



Taxonomic revision of *Murraya J. Koenig* (Rutaceae) based on the molecular phylogeny and morphological characters

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ABSTRACT: Two sections of the genus *Murraya J. Koenig* were generic rather than sectional. *Murraya s.s.* was comprehensively revised based on the molecular phylogeny and morphological data. In addition, systematic relationship about all species of *Murraya s.s.* and an identification key of species, morphological description, images of useful distinguishing characters from fields and laboratory, were provided. As a result, eight species of *Murraya s.s.* belonging formerly to *M. sect. Murraya* are identified and revised except *M. alternans*. One new combination, *Murraya zollingeri* (Tanaka) F. J. Mou is proposed here. The lectotype of three names and the neotype of two names were designated here.

KEY WORDS: Molecular phylogeny, morphological character, *Murraya*, taxonomic revision.

INTRODUCTION

The genus *Murraya J. Koenig* (named *Murraea*) was first published based on *Murraya exotica* L. (named *Murraea exotica*) while the genus *Berbera J. Koenig* based on *Berbera koenigii* L. (Linnaeus, 1771). Then, *B. koenigii* was incorporated into *Murraya* by Sprengel in 1825. All species of the genus was morphologically divided into two sections (Tanaka, 1929; But *et al.*, 1986; Huang, 1997). According to a combination of several morphological characters, Tanaka (1929) first divided the genus *Murraya* (named *Chalcas*) into two groups, namely sect. *Euchalcas* having cymes with a few large flowers and filiform filaments and sect. *Berbera* having cymes with many small flowers and dilated filaments. But *et al.* (1986) proposed that eight species of this genus in China can also be divided into two sections, namely sect. *Murraya* (sect. *Euchalcas* of Tanaka) and sect. *Berbera*, differing from each other on morphology. Generally, plants of *Murraya* are characterized with the straw to light greyish yellow stem, old branches and root bark, leaflets distributing with oil glands, larger petals (1–2 cm long), red and ellipsoid fruits, and hard testa covered with greyish hairs, while those of sect. *Berbera* have dark brown stems and root bark, in and at margin of leaflets with oil glands, smaller petals (4–7 mm long), purplish black or red globular to ellipsoid fruits, and membranous and glabrous testa (But *et al.*, 1986; Huang, 1997; Zhang *et al.*, 2010). This dichotomy was also supported by the phytochemical data (But *et al.*, 1986, 1988; Kong *et al.*, 1986; Li *et al.*, 1988) and was justified by the noticeable difference of secondary metabolites with 3-prenylindoles in sect. *Murraya* and carbazoles in sect. *Berbera* (Kinoshita, 2014).

The genus *Murraya s.l.* is not a natural group, in which sect. *Murraya* is much closer to *Merrillia* in the tribe Citreae, while sect. *Berbera* is a sister to the genus *Micromelum* (Kong *et al.*, 1986, 1988a, 1988b) or *Clausena* (But *et al.*, 1988; Samuel *et al.*, 2001; Kinoshita, 2014) in that carbazoles was found in both genera. This conclusion is also supported by the cytological characters (Guerra *et al.*, 2000), palynological morphology (Mou and Zhang, 2009), and molecular phylogenetic evidences (Samuel *et al.*, 2001; Bayer *et al.*, 2009; Morton, 2009; Mou *et al.*, 2018). It was suggested that the dichotomy of *Murraya s.l.* should be generic rather than sectional (Kinoshita, 2014; Mou *et al.*, 2018). Based on results of molecular phylogenetic analysis, *Murraya s.s.* is monophyletic and closer to *Merrillia* (Mou *et al.*, 2018; Nguyen *et al.*, 2019). The genus *Murraya s.s.* now comprises a handful of species native to the Indopacific (Mabberley, 2013) and in need of a modern revision (Mabberley, 2016a). In this paper, the genus *Murraya s.s.* is revised based on the morphological and phylogenetic evidences.

MATERIALS AND METHODS

Molecular phylogeny

Taxon sampling

All sampled species in molecular phylogeny belong to the genus *Murraya* from China, Timor island, Australia and Sri Lanka, along with a species of *Merrillia*. One species *Murraya elongata* has multiple accessions sampled from different populations due to the marked morphological differences. Two species, *Poncirus polyandra* and *Citrus medica* of the tribe Citreae were selected as the out-groups based on the new phylogeny of

**Table 1.** Voucher information of *Citrus*, *Murraya* and *Poncirus* species in phylogenetic studies.

Taxon	Vouchers	Location
<i>Citrus medica</i>	F.J. Mou 589, SWFC	Kunming World Horti-Expo Garden, Kunming, Yunnan, China (cultivated)
<i>Murraya alata</i>	F.J. Mou 523, SWFC	South China Botanical Garden, Guangzhou, Guangdong, China (cultivated from Hainan)
<i>Murraya elongata</i>	F.J. Mou 448, SWFC	Mengla, Yunnan, China (YNML)
<i>Murraya elongata</i>	F.J. Mou 498, SWFC	Napo, Guangxi, China (GXNP)
<i>Murraya elongata</i>	F.J. Mou 507, SWFC	Longlin, Guangxi, China (GXLL)
<i>Murraya elongata</i>	F.J. Mou 524, SWFC	South China Botanical Garden, Guangzhou, Guangdong, China (cultivated) (SCBG)
<i>Murraya elongata</i>	F.J. Mou 542, SWFC	Libo, Guizhou, China (GZLB)
<i>Murraya elongata</i>	F.J. Mou 557, SWFC	Mengzi, Yunnan, China (GZMZ)
<i>Murraya elongata</i>	F.J. Mou 570, SWFC	Simao, Yunnan, China (YNSM)
<i>Murraya elongata</i>	T.Y. Tu 4474, IBSC	Wanning, Hainan, China (HNWN)
<i>Murraya lucida</i>	F.J. Mou 572, SWFC	Queensland, Australia
<i>Murraya omphalocarpa</i>	F.J. Mou 574, SWFC	Xishuangbanna Tropical Botanical Garden, Mengla, Yunnan (cultivated from Taiwan)
<i>Murraya paniculata</i>	F.J. Mou 592, SWFC	Guangxi Botanical Garden of Medical Plants, Nanning, Guangxi, China
<i>Murraya sumatrana</i>	F.J. Mou 611, SWFC	Dongfang, Hainan, China (HNDF)
<i>Murraya zollingeri</i>	F.J. Mou 571, SWFC	Timor Island
<i>Poncirus polyandra</i>	F.J. Mou 575, SWFC	Kunming World Horti-Expo Garden, Kunming, Yunnan, China (cultivated)

