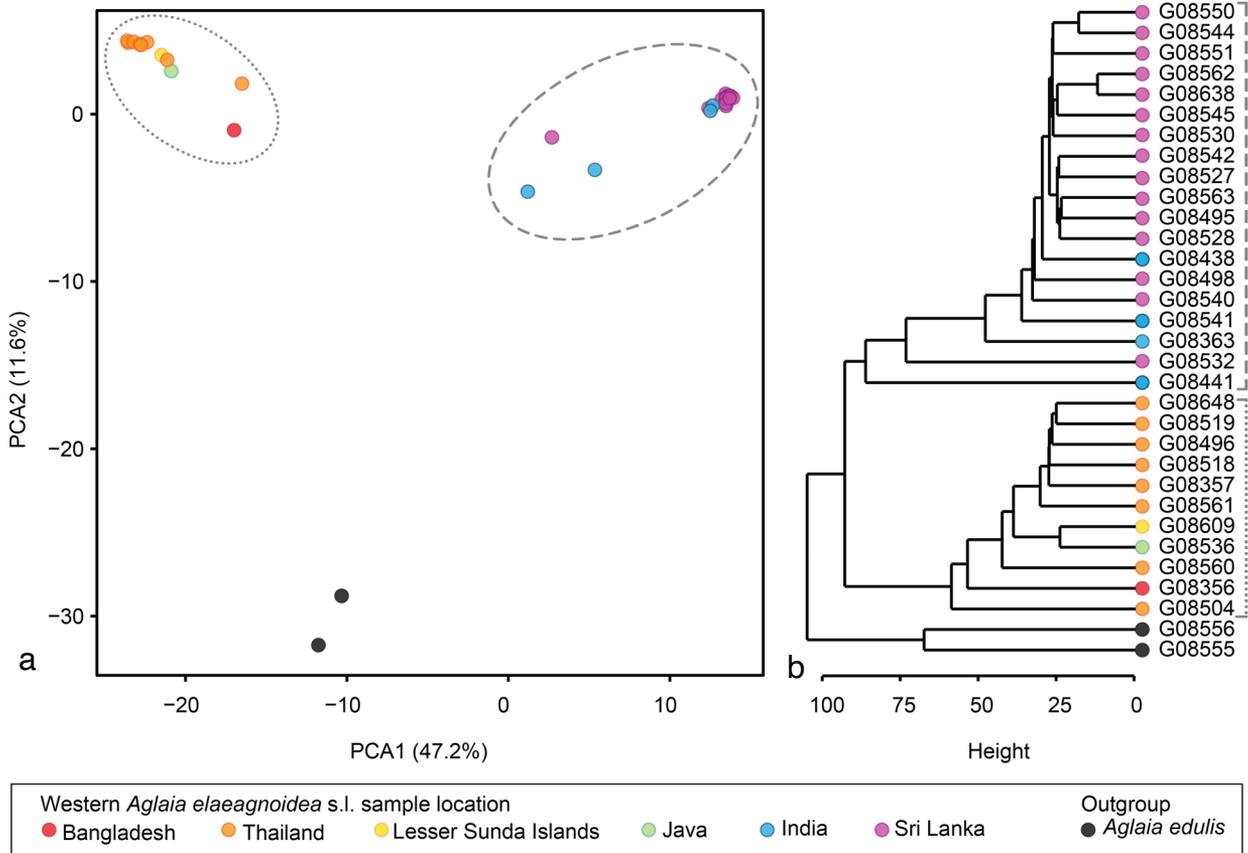
#### **Morphological study**

The species identity of all specimens sampled for molecular analysis was confirmed by the last or first author, and notes on morphology and locality were made and a photograph was taken of every specimen. The morphology of *A. elaeagnoidea* s.lat. specimens was also studied at BO, K, M and SING. Biometrics were recorded for a haphazardly-selected subset of specimens from all visited herbaria.

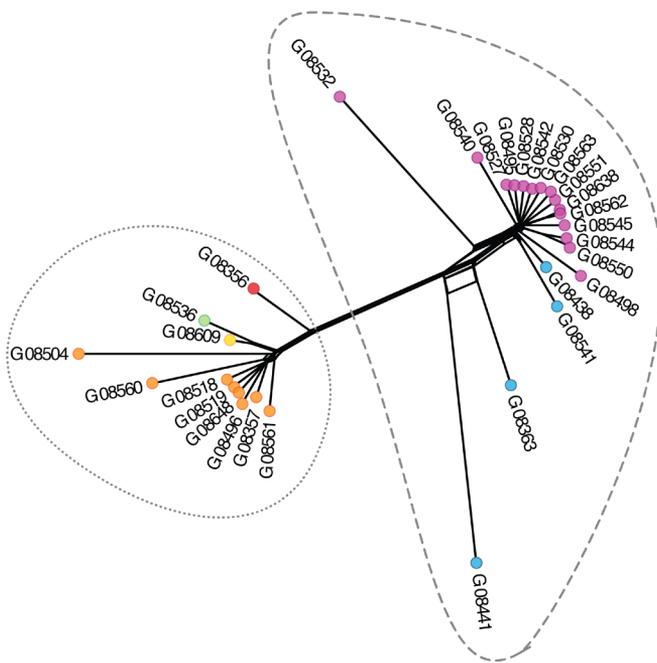
## **RESULTS**

A total of 176331 SNPs were recovered from 90456 loci. After removing poor-quality SNPs, 22834 loci were retained.

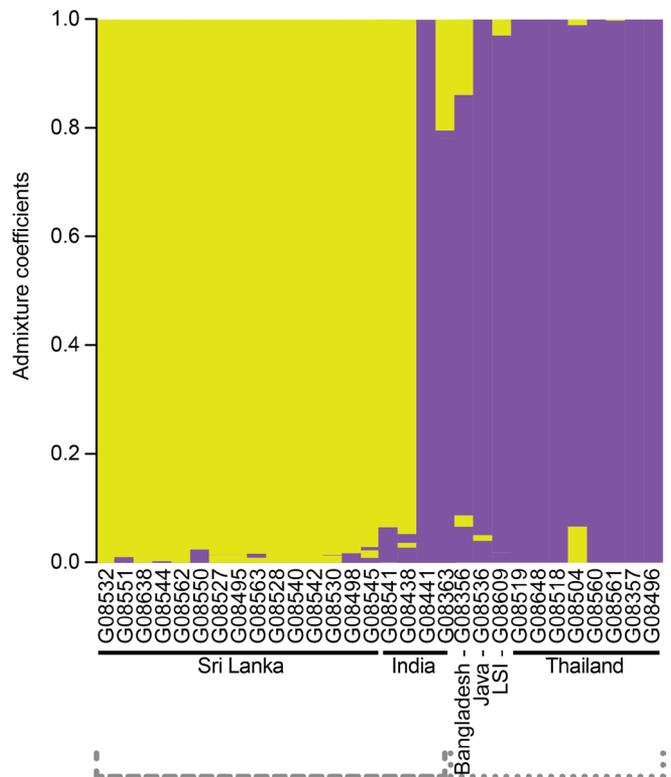
In the PCA (Fig. 2a), PCA1 accounted for 47.2 % of the genetic variation, and PCA2 explained 11.6 % of the variation. Western *A. elaeagnoidea* is most clearly separated from *A. edulis* along PCA2. Genetic discontinuity within western *A. elaeagnoidea*