Table 2. The sequence of all primers in phylogenetic studies

Sequences Name	Primer name	Primer Sequence	Annealing temperature	Conferences
ITS	ITS4	5'- TCCTCCGCTTATTGATATGC -3'	55°C	White <i>et al.</i> , 1990
	ITS5	5'-GGAAGTAAAAGTCGTAACAAGG -3'		
<i>trnL-F</i>	A50272	5'- ATTGAACTGGTGACACGAG -3'	53°C	Taberlet <i>et al.</i> , 1991
	B49317	5'- CGAAATCGGTAGACGCTACG -3'		
<i>atpB-rbcL</i>	Oligo2	5'- TACAGTTGTCCATGT ACCAG -3'	54°C	Manen <i>et al.</i> , 1994
	Oligo5	5'- GAAGTAGTAGGATTGATTCTC -3'		
<i>rbcL</i>	1F	5'- ATGTCACCACAAACAGAAAC -3'	54°C	Kress and Erickson, 2007
	724r	5'- TCGCATGTACCTGCAGTAGC -3'		
<i>matK</i>	matK1F	5'-ACCGTATCGCACTATGTATC -3'	53°C	Penjor <i>et al.</i> , 2013
	matK1R	5'-GAACTAGTCGGATGGAGTAG -3'		
<i>psbH-petB</i>	7L	5'-ATGTTGACATGAGGAGGAAC -3'	54°C	Reverdatto <i>et al.</i> , 1989
	7U	5'-GGCTACACAAACCGTTGAAG -3'		
<i>psbA-trnH</i>	psbAF	5'-GTTATGCATGAACGTAATGCTC -3'	58°C	Sang <i>et al.</i> , 1997
	trnHR	5'-CGCGCATGGTGGATTACAAATC -3'		

the tribe Clauseneae (Mou *et al.*, 2018). In addition to *Murraya gleniewii* and *Merrillia caloxylon* downloaded from GenBank, the data set contains 18 accessions of 10 species totally. A full list of taxa and vouchers are provided in Table 1.

DNA extraction, amplification and sequencing

Total DNA was isolated from fresh leaves or silica-dried leaves collected in the field ground in liquid nitrogen using the modified CTAB method (Doyle and Doyle, 1987). The primers for amplification are listed in Table 2. The PCR amplification was performed using a 5 min denaturing step at 95 °C followed by 38–40 cycles of denaturing for 1.0–1.5 min at 95 °C, primer annealing for 1.0–1.5 min at 53–58 °C, and elongation for 1.5 min at 72 °C, with a final 8 min elongation step at 72 °C. The PCR products were subjected to electrophoresis in 1.2 % agarose gels. The PCR products and the PCR primers were used for cycle sequencing reactions with BigDye 3.1 in 10 µl volumes. Cycle sequencing conditions started at 96°C for 1 min, followed by 30 cycles of 96 °C for 10 sec, 50 °C for 5 sec, 60 °C for 2 min, and a final extension of 60 °C for 2 min. Sequencing was run in an ABI 3730XL automated sequencer (Applied Biosystems, Foster City,

California) at Tsingke Biological Technology (Kunming). A full list of taxa GenBank accessions in Table 3.

Data analysis

Sequences analyzed in this study were almost generated anew and all sequences of *Merrillia caloxylon* obtained from GenBank, ITS (FJ434149), *trnL-F* (AY295296), *atpB-rbcL* (AF320871), *rbcL* (AB505907), *matK* (AB762388) (Samuel *et al.*, 2001; Bayer *et al.*, 2009; Morton, 2009).

Base confirmation and editing of raw sequences were performed using Sequencher 4.9 (Gene Codes Corp., Ann Arbor, MI, USA). Confirmed sequences were initially aligned and adjusted manually with MEGA 7.0.21 (Kumar *et al.*, 2016). Some accessions are relatively incomplete and have extensive missing data due to the fact that sequencing was not successful for some fragments using the available herbarium specimens, or sequences were not available GenBank for all the seven DNA regions in some OTUs. Those data failed in sequencing program were encoded as missing data in the matrix. An ILD test (Farris *et al.*, 1995) was conducted before ITS and six cpDNA sequences were combined.

Seven fragments of 18 samples (15 samples of the

**Table 3.** GeneBank accession numbers, including previously published sequences in phylogenetic studies

Taxon	ITS	<i>trnL-F</i>	<i>atpB-rbcL</i>	<i>rbcL</i>	<i>matK</i>	<i>psbH-petB</i>	<i>psbA-trnH</i>
<i>Citrus medica</i> 589	MZ824496	MZ824512	MZ824528	MZ824544	MZ824573	MZ824558	MZ824589
<i>Merrillia caloxylon</i>	FJ434149	AY295296	AF320871	AB505907	AB762388	-	-
<i>Murraya alata</i> 523	MZ824483	MZ824498	MZ824514	MZ824530	MZ824560	MZ824546	MZ824575
<i>M. elongata</i> 448-YNML	MZ824484	MZ824499	MZ824515	MZ824531	MZ824561	-	MZ824576
<i>M. elongata</i> 498-GXNP	MZ824485	MZ824500	MZ824516	MZ824532	MZ824562	MZ824547	MZ824577
<i>M. elongata</i> 507-GXLL	MZ824486	MZ824501	MZ824517	MZ824533	MZ824563	MZ824548	MZ824578
<i>M. elongata</i> 524-SCBG	MZ824487	MZ824502	MZ824518	MZ824534	MZ824564	MZ824549	MZ824579
<i>M. elongata</i> 542-GZLB	MZ824488	MZ824503	MZ824519	MZ824535	MZ824565	MZ824550	MZ824580
<i>M. elongata</i> 557-YNMZ	MZ824489	MZ824504	MZ824520	MZ824536	MZ824566	MZ824551	MZ824581
<i>M. elongata</i> 570-YNM	MZ824490	MZ824505	MZ824521	MZ824537	MZ824567	MZ824552	MZ824582
<i>M. elongata</i> 4474-HNWN	MZ824491	MZ824506	MZ824522	MZ824538	MZ824568	MZ824553	MZ824583
<i>M. gleniei</i>	-	-	AF320869	-	-	-	-
<i>M. lucida</i> 572	MZ824492	MZ824507	MZ824523	MZ824539	MZ824569	MZ824554	MZ824584
<i>M. omphalocarpa</i> 574	MZ824493	MZ824508	MZ824524	MZ824540	MZ824570	MZ824555	MZ824585
<i>M. paniculata</i> 592	MZ824494	MZ824509	MZ824525	MZ824541	MZ824571	MZ824556	MZ824586
<i>M. sumatrana</i> 611-HNDF	MZ824495	MZ824510	MZ824526	MZ824542	MZ824572	MZ824557	MZ824587
<i>M. zollingeri</i> 571	-	MZ824511	MZ824527	MZ824543	-	-	MZ824588
<i>Poncirus polyandra</i> 575	MZ824497	MZ824513	MZ824529	MZ824545	MZ824574	MZ824559	MZ824590

genus *Murraya*, one of *Merrillia* and two samples of outgroups) were linearly connected separately using the program MEGA 7.0.21. Those data failed in sequencing program were encoded as missing data in the matrix. Bayesian inference (BI) and Maximum likelihood (ML) methods were used to reconstruct the phylogenetic trees based on data matrices containing the combination of ITS and cpDNA sequences, using MrBayes v3.2.7 (Ronquist *et al.*, 2012) and PhyML 3.0 (Guindon *et al.*, 2010), respectively. For BI analysis, two independent Markov Chain Monte Carlo (MCMC) runs were conducted simultaneously, each with four linked chains, for 1,000,000 generations, sampling one tree every 100 generations, and starting with a random tree. PhyML analysis was conducted with the GTR substitution model, executing 1000 rapid bootstrap inferences before a thorough ML search.

Morphology

The relevant literatures concerning the genus *Murraya* were carefully reviewed. Plant materials for this study were collected from Yunnan, Guangxi, Guizhou, Guangdong, Hainan provinces in China and Australia during fieldworks from 2014 to 2020. At the same time, the specimens deposited in KUN, IBSC, IBK, HITBC, SYS, CANT, SWFC, YUKU, GXMI, GXMG herbaria and the digital specimens from PE, NAS, TAI, K, P, E, BM, L, U, WAG, GDC, GOET, US, GH, ECON, NY, TNS, FR, and MEL herbaria were examined. Almost all type specimens were checked. Additionally, all specimens previously collected from China and neighboring countries were checked according to the relevant literature (Tanaka, 1928, 1929; Swingle and Reece, 1967; Huang, 1959, 1997; Zhang *et al.*, 2010). In addition, the specimens collected during the study were deposited in IBSC (Herbarium, South China Botanical

Garden) and SWFC (Herbarium, Southwest Forestry University). Morphological features were obtained and photographed in field and laboratory studies, such as paraffin section of ovary.

RESULTS

Molecular phylogeny

Using BI and ML methods, all accessions of *Murraya* species form a separate branch related to the genus *Merrillia* (PP=1, BS=100%) and consists of three groups, based on the combination data of ITS and six cpDNA fragments, including *trnL-F*, *atpB-rbcL*, *rbcL*, *matK*, *psbH-petB* and *psbA-trnH* (Fig. 1). The clade A comprising four species, *M. zollingeri*, *M. omphalocarpa*, *M. lucida*, and *M. gleniei* is a sister to cluster consisting of other accessions (PP=1, BS=99.6%). The clade B consists of all accessions of *M. elongata* from mainland of China (PP=0.71), Accessions of *M. elongata* from Yunnan, Napo in Guangxi are separated from these from Longling in Guangxi, Guizhou, Guangdong and Wanning in Hainan. The clade C includes *M. alata*, *M. paniculata*, and an accession of *M. sumatrana* from Dongfang County in Hainan Province (PP=1, BS=78.0%).

Morphology

For the species *Murraya elongata*, the leaflets are much longer and more lanceolate and fruits are 1.5 cm long and narrowly ellipsoid; plants from different localities varies on many morphological characters (Fig. 2C-F). The typical plants have the thinner leaflets and oval fruits (Fig. 2C-E), but the plants from Mengzi, Yunnan Province (China) have smaller oval leaflets which looks like *M. lucida* from Queensland in Australia (Fig. 2E). The plants of *M. sumatrana* growing in limestone of Dongfang County, Hainan Island (China)

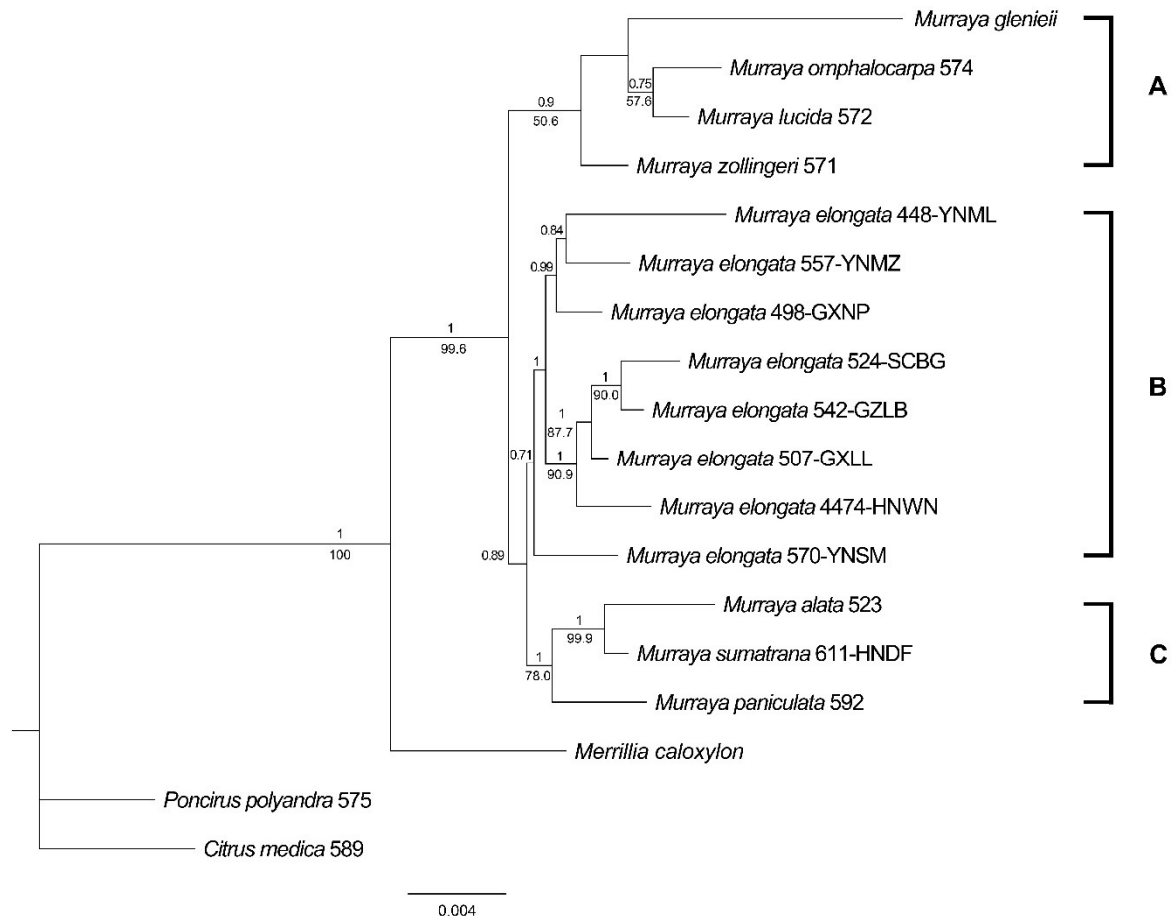


Fig. 1. Bayesian tree based on nuclear of ITS and plastid data of some representatives of the genus *Murraya*, along with *Merrillia caloxylon*, and *Poncirus polyandra* and *Citrus medica* as out-groups. Branch lengths are proportional to the number of nucleotide changes. Bayesian posterior probabilities (PP) above the branches and bootstrap support (BS, %) values for maximum likelihood (ML) analysis below the branches are given, respectively.