**Fig. 2** a. Principal Component Analysis (PCA); b. UPGMA dendrogram of western *Aglaia elaeagnoidea* s.lat. individuals and outgroup species *A. edulis* (black dots) from 22834 loci. Labels refer to DNA number; for full specimen details see Table 1. Point colour represents sample locality, and grey lines correspond to new taxonomic boundaries resulting from this study: dotted and dashed lines demarcate the taxa designated as *A. wallichii* and *A. roxburghiana*, respectively.



**Fig. 3** SplitsTree network of 22834 loci from western *Aglaia elaeagnoidea* s.lat. individuals. Labels refer to DNA number; for full specimen details see Table 1. Point colour represents sample locality as in Fig. 2; dotted and dashed lines demarcate the taxa designated as a result of this study as *A. wallichii* and *A. roxburghiana*, respectively.



**Fig. 4** Results of LEA analysis showing genetic structure across the distribution of western *Aglaia elaeagnoidea* s.lat. Labels refer to DNA number; for full specimen details see Table 1. Bar plot of Q-value admixture coefficient (y-axis) for each individual (x-axis) represents each individual's ancestry proportion when modelled with two ancestral populations ( $k = 2$ ), with colours representing different ancestral populations. Dotted and dashed lines demarcate the taxa designated as a result of this study as *A. wallichii* and *A. roxburghiana*, respectively.

is evident across PCA1, with individuals from Sri Lanka and India clustering separately from individuals from Bangladesh, Thailand, Java and the Lesser Sunda Islands. UPGMA clustering analysis retrieved the same two groups in western *A. elaeagnoidea* (Fig. 2b).

SplitsTree analysis also retrieved strong genetic structure within western *A. elaeagnoidea*, indicating high genetic difference between individuals from India and Sri Lanka compared to individuals from Bangladesh, Thailand, Java and Bali, with little intermixing (Fig. 3). LEA analysis suggests for the first time that western *A. elaeagnoidea* has two ancestral populations ( $k = 2$ ), with individuals from Sri Lanka having little shared ancestry with individuals from Bangladesh, Thailand, Java and Bali in the Lesser Sunda Islands (Fig. 4). The ancestry of individuals from India was mixed, with two individuals showing a strong signal of shared ancestry with individuals from Bangladesh, Thailand, Java and Bali, and the rest indicating a shared ancestry with Sri Lankan individuals (Fig. 4).

## DISCUSSION

The phenetic analyses (PCA and UPGMA) and the network analysis (SplitsTree) all indicate that western *A. elaeagnoidea* comprises two distinct genetic groups: 1) individuals from India and Sri Lanka; and 2) individuals from Bangladesh, Thailand, Java and Bali. In combination with the strong genetic divergence between eastern and western *A. elaeagnoidea* demonstrated in Joyce et al. (2021), we herein divide *A. elaeagnoidea* s.lat. into three species. *Aglaia elaeagnoidea* (A.Juss.) Benth. is recircumscribed to include only individuals recognised as 'eastern *A. elaeagnoidea*' by Joyce et al. (2021), occurring in Borneo, Sulawesi, the Philippines, The Lesser Sunda Islands (Bali, Timor), Moluccas, New Guinea, Australia and islands of the western Pacific. *Aglaia roxburghiana* (Wight & Arn.) Miq. is reinstated for individuals from India and Sri Lanka only, and *A. wallichii* Hiern is reinstated and its circumscription greatly expanded, to include individuals from Bangladesh, Thailand, Java and Bali.

While the three species were primarily recognised using genetic markers, all are recognisable morphologically, although they have some geographical, morphological and ecological overlap. *Aglaia wallichii* and *A. roxburghiana* can usually be distinguished from *A. elaeagnoidea* s.str. using indumentum and fruit characters. Stellate scales are often present in the indumentum of inflorescences and leaflets of *A. wallichii* and *A. roxburghiana*, (particularly on young growth but often wearing off on older growth), but are absent from the indumentum of *A. elaeagnoidea* s.str. Stellate scales are also shared with *A. edulis*, which was retrieved as being more closely related to *A. wallichii* and *A. roxburghiana* than to *A. elaeagnoidea* s.str. in Joyce et al. (2021). Pannell (1992: 150) also highlighted the morphological similarity between western *A. elaeagnoidea* s.lat. and *A. edulis* in this respect. Fruits of *A. wallichii* and *A. roxburghiana* are also distinct from *A. elaeagnoidea* s.str., being obovoid when immature, ellipsoid to subglobose when ripe, and having a brown, yellow or orange pericarp with a dense indumentum on the outer surface and a seed with a complete gelatinous aril. In contrast, fruits of *A. elaeagnoidea* s.str. are subglobose to globose when both immature and ripe, have a fleshy, red pericarp with a sparse indumentum of scattered peltate scales, and (at least in some parts of Australia), a seed with a vestigial gelatinous aril. The difference in fruit morphology correlates with observed differences in vertebrate dispersers between the taxa. In Sri Lanka, fruits of *A. roxburghiana* are eaten by Grey Langurs (*Semnopithecus priam thersites*) and Toque Macaques (*Macaca sinica sinica*), that use their fingers to peel off the yellow-brown pericarp and ingest the seeds with

their fleshy arils (Dittus 1974; Dittus pers. comm. 2019). Likewise, in Thailand, the seeds of *A. wallichii* with their adherent fleshy aril are ingested by gibbons (*Hylobates* spp.; Brockelman pers. comm. 2020). Dispersal of *A. roxburghiana* and *A. wallichii* therefore conform to the primate dispersal syndrome described in Pannell & Koziol (1987), Pannell (1992, 1997) and Hopkins et al. (1998). Primates do not occur over most of the range of *A. elaeagnoidea* s.str., and the only recorded dispersers are Pied Imperial Pigeons (*Ducula bicolor*, in Australia), which swallow the fruits whole, including the fleshy red pericarp (Kenneally & McKenzie 1989). *Aglaia wallichii* can usually be further separated from *A. elaeagnoidea* s.str. by a difference in habitat, with *A. wallichii* usually found in inland rainforests and *A. elaeagnoidea* s.str. in coastal forests. However, as with the morphological characters, exceptions to these habitats occur where the ranges of the taxa overlap in West Malesia and Bali.

*Aglaia wallichii* and *A. roxburghiana* can be separated primarily by leaflet shape, indumentum and geography. The leaflets of *A. roxburghiana* are obovate, usually lack a drip tip, and generally have somewhat prominent tertiary venation in herbarium specimens. *Aglaia wallichii* leaflets are usually elliptic, characteristically feature a drip tip, and usually have less prominent venation than in *A. roxburghiana*. The indumentum of *A. roxburghiana* is sparser than that of *A. wallichii*, and the peltate scales are paler. The fruits of both *A. roxburghiana* and *A. wallichii* are obovoid when young. When ripe they are subglobose in *A. wallichii* and either subglobose or ellipsoid in *A. roxburghiana*.

Given the overall morphological similarity of *A. wallichii* and *A. roxburghiana*, we hypothesise that they are sister species; however, additional phylogenetic analysis inclusive of all affiliated taxa are needed to confirm this. If *A. roxburghiana* and *A. wallichii* are sister species, it would be interesting to investigate the effect of historical biogeographic events on their divergence such as the aridification of India producing a disjunction in distributions of mesic species at the Deccan Plateau (e.g., Ray et al. 2021).

The SplitsTree analysis and PCA indicate that *A. roxburghiana* is genetically more variable than *A. wallichii*, and the LEA analysis retrieved some Indian individuals as having a different ancestry to other Indian and Sri Lankan individuals. Anecdotal field observations also suggest that *A. roxburghiana* is diverse in its habit and habitat across the Western Ghats (Machado pers. comm. 2019, Singh Ramesh pers. comm. 2019). Habitat and habit information is often not captured with herbarium specimens, hence the sampling used in this study may not encompass the full extent of morphological, genetic and ecological variation within *A. roxburghiana*. Gamble (1915) recognised two varieties of *A. roxburghiana* within India (later synonymised as varieties of *A. elaeagnoidea* by Nair (1981)) distinguished by locality, leaflet number and fruit size. It is therefore possible that *A. roxburghiana* comprises multiple taxa, but the sampling in this study was not dense enough to test this. Taxonomy of *Aglaia* in India warrants further investigation using field data and more intensive sampling.

## TAXONOMIC TREATMENT

### Key to the species

The most reliable diagnostic morphological characters that distinguish the three species recognized here are found in the fruits, which are often absent from living and dried specimens and, in any event, can only be found on pistillate plants in this dioecious genus. The key is constructed using morphological characters that agree with the molecular results and known fruit morphology. Geographical occurrence is included for guidance,

**Table 2** Morphological characters of the segregate species formerly included within *Aglaia elaeagnoides* s.lat.

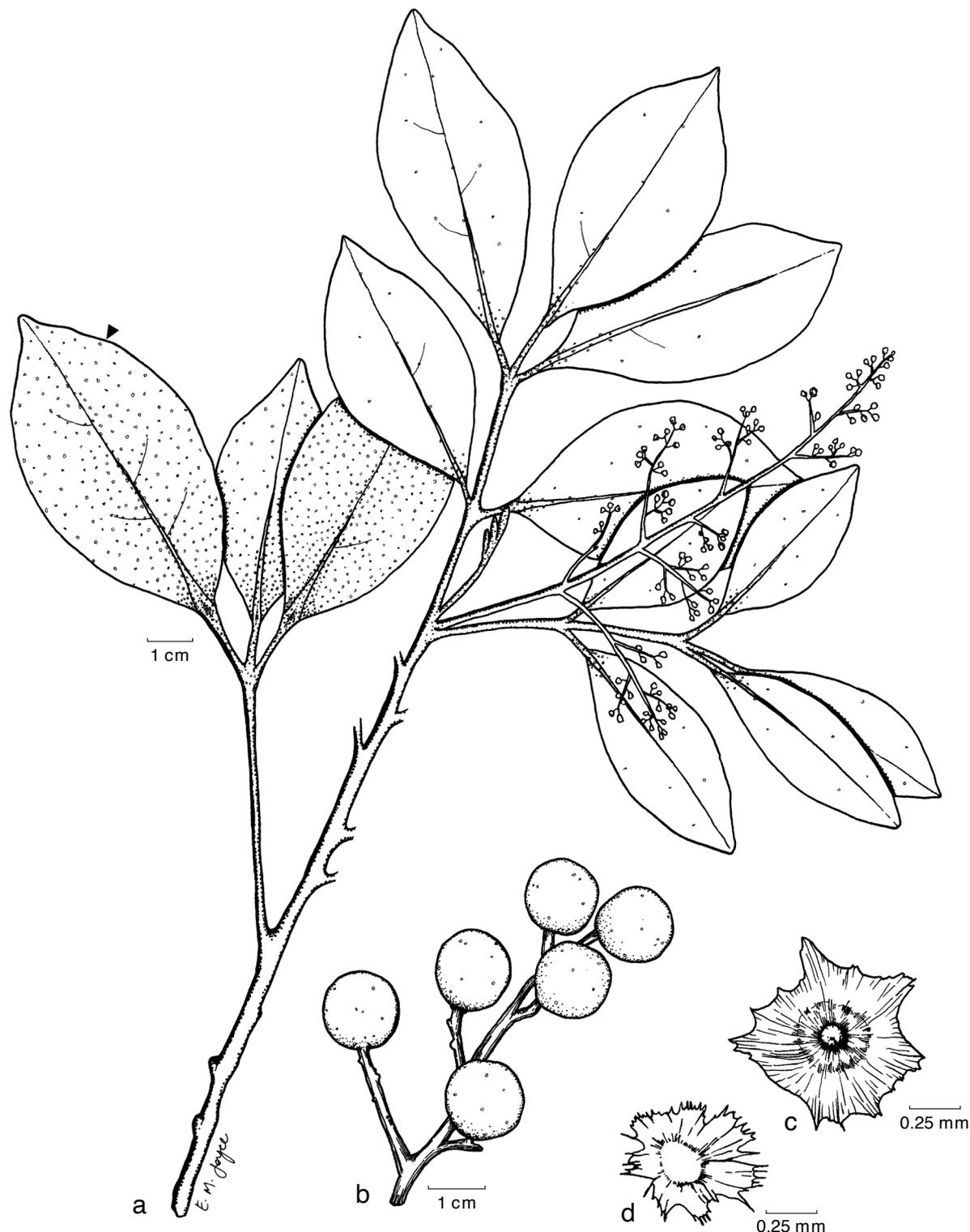
Species	Distribution and habitat	Leaflet apex	Leaflet shape	Leaflet base	Leaflet indumentum	Flower indumentum	Fruit and seed
<i>A. elaeagnoides</i> (A. Juss.) Benth.	Taiwan, Philippines, Borneo, Bali, Timor, Sulawesi, Maluku, New Guinea, Australia (Queensland and Western Australia), to the Samoan Islands in the western Pacific	Absent or with a short broad rounded acumen triangular in outline. Occasionally leaflet margin concave at the base of the acumen, but then the acumen shape is short, broad and triangular (not a drip tip)	Elliptical or broadly obovate, usually less than twice as long as wide. Widest point usually at the midpoint of the lamina. The exception is in inland populations, where the leaflet shape resembles that of <i>A. wallichii</i> and <i>A. roxburghiana</i>	Rounded or shortly cuneate	Scales peltate, large, usually pale brown or white with a pale brown centre, margin usually entire or sometimes shortly fimbriate, sparse to numerous on lower leaflet surface, densely covering midrib below; occasionally deep reddish brown, giving leaflets and young parts of the plant a rusty or coppery colour	Scales characteristically present on the exposed outer surface of the petals	Globose, red, with scattered large peltate scales, pale brown or white with a pale brown centre, margin entire or shortly fimbriate. Pericarp of mature fruit wrinkled when dry. Seeds completely or partially covered with a gelatinous aril
<i>A. roxburghiana</i> (Wight & Arn.) Miq.	Western Ghats and Sri Lanka, Odisha and West Bengal, mostly inland forest	Acumen usually absent; occasionally some leaflets on Indian specimens have a distinct acumen (drip tip)	Obovate, usually at least twice as long as wide, widest point usually distal to the midpoint of the lamina	Cuneate	Scales peltate, brown or orange-brown, sometimes with a fimbriate margin, sparse on lower leaflet surface. Stellate scales usually present on young growth, occasionally persisting on mature leaflets	Scales almost always absent from the petals	Subglobose or ellipsoid when ripe, obovoid when unripe, yellow or orange or brown, densely covered with brown or orange-brown peltate scales with a fimbriate margin. Pericarp of mature fruit smooth and brittle when dry. Seeds completely covered with a fleshy gelatinous aril
<i>A. wallichii</i> Hiern	Mainland Asia, Java, Bali, usually inland forest on limestone or sandstone bedrock, sometimes coastal in Java and Bali	Usually with distinct, narrow, tapering or parallel sided acumen (drip tip), with leaflet margin narrowing markedly and concave at the base of the acumen. Coastal specimens have a short broad rounded acumen, triangular in outline	Obovate, usually at least twice as long as wide. Widest point usually distal to the midpoint of the lamina. The exception is in coastal populations, where leaflet shape resembles that of <i>A. elaeagnoides</i> s.str.	Cuneate (or rounded in some coastal specimens)	Scales peltate, brown or orange-brown, sometimes with a fimbriate margin, sparse on lower leaflet surface. Stellate scales sometimes present. One known exception to this is coastal specimens from W. Java and offshore islands which have the indumentum of <i>A. elaeagnoides</i> s.str.	Scales almost always absent from the petals, except on the Javanese specimens that resemble <i>A. elaeagnoides</i> s.str.	Subglobose, ellipsoid when ripe, obovoid when unripe, yellow, orange or brown, densely covered with brown or orange-brown peltate scales with fimbriate margin. Pericarp of mature fruit smooth and brittle when dry. Seeds completely covered with a fleshy gelatinous aril