have the thicker leaflets and fruits with tip (Fig. 2Q). The species *M. paniculata* has the obovate leaflets, as well as more flowers and fruits with sparse and big oil glands (Fig. 2N-P). *M. omphalocarpa* differs others species by the large broad leaflets, larger flowers and berries with attenuate tip and dense and big oil glands on the pericarp (Fig. 2J-M). *M. lucida* is characterized by broadly oval or ovate leaflets with more numerous and larger oil-dots and often decidedly hirsute and tomentose and the twigs, calyx, petals, and ovary are hirsute (Fig. 2G-I). *M. zollingeri* has the declined rachis, smaller and thinner leaflets with revolute margin, and globose fruits covered with white hairs (Fig. 2R-T). *M. alata* has obvious wings at both sides of rachises, smaller leaflets and smooth berries (Fig. 2A-B), as well as flowers with different odor compared with other species.

TAXONOMIC TREATMENT

Murraya J. Koenig, Linnaeus, Mant. Pl. Altera 2: 554-555, 563 (1771) (as '*Murraea*', nom. et orth. cons.).

Type species: *Murraya exotica* L.

≡ *Chalcas* L., Mant. Pl. 1: 68. 1767, et Syst. Nat. 2: 293. 1767.

≡ *Marsana* Sonn., Voy. Indes Orient. (Sonnerat) 2: 245, et 3: 282. 1782.

Unarmed trees. Stem bark whitish to greyish yellow. Leaves odd-pinnate, alternate. Cymes few-flowered, either axillary or terminal; flower buds cylindrical or long-ovoid; flowers rather large, 5-merous. Calyx 5, ovate or lanceolate; sepals united at the base or only in the lower third. Petals 5, rather large, lanceolate or linear, imbricate. Stamens 10, alternately shorter, free, elongate, filaments filiform, anthers small, broadly elliptic or oval. Disk annular, cushion-shaped or cylindrical, short. Ovary ovoid, with 2 or 4-5 locules, each with 2 or 1 superimposed or almost collateral ovules; style rather long and slender, finally falling off, stigma capitate. Berry small, ovoid or subglobose, with mucilaginous pulp. Seeds medium-sized, testa hard and villous, cotyledons plano-convex with oil glands.

Distribution, habitat, and species

The genus *Murraya* is endemic to south and eastern mainland in Asia (India, Andaman Islands, Indo-China Peninsula, Southern China, Malay Peninsula, Indonesian Archipelago, Philippines), New Guinea, New Caledonia, to Northeastern Australia.

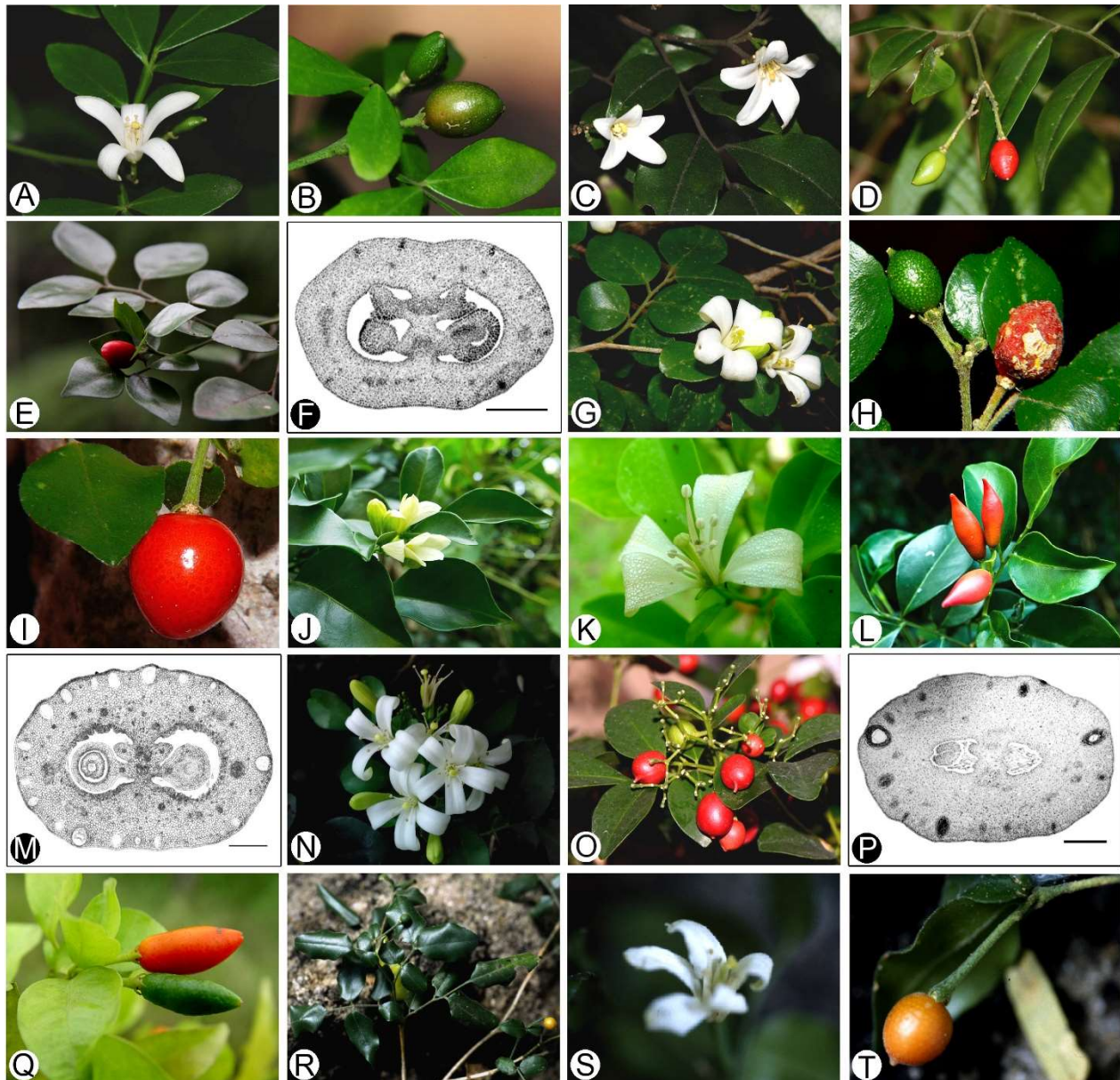


Fig. 2. General leaves, flowers, ovary and fruits of *Murraya*: A-B. *M. alata*, C-F. *M. elongata*, G-I. *M. lucida*, J-M. *M. omphalocarpa*, N-P. *M. paniculata*, Q. *M. sumatrana*, R-T. *M. zollingeri*

This genus includes all species previously in *Murraya* sect. *Murraya* except *M. alternans* (Kurz) Swingle. Although this species was included in *Murraya* sect. *Murraya* based on the incomplete morphological and phytochemical data (But *et al.*, 1986), our study found that it should be one species in *Murraya* sect. *Bergera* (namely the genus *Bergera*) based on the dark brown stems and root bark, cymes with many small flowers, and the leaves and branches getting little brown after dried under shady and well ventilated area. Most *Murraya* species have a ovary with 2 locules (Fig. 2F, M, P) except a prominent species *M. gleniei* with 4–5 locules. According to the morphological, biochemical, and DNA data, the genus *Murraya* is much closer to *Merrillia* and

the tribe Citreae (Kong *et al.*, 1986, 1988a,b; Samuel *et al.*, 2001; Mou *et al.*, 2018; Nguyen *et al.*, 2019). Two genera *Murraya* and *Merrillia* originated in Sundaland and the former diverged from the latter during the Miocene (23–5 Ma) with the *Murraya* speciating and dispersing during the Middle Miocene onwards (Nguyen *et al.*, 2019).

Key to the species of *Murraya*

- 1a. Leaf rachises not winged 2
- 1b. Leaf rachises winged *M. alata*
- 2a. Fruits not lobed or angled 3
- 2b. Fruits 4- or 5-lobed or bluntly 4- or 5-angled, flat-topped . *M. gleniei*
- 3a. Fruits covered with hairs 4
- 3b. Fruits glabrous 5



- 4a. Leaflets oblique, undulate and revolute; fruits orange .. *M. zollingeri*
 4b. Leaflets ovate to broadly ovate, flat; fruits red *M. lucida*
 5a. Leaflets thin, papyraceous, fruits without rostrate6
 5b. Leaflets thick, thin coriaceous, blades 0.5–3.0 cm wide; fruits with
 rostrate *M. omphalocarpa*
 6a. Leaflets lanceolata or ovate, acuminate or obtuse; fruits ovoid or
 apiculate 7
 6b. Leaflets elliptic-obovate or obovate; fruits ovoid *M. paniculata*
 7a. Leaflets ovate *M. sumatrana*
 7b. Leaflets lanceolate *M. elongata*

Murraya alata Drake, Morot, J. Bot. 6(15/16): 276. 1892.

Fig. 2A–B

Type: VIET NAM (French Indo-China), Hanoi (Tonkin), Tan-keuin, *B. Balansa 1118* (lectotype: P MNHN-P-P05185441 image!; isolecotype: K K000736099 image!, US 01108293 image!); VIET NAM, Hanoi, Tan-keuin, *B. Balansa 1119* (syntype: P MNHN-P-P05185446 image!, G G00096632, G00087526 image!, US 01108293 image!).

≡ *Chalcas alata* (Drake) Tanaka, Bull. Soc. Bot. Fr. 75: 711. 1928.

≡ *Murraya alata* Drake var. *hainanensis* Swing., J. Wash. Acad. Sci. 32: 26. 1942. Type: CHINA, Hainan, *F. A. McClure 7611* (holotype: A, isotype: BARC).

Shrubs, 1–3 m high. Branches glabrous, bark yellowish gray to grayish white. Leaves 5–9-foliolate, up to 10 cm long; rachis narrowly winged; petiolules short or leaflets sessile; leaflet blades obovate to obovate-elliptic, 1–3 × 0.6–1.5 cm, margin entire or crenulate, apex rounded or rarely obtuse. Cymes, axillary, 2–3 cm long, pedicels 9 mm long, few-flowered, puberulous; flowers 5-merous. Sepals 1.5–2.0 mm long, pubescent; petals oblong, glabrous, white, 10–15 × 3–5 mm, with parallel veins. Stamens 10, filaments linear, glabrous, the 5 longest a little shorter than the petals, and reaching to the stigma; anthers very small. Ovary glabrous, 2-loculed, each with a single ovule; style subulate, ca. 2 × as long as ovary; stigma capitate. Berry vermilion when ripe, long ovoid to globose, ca. 1 cm in diam., 1–2-seeded. Seed testa parchment-like, yellowish-brown, villous with brown hairs; embryo single-straight with fleshy plano-convex cotyledons.

Distribution: Viet Nam (Tonkin: Tan-keuin, Kien-khé, and Bac-bat), China (southern Hainan, southwest Guangdong: Leizhou Peninsula, southwest Guangxi: Beihai).

Ecology and phenology: The species is usually found in the thickets along the beaches or in the forests from sea level to alt. 1 300 m, or in limestone. Flowering May to July; fruiting October to June.

Note: Besides the alate rachis, the narrow calyx lobes and shallow disk ring quite conspicuous when fruiting, are characteristic features of *Murraya alata*. The wing of the rachis is sometimes very conspicuous, but is often reduced into a slight degree in certain specimens; the cymes have few flowers, the calyx lobes of are pubescent, the staminal filaments are glabrous. The species is very close to *M. paniculata* in having similar texture of the

leaflets. Based on DNA data, *M. alata* is closely group with accessions of *M. paniculata* and *M. elongata* in accordance with the results of Nguyen *et al.* (2019), but this study found that *M. alata* is closer to *M. sumatrana* than *M. paniculata*.

Conservation: *Murraya alata* is a highly range restricted species, known only from northern Viet Nam to southwest Guangdong and Hainan Island in China. Most plants grow in sand-land near the sea line, where ecological environment is very fragile. Due to the ornamental plant and medicinal efficacy, the plants in the wild have been collected in large quantities. It's urgent to resolve the resources depletion by further studies about the low natural reproduction rate.

(All examined specimen list in supplementary)



Fig. 3. A. Holotype of *Murraya elongata* (K001132323) and **B.** Neotype of *M. sumatrana* (K001123696).

Murraya elongata A. DC. ex Hook. f., Fl. Brit. India [J. D. Hooker] 1(3): 503. 1875.

Fig. 2C–F & 3A

Type: MYANMAR, Ava, Taong-dong (Thandaung). *s. coll. Cat. no. 6369* (holotype: K K001132323, image!). (Fig. 3A).

The slender branches pale-yellow. Leaves pinnately 4–6-foliolate, glabrous; petiole with rachis 7.5 cm long, angular; leaflets coriaceous, shining, ovate or elliptically lanceolate, 5–10 cm long, bluntish and notchedly obtusely caudate-acuminate, or acuminate, pale bright-brown in a dried state. Cymes close, few-flowered. Fruits 1.5–2.0 cm long, oval or narrowly ellipsoid.