especially when the diagnostic characters are not present. A comparison of key features is also presented in Table 2.

1. Fruits subglobose when immature and mature, red, with sparse pale brown or white peltate scales; indumentum of large peltate scales, pale brown or white with pale brown centres and entire or shortly fimbriate margins, the scales sparse to numerous on lower leaflet surface, densely covering the midrib below, occasionally deep reddish brown, giving leaflets and young parts of the plant a rusty or coppery colour; leaflet acumen usually absent or short, broad-rounded and triangular in outline (i.e., not a 'drip tip'); petals with peltate scales on the exposed surfaces; immature and mature fruits subglobose, red, with sparse

pale brown or white peltate scales. — Taiwan, Philippines, Borneo, Sumatra, Bali and islands eastwards to the Samoan Islands, Queensland and Western Australia . . . . .

1. Fruits obovoid when immature, ellipsoid or subglobose when mature, orange, yellow or brown and densely covered with orange-brown or pale brown peltate scales with fimbriate margins; indumentum of brown or orange brown peltate scales with fimbriate margins, sparse on lower leaflet surface; leaflets with distinct acumen ('drip tip') present or absent; petals usually without peltate scales on the exposed surfaces. — Sri Lanka, India, Bangladesh, Myanmar, China, Indo-China, Thailand, Peninsular Malaysia, Java, Bali . . . . . 2



**Fig. 5** *Aglaia elaeagnoidea* s.str. a. Branch with inflorescence, with arrow indicating leaf lower surface; b. mature fruit; c. peltate scale with entire margin; d. peltate scale with fimbriate margin (a, c–d: Ford & Bradford 5776; b: Croft & Lelean LAE 68520, all CNS). — Illustration by E.M. Joyce.

2. Apex of leaflet usually rounded, rarely with a distinct acumen; occasional stellate scales interspersed amongst the peltate scales. — Sri Lanka, Western Ghats, Odisha and West Bengal of India . . . . . 2. *A. roxburghiana*
2. Apex of leaflet with a distinct acumen (drip tip) demarcated by a markedly convex margin at the junction between the main lamina and the acumen. — Mainland Asia (Myanmar, China, Indo-China and Thailand), Peninsular Malaysia and the western Malesian islands of Java and Bali; historically in Bangladesh . . . . . 3. *A. wallichii*

### 1. *Aglaia elaeagnoidea* (A.Juss.) Benth. — Fig 5

- Aglaia elaeagnoidea* (A.Juss.) Benth. (1863) 383; Koord. & Valetton (1913) t. 154; Pannell (1992) 143, p.p. pro type; (1995a) 243, p.p. pro type; (2007) 49; Kenneally & N.L.McKenzie (1989) 52; W.Cooper & W.T.Cooper (2004) 285; Pannell (2013b) 38. — *Nemedra elaeagnoidea* A.Juss. (1830) 239; (1832 '1830') 223, t. 14. — Lectotype (designated by Pannell 1992): *Leschenault* in *Baudin s.n.* (lecto P; isolecto BM, G, K), Australia.
- Aglaia lepidota* Miq. (1861) 507. — Type: *Anonymous HB 4485* (holo U), S. Sumatra, Lampong Province, Pulau Lebuku.
- Aglaia canariifolia* Koord. (1898) 380, 633. — Lectotype (designated by Pannell 1992): *Koorders 17899* (lecto BO; isolecto L), Sulawesi, Minahassa, Menado.
- Aglaia elaeagnoidea* (A.Juss.) Benth. var. *glabrescens* Valetton (1905) 65. — Lectotype (designated here by Pannell): *Teijsmann 323* (lecto L; isolecto K), cultivated in Bogor Botanical Garden.
- Aglaia parvifolia* Merr. (1905) 21. — Lectotype (designated by Pannell 1992): *Clark For. Bur. 986 [968]* (lectotype (designated by Pannell 1992) NY; isolectotypes BM, G, K, US), Philippine Islands, Island of Burias, June 1904.
- Aglaia elaeagnoidea* (A.Juss.) Benth. var. *formosana* Hayata (1906) 78. — *Aglaia formosana* (Hayata) Hayata (1913) 52. — Type: *Owataru s.n.* (holo K), Taiwan, near Chokachiraisha.
- Aglaia elaeagnoidea* (A.Juss.) Benth. var. *pallens* Merr. (1908) 413. — *Aglaia pallens* (Merr.) Merr. (1918) 297. — Lectotype (designated by Pannell 1992): *BS (Fénix) 4122* (lecto NY), Philippines, Camiguin Island, Babuyan.
- Aglaia cupreolepidota* Merr. (1922) 393. — Lectotype (designated by Pannell 1992): *BS (Ramos) 39579* (lecto A; isolecto BM, BO, GH, K US), Philippines, Mindoro, Paluan.
- Aglaia odoratissima* auct. non Blume: Benth. (1843) 213, quoad specimens: *Barclay s.n.* (K), Tobie Island; *Hind 1841* (K!), New Guinea.

Small trees, to 20 m tall, without or sometimes with buttresses. *Bark* pale brown, greyish brown or mottled, with fine vertical fissures, shedding in large flakes which curl back; inner bark pink grading to cream; wood pink or yellow. *Twigs* densely covered with large white, pale brown or sometimes coppery brown peltate scales often with an irregular margin. *Leaves* alternate, imparipinnate, 4.5–22(–26) by 9–20(–26) cm; petiole to 4.3(–5.5) cm long. Leaflets (1–)3–7; lamina elliptical or obovate, 2–16 by 1–6.5 cm, mostly twice as long as wide or less, base cuneate, apex rounded or with a short broad acumen, with scales (like those on the twigs) usually densely covering the lower leaflet surface and few to numerous on the upper surface, with numerous faint or conspicuous pits on both surfaces, lateral veins 5–10 on each side of midrib, ascending and curved upwards near the margin, anastomosing, midrib prominent and lateral veins subprominent on the lower leaflet surface, reticulation usually not visible (except sometimes in inland specimens and on other specimens with sparse indumentum); petiolules 0.4–2 mm long on lateral leaflets, to 2.5(–4.5) cm long on terminal leaflet. *Flowers* depressed globose, 1.5–2 by c. 2 mm. *Calyx* cup-shaped, divided into 5 rounded lobes, densely covered on the outside with scales (like those on the twigs). *Petals* usually 5, white or yellow, quincuncial, with scales (like those on the twigs) few to numerous on the petals, sometimes with a short-fimbriate margin. *Staminal tube* subglobose, c. 1 by 1.5 mm wide, the aperture 0.6–1 mm diam; anthers 5, broadly ovoid, c. 0.4 by 0.5 mm, inserted half way up the tube, included within or just protruding through the aperture. *Fruits* subglobose, 1–2 by 1.3–1.5 cm, indehiscent;

pericarp red, often wrinkled when dry, with few scales (like those on the twigs), sometimes with a short-fimbriate margin; locules 2, each with 0 or 1 seed. *Seeds* partly or completely surrounded by a gelatinous white or yellow aril.

Distribution — *Aglaia elaeagnoidea* is found in Taiwan, the Philippines, Borneo, Bali, Sulawesi, Maluku, Timor, New Guinea, Australia (Queensland and Western Australia), Melanesia and in the Western Pacific to the Samoan Islands.

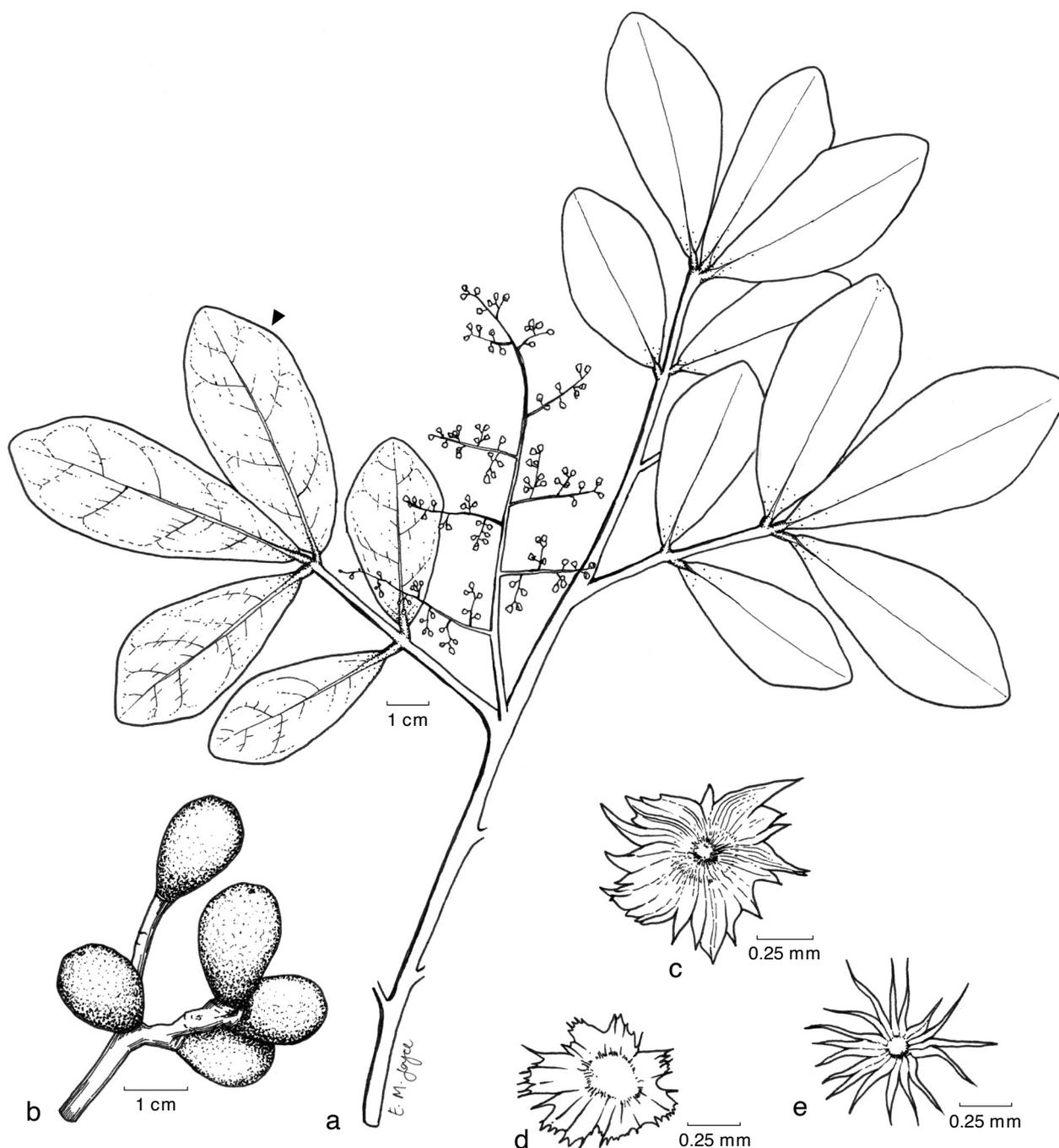
Habitat & Ecology — Grows in coastal rainforest, monsoon forest, strand forest on dunes, shingle ramparts, rocky hillside, semi-deciduous vine forest, vine scrub or wind-swept vine forest, and riparian forest, from sea level to 400 m elevation. Occurs on sandy soils and sand dunes, soils derived from metamorphic rocks, lateritised basalt or basic igneous rocks, basalt flows or red clay over basalt, and alluvia. *Aglaia elaeagnoidea* is usually coastal, but two of four specimens sequenced from the Philippines, and one of two specimens sequenced from Borneo, are from inland localities at 84–133 m elevation. Inland specimens of *A. elaeagnoidea* s.str. sometimes resemble *A. wallichii* in having a distinct drip tip on their leaves. Specimens sequenced from Timor were from inland populations up to 380 m elevation (an additional unsequenced specimen was collected at 400 m). Those sequenced from the Kimberley region of Western Australia were inland at or near sea level.