Distribution: From Pakistan through India (including the Andaman Islands), Myanmar, Thailand, peninsular Malaysia (including the Langkawi islands), Laos, Viet Nam to southern China.

Ecology and phenology: Limestone hills and rocky terrains.

Note: The species *Murraya elongata* is associated with limestone (Karst) hills and rocky terrains from Pakistan through India (including the Andaman Islands),



Myanmar, Thailand, Laos, Việt Nam to southern China, and peninsular Malaysia (including the Langkawi islands) (Nguyen *et al.*, 2019). All accessions of this species from mainland of China have a closer relationship with another cluster consisting of *M. alata*, *M. paniculata*, and *M. sumatrana*. An oval and very small leaf variant from Mengzi, Yunnan (China) falls in the *M. elongata* clade although it is morphologically similar to *M. lucida* from Queensland (Australia). It is a very different species, such as pale-yellow bark on the slender branches, rachis 7.5 cm long, angular; leaflets pale bright-brown when dry, much longer and more lanceolate than *M. paniculata*, fruits 1.5 cm long, narrowly ellipsoid. It is distributed widely, and varies on many morphological characters, such as shrubs to small trees, leaflets size, as well as fruits shape and size. This species are usually confused with *M. paniculata*, but widest of leaflets of the former is at the lower part while that of the latter is at the upper part.

(All examined specimen list in supplementary)

Murraya gleniei Thwaites ex Oliv., J. Proc. Linn. Soc. Bot. 5(supple 2): 29, plate 22. 1861.

Fig. 4

Type: SRI LANKA (Ceylon), Trincomalee, April 1860, *S.O. Glenie s.n.* (lectotype: K K000382452, image!; syntype: K K000382451, image!, G G00096634, image!).

≡ *Murraya exotica* var. *glenieii* (Thwaites ex Thwaites) Hook., Die Nat. Pflanzenfam. 3(4): 188. 1896.

= *Chalcas gleniei* (Thwaites ex Oliv.) Tanaka, Bul. Soc. Bot. Fr. 75: 710. 1928.

Shrubs. Much branched, bark very white, young twigs strongly pubescent. Leaves pinnate, 3.8–10.0 cm long; rachis strongly pubescent, leaflets 3–7, upper ones much the longest, rhomboid-lanceolate, obtuse, emarginate, lower ones rotundate, all slightly crenate, glabrous, margin reflexed slightly. Cymes axillary and terminal, short; flowers 13–19 mm in diam., ca 3–7; pedicels very pubescent. Sepals very small, densely tomentose; petals 13 mm long. Ovary on a distinct cylindrical stalk, 4- or 5-lobed, 4- or 5-celled. Berry orange, inflated star-shaped, large, 1 cm in diam., somewhat pyriform or urn-shaped, flat-topped, but mammillate in centre, 4- or 5-lobed or bluntly 5-angled, rough with large glands, shining green, 5- or 4-celled, the large inflated cell; 1–3-seeded. Seeds globose, green.

Distribution: Only endemic to Sri Lank.

Ecology: The species was found in thickets and forests of dry areas at lower altitudes.

Note: *Murraya gleniei* is a very distinct species by its peculiar 5-angled ovary (Dassanayake and Fosberg, 1985) and fruits are much close to *Murraya paniculata* instead of *M. exotica*, based on *atpB-rbcL* intergenic spacer (Samuel *et al.*, 2000), although it resembles *M. elongata* very much based on the vegetative characters, such as leaves.

(All examined specimen list in supplementary)



Fig. 4. Branches, leaves and fruit of *Murraya gleniei* (Thwaites C.P. 3627) from Lectotype, K, K000382452 (A); Syntype G, G00096634 (B), K, K000382451 (C).

Murraya lucida (G. Forst.) Mabb., Mabblerley's Pl.-Book: 1102. 2017.

Fig. 2G–I

≡ *Limonia lucida* G. Forst., Fl. Ins. Austr. 33. 1786. **Type:** VANUATU, Malakula, July 1774, *J. R. Forster and G. Forster s. n.* (lectotype: BM BM000798433, image!); *J. R. Forster and G. Forster s. n.* (isolecotype: BM BM000798434, BM001015580, image!, GOET GOET012627, image!).

≡ *Murraya heptaphylla* Span., Linnaea 15(2): 178. 1841. **Type:** TIMOR, *Anonymous s.n.* (Isotype: L L0062742 image!).

≡ *Murraya exotica* var. *ovatifoliolata* Engl., Die Nat. Pflanzenfam. 3(4): 188. 1896. **Type:** AUSTRALIA, Queensland, Rockhampton, *A. Dietrich 928* (neotype: MEL 2100755A, image!). Domin (1927) didn't designate holotype, although a few specimens were listed. Designated here.

= *Murraya ovatifoliolata* (Engl.) Domin, Biblioth. Bot. 89(4): 296. 1927.

≡ *Murraya banati* Elmer, Leafl. Philipp. Bot. 8: 2812–1823. 1915. **Type:** PHILIPPINES, Cabadbaran (Mt. Urdaneta), Province of Agusan, Island of Mindanao, August 1912, *A. D. E. Elmer 13647* (lectotype: K K000736098 image! designated here; isolecotype: U U1585154 image!, BISH BISH1004847 image!, US US00101717 image!, NY NY00055921 image!).

Shrub or small trees, ca. 2–3 m high. Twigs, calyx, petals, and ovary hirsute. Leaves 3–9-foliolate; leaflets broadly oval or ovate, with more numerous and larger oil dots, and often decidedly hirsute and tomentose; petiolules 2–3 mm long, hairless or with fine hairs; leaflets ovate to broadly ovate, 1.2–4.5 cm × 0.9–3.0 cm, apex bluntly acuminate or obtuse, base rounded, usually oblique, margin irregularly crenulate, conspicuously glandular-punctate, upper surface dark green, hairless and glossy, lower surface dull and paler. Cymes terminal or upper axillary, few-flowered. Sepals ca. 1 mm long; petal oblong-obovate, white, 7–12 mm long, dispersing oil dots at the upper. Filaments white; anthers with sparse hairs, a yellow spike at the top; disks yellow, obvious. Style much longer than stamens; stigma yellow, capitate,



sharply expanded, 2-lobes; style and stigma with sparse hairs. Berry green at first, red when ripe, globose or ellipsoid, ca. 10 mm long, with oil dots.

Distribution: Eastern and central islands of the Malay Archipelago and Australasia, east to Vanuatu.

Ecology and phenology: The species was found in depauperate rainforest or mixed woodland on clayey soil, particularly along forest edges, drought tolerant and adaptable to both full sun and partial shade. Flowering December to January; fruiting February to June.

Note: The species *M. lucida* also includes the small- and large leafleted types, distributing in north and north-eastern Australia, east to Vanuatu. An accession of small leafleted *M. lucida* from Queensland (Australia) is close to *M. omphalocarpa* based on molecular phylogeny.