Note — The large, almost white, peltate scales, and pale brown or coppery scales are conspicuous on the stems and leaves, giving the plant a pale or coppery appearance. The indumentum is more often copper-red in western parts of the range of the species. The outer surfaces of the petals always have some peltate scales. The single decisive diagnostic character that separates *A. elaeagnoidea* s.str. from *A. wallichii* and *A. roxburghiana* is the red fruit with few peltate scales. In the Kimberley (Western Australia), the aril is vestigial, the pericarp has few scales and the fruits are eaten by birds, especially Pied Imperial Pigeons *Ducula bicolor*, which swallow them whole.

### 2. *Aglaia roxburghiana* (Wight & Arn.) Miq. — Fig. 6

- Aglaia roxburghiana* (Wight & Arn.) Miq. (1868) 41, p.p. pro type; non Koorders (1912) 444 (= *A. wallichii*); non Koorders & Valetton (1913) t. 161 (= *A. wallichii*); Hiem (1875) 555, p.p.; C.DC (1878) 604, p.p. — *Milnea roxburghiana* Wight & Arn. (1834) 119. — Lectotype (designated by Pannell 1992): *Herb. Wight 311* (lecto K; isolecto BM, CGE, G, K-W, MO), India.
- Walsura lanceolata* Wall. (1831–1832) n. 4886, nom. nud.]
- [*Aglaia grata* Wall. ex Voigt (1845) 136, nom. nud.]
- [*Aglaia midnaporensis* Carey ex Voigt (1845) 136, nom. nud.]
- [*Sapindus lepidotus* Wall. (1847) n. 8036, nom. nud.]
- Aglaia roxburghiana* (Wight & Arn.) Miq. var. *obtusa* C.DC (1878) 605. — Lectotype (designated by Pannell 1992): *Anon.* in *Thwaites C.P. 1148* (lecto G-DC), Ceylon [Sri Lanka].
- ?*Aglaia littoralis* Talbot (1902) 76, non Miq. (1868) 45 (= *Aglaia lawii*). — Syn-types: *Talbot 2955* (syn BSI), Mysore State (N. Kanara District), Kumpta; *Talbot s.n.* (syn BSI), Mysore State.
- Aglaia roxburghiana* (Wight & Arn.) Miq. var. *beddomei* Gamble (1915) 180; Beddome (1871) 130A. — *Aglaia elaeagnoidea* (A.Juss.) Benth. var. *beddomei* (Gamble) K.K.N.Nair (1981) 426. — Lectotype (designated by Pannell 1992): *Beddome s.n.* (lecto BM), S. India, Tamil Nadu, Annamallays.
- Aglaia roxburghiana* (Wight & Arn.) Miq. var. *courtallensis* Gamble (1915) 180. — *Aglaia elaeagnoidea* (A.Juss.) Benth. var. *courtallensis* (Gamble) K.K.N.Nair (1981) 426. — Type: *Barber 8388* (holo K), S. India, Tamil Nadu, Courtallam, Hills of Tinnevely.
- ?*Aglaia talbotii* Sundararagh. (1969) 184, nom. nov. pro *Aglaia littoralis* Talbot, non Miq. (1868) 45 (= *Aglaia lawii*).
- Aglaia elaeagnoidea* auct. non (A.Juss.) Benth.: Pannell (1992) 148, t. 34 & t. 35, p.p.; Pannell (1995b) 256.

Trees, to 15(–30) m high, with buttresses outwards from the base to 1.5 m and up the bole to 75 cm, tapering into a fluted bole with occasional bosses. *Bark* pale orange-brown or reddish brown, smooth or flaking in scales, exposing the orange-brown bark underneath; inner bark reddish brown or pink. *Twigs*



**Fig. 6** *Aglaia roxburghiana* (Wight & Arn.) Miq. a. Branch with inflorescence, arrow indicating leaf lower surface; b. immature fruit; c. peltate scale; d. peltate scale with fimbriate margin; e. stellate scale (a, c–e: Barber 2551, K; b: Wight 140, NY). — Illustration by E.M. Joyce.