The plants of large leafleted types looks very similar to *M. sumatrana*, and is distinguished by broadly oval or ovate leaflets with more numerous and larger oil-dots and often decidedly hirsute and tomentose and the twigs, calyx, petals, and ovary are hirsute. This species has a close relationship with *M. omphalocarpa*, as well as *M. gleniei* and *M. zollingeri* based on the DNA phylogeny of *Murraya*.

(All examined specimen list in supplementary)

Murraya omphalocarpa Hayata, Icon. Pl. Formos. 3: 51. 1913.

Fig. 2J–M

Type: Taiwan (Formosa), Kotosho, Taito, October 1912, *T. Kawakami* and *S. Sasaki s.n.* (lectotype: TI TI00011271, image! designated here); Kotosho, February 1906, *T. Kawakami* and *G. Nakahara 1010* (syntype: TI TI00011270, image!); Kotosho, June 1911, *S. Sasaki s.n.* (syntype: TI TI00011273, image!).

≡ *Chalcas paniculata* L. var. *omphalocarpa* (Hayata) Tanaka, J. Soc. Trop. Agr. 1: 27. 1929.

= *Murraya paniculata* (L.) Jack. var. *omphalocarpa* (Hayata) Swingle, Webber H. J. et Batchelor L D., Citrus Indust. 1: 197. 1943.

Shrubs or small trees, green. Branchlets yellow, brownish. Rachis 5–8 cm long, striated; leaves 5–7-foliolate; leaflets broad-oval, terminal one about 7.0 × 4.5 cm, lateral ones smaller, measuring about 6 × 4 mm, the largest being 8.0 × 4.7 cm; margin entire or slightly crenulate; midrib prominent on lower side; thick, glabrous, thin coriaceous. Flowers solitary or fascicled, terminal or axillary, larger, at least near the end of the branchlets; pedicels 1.3–1.5 cm long. Calyx long-lobed, body campanulate, lobes ovate to linear-oblong, 3 mm long, obtuse and pubescent at the apex; petals oblong-obval, almost oblanceolate, 13 × 4 mm, narrowed at the base, obtuse at the apex. Stamens 10, filaments alternately shorter, longer ones about 9 mm, shorter ones about 6 mm. Pistil as long as the filaments; style fine, filiform; stigma capitate, ca. 1 mm diam. Berry ovoid, apiculate, with attenuate tip, about 21 × 12 mm, very much rostrate when immature, about 15 × 15 mm.

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Distribution: Taiwan (Orchid Island, Green Island); Philippines, northern Luzon and Batanes.

Ecology and phenology: The species was found near the margin of forests alt. up to 500 m. Flowering March to July; fruiting December to February.

Note: The species *Murraya omphalocarpa* is previously treated as the variety of *M. paniculata* in Swingle and Reece (1967), and Huang (1997), namely *Chalcas paniculata* in the studies of Tanaka (1929). According to Nguyen *et al.* (2019), *Murraya omphalocarpa* (syn. *M. paniculata* var. *omphalocarpa*) was identified as putative natural hybrids, which female parent was *M. paniculata* in Papua and *M. lucida* on Orchid Island in Taiwan respectively. According to the plenty specimens studied, this species is naturally distributed in southern Taiwan (Orchid Island and Green Island), Batanes and northern Luzon in the Philippines, not in Papua. It occurs within the naturally overlapping distributions of *M. sumatrana* and *M. lucida*. Based on molecular phylogeny (Fig. 1), this species is closer to *M. gleniei* and *M. zollingeri* than *M. paniculata*. It differs from other species (including the typical *M. paniculata*) by the large broad and thickest leaflets, larger flowers with narrow petals with attenuate base and elongated calyx lobes, and larger rostrate berry with apiculate tip. All evidences support the species status of *M. omphalocarpa* instead of hybrid.

(All examined specimen list in supplementary)

Murraya paniculata (L.) Jack, Malay. Misc. 1: 31. 1820.

Fig. 2N–P

≡ *Chalcas paniculata* L. Mant. Pl. 1: 68. 1767; Syst. Nat. 2: 293. 1767. **Type:** CHINA, Guangdong, Guangzhou, *C. G. Ekeberg s.n.* (lectotype: SBT SBT12151, image!).

= *Murraya exotica* L., Mant. Pl. Altera 563. 1771. **Type:** INDIA (likely cultivated in Tamil Nadu), *J. G. König '3'* (holotype: LINN 539.2 image!).

= *Camunium exoticum* (L.) Kuntze, Revis. Gen. Pl. 1: 99. 1891.

= *Chalcas exotica* (L.) Millsp., Publ. Field Columbian Mus., Bot. Ser. 1: 25. 1895.

= *Murraya paniculata* var. *exotica* (L.) C. C. Huang, Acta Phytotax. Sin. 8(1): 100, Pl. 11, 12. 1959; *Murraya paniculata* var. *exotica* (L.) M. R. Almeida, Fl. Maharashtra 1: 209. 1996.

≡ *Murraya amoena* Salisb., Prodr. Stirp. Chap. Allerton: 320. 1796. nom. illeg.

≡ *Murraya odorata* Blanco, Fl. Filip. 2: 256. 1845.

≡ *Murraya scandens* Hassk., Abh. Naturf. Ges. Halle 9: 233, l. 20. 1866.

Shrubs or trees, up to 8 m tall. Older branchlets grayish white to pale-yellowish gray. Leaves 3–7-foliolate, lower ones smaller; petiolules rather short; leaflet blades elliptic-obovate or obovate, 1–6 × 0.5–3.0 cm, shining green, margin entire, apex rounded or obtuse, base rounded; upper surface hairless and glossy, lower surface dull and paler, hairless or with fine hairs on petiolules, lower surface and margins. Cymes terminal or terminal and axillary, more flowers, 5-merous, fragrant. Sepals ovate, ca. 1.5 mm; petals white, oblong, 1.0–1.5 cm. Stamens 10. Berry broadly ovoid, 8–12 × 6–10 mm,



orange to vermilion when mature; 1–2-seeded. Seeds villous, with gray white hairs.

Distribution: Widely cultivated in tropical and subtropical areas, including India, southern China (Yunnan, S Fujian, Guangdong, Guangxi, S Guizhou, Hainan), possibly northern Việt Nam, Australia (North from Kilkivan in Queensland).

Ecology and phenology: The species was found in maritime sites on red, acid soils; cultivated widely in subtropical and tropical areas. Flowering April to August; fruiting September to December.

Note: The species *Murraya paniculata* has been distributed around the world as an ornamental plant. It was recently confirmed as the specific name for the species that includes cultivars of the tropical to warm temperate ornamental known as orange jasmine (Mabberley, 2016a,b). Nguyen *et al.* (2019) proposed that *M. paniculata* complex can be separated into four species with a rare hybrid also confirms morphological studies: *M. paniculata* s.s., *M. elongata*, *M. sumatrana*, and *M. lucida*. In addition, *M. omphalocarpa* was identified as a putative hybrid of *M. paniculata* and *M. lucida* with two geographically isolated nothovarieties representing reciprocal crosses. Accessions of *M. paniculata* and *M. elongata* closely group with *M. alata* (Nguyen *et al.*, 2019). It is characterized with the obovate leaflets and more flowers and fruits, which is different from *Murraya exotica*. Based on molecular phylogeny, it is much closer to *M. alata*.

(All examined specimen list in supplementary)

Murraya sumatrana Roxb., Bot. Reg. 5: sub t. 434. 1819; Fl. Ind. 2: 375. 1832.

Figs. 2Q & 3B

Type: BANGLADESH, Sylhet (introduced from Kolkata [Calcutta], West Bengal, INDIA, native to Sumatra in Indonesia), *F. De Silva Cat. no. 6369.B* (neotype: K K001123696 image!). According to the original description of W. Roxburgh in 1819 and 1832, the plant of this species was native to Island Sumatra, and from thence sent to the Botanic Garden at Calcutta by Dr. C. Campbell. Designated here (Fig. 3B).

- ≡ *Chalcas sumatrana* (Roxb.) Roem. Syn. Hesper. i: 49. 1846.
- ≡ *Chalcas camuneng* Burm. f., Fl. Ind. (Burman N. L.) 104. 1768.
- ≡ *Murraya cycloperensis* Astuti & Rugayah, Reinwardtia 15(2): 112. 2016. Type: INDONESIA, Java, Bogor Botanic Gardens (introduced from Kemiri Said Nature Reserves, Cyclops Mountain Papua), plot XXIV. A. 249, *Frisca Damayanti* 009 (holotype: BOHB; isotype BO).

Large shrubs. Leaves alternately pinnate and odd; leaflets 5–7, ovate or ovate-oblong, emarginate or acuminate at the tip, smooth, deep shining green; 3.5–5.0 cm long, ca. 2.5 cm broad, lowermost smallest; petioles glandular, round. Cymes terminal, flowers crowded, purely white. Calyx 5-parted, glandular. Pistil 2-celled with 2 ovule in each cell vertically attached to the uppermost part of the partition. Berry superior; rind

leathery, beset with small miliary glands. Seeds solitary, 1–2, oblong, pointed above, flat on one side, woolly; embryo inverted.

Distribution: Western (Indonesia, excluding New Guinea) and central (Borneo and the Philippines) islands of the Malay Archipelago, to Hainan Island and Taiwan Island.

Ecology and phenology: On rocky soils or limestone. Flowering and fruiting at various times through the year.

Note: The natural distribution of *Murraya sumatrana* appears to include the western (Indonesia, excluding New Guinea) and central (Borneo and the Philippines) islands of the Malay Archipelago, usually growing on rocky soils or limestone in Borneo (Nguyen *et al.*, 2019). *M. sumatrana* from Dongfang County in Hainan is closer to *M. alata*, another Indochinese-southeast China species recorded from northeast Viet Nam and south China (southwest Guangxi, southwest Guangdong, and Hainan).

The species is native to Sumatra Island in Indonesia and a very ornamental, with beautiful flowers which is pretty large, purely white and exquisitely fragrant. It is a wood most highly valued for making handles of kresses in Sumatra. It differs from *M. paniculata* in being much less bushy, and much thinner of branches, with larger leaves, fewer but much bigger flowers, and a very distinct habit.

(All examined specimen list in supplementary)

Murraya zollingeri (Tanaka) F.J. Mou, *comb. nov.*

Fig. 2R–T

- ≡ *Chalcas paniculata* L. var. *zollingeri* Tanaka, Bul. Soc. Bot. Fr. 75: 710. 1928. Type: INDONESIA, Nusa Tenggara Barat, Sumbawa, Bima, 8 August 1847, *H. Zollinger 3351* (lectotype: P MNHN-P-P02441042 image! designated here; isolecotype: P MNHN-P-P02441043 image!, L image!).
- ≡ *Murraya paniculata* L. (Jack) var. *zollingeri* (Tanaka) Tanaka, J. Indian Bot. Soc. 16: 232. 1937.

Shrubs. Leaflets 3–6, attached quite apart, small, ca. 3.0 × 1.5 cm, oval, chartaceous, thin, pellucid-dotted; puberulent on both sides, elliptic, tips acuminate or obtuse, base oblique, margin considerably undulate and revolute; rachis very thin and declined, slightly pubescent. Inflorescence axillary, few-flowered, often pendulous after flowering; peduncle about 1.8 cm long, pedicel slender, continuous to calyx, about 1.0–1.5 cm long, covered with very short soft hairs. Calyx small, well-lobed, lobes elongated-triangular, copiously tomentose, not glandular; disk short. Ovary oval after flowering, tomentose. Immature fruit often pendulous, globose or oboval, short, apex rounded, not apiculate, with a short part of style, densely dotted with large pellucid glands, covered with short white hairs; orange when ripe.

Distribution: Islands of the Philippines, Indonesia (Island Bima), Timor island.

Note: Following recent retypification of the genus *Murraya* by Mabberley's (2016a) and synonymy of *M. heptaphylla* with *M. lucida* (Mabberley, 2017), Nguyen



et al. (2019) thought that *M. lucida* (syn. *M. ovatifoliolata*) also incorporates *M. zollingeri* (syn. *M. paniculata* var. *zollingeri*) from Indonesia (Nusa Tenggara, Sulawesi and Maluku regions), islands of the Philippines, and Timor Island. However, this species is distinct from other species by the declined rachis, smaller and thinner leaflets with revolute margin, and globose fruits covered with white hairs. Meanwhile, it has a close relationship with a cluster of *M. omphalocarpa* in Taiwan, *M. lucida*, and *M. gleniei* from Sri Lanka based on the DNA phylogeny, which show that *M. zollingeri* should be a species, instead of the varieties of *M. paniculata* (Tanaka, 1929; Swingle and Reece, 1967) or the synonym of *M. lucida* (Nguyen et al., 2019).

(All examined specimen list in supplementary)

CONCLUSION

Based on the results of molecular phylogeny and morphological characters, the species status of *M. zollingeri* from Timor Island and *M. omphalocarpa* from Taiwan are stated here. There are eight species of the genus *Murraya* s.s. worldwide, and one new combination was proposed here, namely *Murraya zollingeri* (Tanaka) F.J. Mou. Meanwhile, the lectotype of three names (*Murraya omphalocarpa* Hayata, *Murraya banati* Elmer, and *Chalcas paniculata* L. var. *zollingeri* Tanaka) and the neotype of two names (*Murraya sumatrana* Roxb. and *Murraya exotica* var. *ovatifoliolata* Engl.) were designated here.

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