densely covered with orange-brown peltate scales with fimbriate margins. *Leaves* alternate, imparipinnate, 11–23 cm long, 10–23 cm wide; petiole 2.5–5 cm long. *Leaflets* 3–7; lamina elliptical, lanceolate or oblanceolate, 2.5–10(–12.5) by 1–3(–5) cm, usually at least twice as long as wide, base cuneate, apex usually rounded, sometimes acuminate, with an obtuse acumen to 10 mm long, with scales (like those on the twigs) present on the midrib below and scattered on the rest of the lower leaflet surface, with numerous faint or conspicuous pits on both surfaces; lateral veins (5–)6–12 on each side of the midrib (sometimes with shorter laterals in between), subprominent, ascending and curved upwards near the margin, anastomosing, visible and slightly raised; midrib prominent below, subprominent above; reticulation conspicuously visible as darker green than rest of leaflet surface when fresh, slightly raised when dried; petiolules 2–10 mm long. *Flowers* c. 1 mm long, c. 1.5 mm wide, depressed-globose, yellow. *Calyx* cup-shaped, divided into 5

rounded lobes, densely covered on the outside with scales (like those on the twigs), but with longer-fimbriate margins. *Petals* 5, free, quincuncial, without peltate scales on the outer surface. *Staminal tube* obovoid, c. 1 by 1 mm; aperture 0.2–0.5 mm diam; anthers 5, ovoid, 0.3–0.5 by 0.25–0.4 mm, inserted either near the base or about half way up the staminal tube, included within or just protruding through the aperture. *Fruit* obovoid when immature, ellipsoid or subglobose when ripe, 1–2.2 by 1–2.2 cm diam indehiscent; pericarp pale brown, orange or yellow, thin and brittle when dry, densely covered on the outside with scales (like those on the twigs); locules 2, each with 0 or 1 seed. *Seeds* surrounded by a translucent gelatinous aril which is edible and tasty.

*Distribution* — Sri Lanka, India (Western Ghats, West Bengal and Odisha).

*Habitat & Ecology* — Occurs in evergreen forest including coastal dry-zone forests and riverine forests (on beaches and

sand-dunes in Sri Lanka), up to 1500 m in the evergreen forests of the Western Ghats of India and 600 m in West Bengal.

Notes — 1. *Aglaia roxburghiana* is sometimes a larger tree than either *A. wallichii* or *A. elaeagnoidea*. The occasional larger-leaved specimens can be almost indistinguishable morphologically from *A. edulis* unless fruits are present. The fruits of *A. edulis* are larger than those of *A. roxburghiana* and are usually 3-locular; the upper surface of the leaflets of *A. roxburghiana* is slightly shiny when dry and is dull in *A. edulis*.

2. The leaflets of *A. roxburghiana* usually have a rounded (rarely acuminate) apex, while the leaflets of *A. wallichii* are usually acuminate, except for some coastal specimens from West Malesia. The flowers of *A. roxburghiana* usually resemble those of *A. elaeagnoidea* and *A. wallichii*, but sometimes differ in that they have an obovoid rather than subglobose staminal tube with a narrower aperture. Both *A. roxburghiana* and *A. wallichii* differ from *A. elaeagnoidea* in the absence of scales on the

outer surface of the petals (on nearly all specimens). The scales on the inflorescence and fruits of *A. roxburghiana* have longer fimbriate margins than in either *A. elaeagnoidea* or *A. wallichii*.

3. The fruits of *A. roxburghiana* and *A. wallichii* have an inedible pericarp, densely covered with orange-brown scales. Seed dispersal differs from that of *A. elaeagnoidea*; primates remove the pericarp and consume the seeds, digesting the gelatinous aril and either spitting out or voiding the cleaned seeds in their faeces.

### 3. *Aglaia wallichii* Hiern — Fig. 7

*Aglaia wallichii* Hiern (1875) 555; C.DC (1878) 606. — Lectotype (designated by Pannell 1992): *Anonymous in Herbarium East India Company 8036* (lecto K-W; isolecto BM, FI, K), Bangladesh, Sylhet [Silhet].

*Aglaia roxburghiana* (Wight & Arn.) Miq. var. *angustata* Miq. (1868) 42. — Lectotype (designated by Pannell 1992): *Teymann s.n.* (lecto U barcode U0004212; isolecto BO, L, U barcode U0004213), Java, Japura Province, Pulau Kellor.

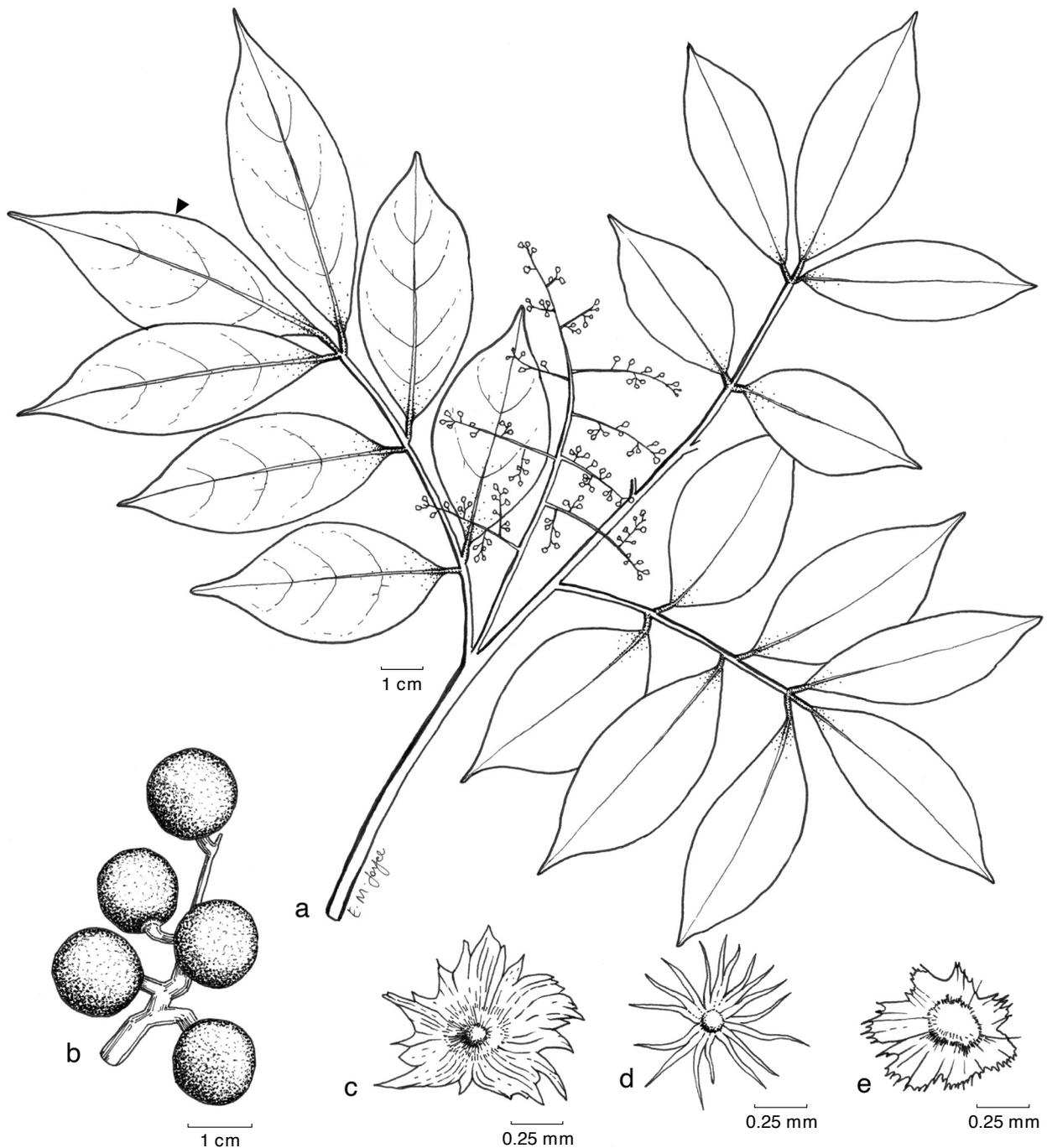


Fig. 7 *Aglaia wallichii* Hiern. a. Branch with inflorescence, with arrow indicating leaf lower surface; b. mature fruit; c. peltate scale; d. stellate scale; e. peltate scale with fimbriate margin (a, c–e: *Murata et al.* T-37072; b: *Petmitr* 516, all A). — Illustration by E.M. Joyce.

*Aglai* *roxburghiana* (Wight & Arn.) Miq. var. *balica* Miq. (1868) 42. — Lectotype (designated by Pannell 1992): *Anonymous s.n.* (lecto U; isolecto L), Bali.

*Aglai* *wallichii* Hiern var. *brachystachya* C.DC (1878) 606. — Type: *Griffith 1045* (holo K).

*Aglai* *hoanensis* Pierre (1895) ante t. 336. — Lectotype (designated by Pannell 1992): *Pierre 2779* (lecto P; isolecto BM, K), S. Vietnam, Bien Hoa province, Sept. 1869.

*Aglai* *poulocondorensis* Pellegr. (1910) 290. — *Amoora poulocondorensis* (Pellegr.) Harms (1940) 128, 176. — Lectotype (designated by Pannell 1992): *Harmand 748* (lecto P), S. Vietnam, Iles de Poulo-Condor.

*Aglai* *poilanei* Pellegr. (1944) 179. — Type: *Poilane 16713* (holo P), Vietnam, Annam, Bu Khang, Province de Vinh.

*Aglai* *abbreviata* C.Y.Wu (1977) 240. — Type: *P.I. Mao 3262* (holo KUN), China, Yunnan, Pingbian.

*Aglai* *roxburghiana* auct. non ((Wight & Arn.) Miq.: Kurz (1875) 147; Miq. (1868) 41, p.p.; C.DC. (1878) 604, p.p.; Koord. & Valetton (1913) t. 161.

*Aglai* *elaeanoidea* auct. non (A.Juss.) Benth.: Backer & Bakh.f. (1965); 128; Pannell (1992) 148, f. 34 & 35 p.p.; (1995a) 243, p.p.; H.Peng & Pannell (2008) 123; Pannell (2013a) 78, f. 5; S.Gardner et al. (2016) 1231, f. 1612.

Small trees or shrubs, 5–12(–20) m tall, fluted at the base, sometimes with small buttresses. *Bark* brown, greyish brown, reddish brown or yellowish grey, with narrow vertical fissures, flaking in thin, irregular, stiff, scroll-like scales; inner bark pink or reddish brown; sapwood white or yellow; heartwood red. *Twigs* grey or pale brown, densely covered with very pale brown or pale orange-brown peltate scales with entire or shortly fimbriate margins. *Leaves* alternate, imparipinnate, 6–22 by 12–24 cm; petiole 2.5–5.5 cm long. *Leaflets* (3–)5–7, subcoriaceous; lamina elliptical, sometimes obovate, (1–)2–10(–13) by 1–3.5(–4) cm, usually at least twice as long as wide, base cuneate, apex acuminate with an acumen 10(–20) mm long, the lower surface densely covered with scales (like those on the twigs) on the midrib and sparsely so elsewhere, with numerous faint or conspicuous pits on both surfaces; lateral veins 5–11 on each side of the midrib, prominent below; lateral veins subprominent on both surfaces; intercostal venation usually subprominent on both surfaces; petiolules 0.5–2 cm long. *Flowers* 1.25–2 by 1.25–3 mm wide, subglobose or depressed-globose. *Calyx* shallowly divided into 5 broadly ovate obtuse lobes, densely covered on the outside with orange-brown peltate scales with long-fimbriate margins. *Petals* usually 5, free, quincuncial, yellow, without scales on the exposed outer surface (except in coastal specimens from Java and adjacent islands with very pale brown peltate scales). *Staminal tube* depressed-globose or ovoid, c. 1 by 1–1.4 mm, with an aperture c. 0.5 mm diam; anthers 5, ovoid, 0.3–0.5 by 0.25–0.4 mm, inserted half way up the tube and just protruding through the aperture. *Fruits* subglobose, ellipsoid or obovoid when young, subglobose when ripe, 1.1–2.5 by 1.3–2.0 cm, indehiscent; pericarp pale yellow, orange or brown, thin and brittle when dry, densely covered on the outside with orange-brown peltate scales with long-fimbriate margins; locules 2, each with 0 or 1 seed. *Seeds* completely covered with a thin, white, gelatinous, sweet aril.

**Distribution** — Widespread in Myanmar, China, Thailand, Cambodia, Laos, Vietnam, Peninsular Malaysia, Java and Bali (and therefore confined to the west of Wallace's Line). Historically in Bangladesh (including the type locality), though now considered extinct there.

**Habitat & Ecology** — *Aglai* *wallichii* is usually found inland, at elevations to 1400 m, in dry evergreen or deciduous forest, including on limestone and granite. In Java and its offshore islands, however, it occurs on the coast, where it resembles *A. elaeagnoidea* in morphology. Primates remove the pericarp and consume the seeds. They digest the gelatinous aril that adheres firmly to the seed and either spit out the cleaned seeds or void them in their faeces.

**Note** — The twigs, petioles, rachises, petiolules, inflorescence and infructescence peduncles, branches and pedicels of *A. rox-*

*burghiana* and *A. wallichii* are more slender than those in *A. elaeagnoidea*. The leaflets of *A. roxburghiana* and *A. wallichii* are mostly more than twice as long as wide. The indumentum is sparse on the leaflets of *A. roxburghiana* and *A. wallichii* and the pits on the leaflet surfaces are less conspicuous than in *A. elaeagnoidea* (except in coastal specimens from Java and adjacent islands, where the indumentum structure and distribution on the leaves and flowers resembles *A. elaeagnoidea*). Coastal specimens of *A. wallichii* sometimes resemble *A. elaeagnoidea* in having leaves with short, broad, rounded apices, rather than having a drip tip, and an indumentum on the exposed surfaces of the petals. Leaflets in *A. wallichii* are less coriaceous than in *A. elaeagnoidea*, and the reticulation is more visible (except in coastal specimens from Java and adjacent islands).

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