

TAXONOMY AND BIOGEOGRAPHY
OF
SUNDALAND *GARDENIA* (RUBIACEAE)

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A DISSERTATION SUBMITTED IN FULFILMENT OF THE
REQUIREMENTS FOR THE DEGREE OF MASTERS OF
SCIENCE

INSTITUTE OF BIOLOGICAL SCIENCES
FACULTY OF SCIENCE
UNIVERSITY OF MALAYA
KUALA LUMPUR, MALAYSIA

2010

UNIVERSITI MALAYA

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ABSTRACT

In Southeast Asia, the genus *Gardenia* J.Ellis (Rubiaceae) is poorly understood and documented due to a lack of country revisions, contentious species delimitations and accumulation of poorly identified material in herbaria. This study reviewed the taxonomic history and position of the genus, and revised the taxonomy of Sundaland species (including those of Sumatra, the Malay Peninsula, Java, Borneo, Palawan and adjacent islands). It includes a survey and cladistic study of morphological characteristics, and phylogenetic analyses using two chloroplast regions (*atpB-rbcL* and *trnT-F*) and the nuclear ITS region of representative species from Sundaland and adjoining regions. Twelve species are native to Sundaland and another two from mainland Asia and Wallacea commonly cultivated. Important generic characters include a woody shrub to tree habit with the growth architectural models of Leeuwenberg and Scarrone; resinous buds; tubular stipules; solitary terminal flowers; and pollen in tetrads. Calyx characters were the most useful for species distinction. Comparative morphological studies allowed two very closely related species, *G. elata* and *G. tubifera*, to be distinguished; *G. tubifera* var. *subcarinata* to be raised to species rank; and *G. dolichantha* to be subsumed under the synonymy of *G. griffithii*. Several new species (*G. beamanii* Y.W.Low and *G. chanii* Y.W.Low) and varieties (*G. subcarinata* var. *sumatrana* Y.W.Low and *G. elata* var. *kinabaluensis* ined.) were diagnosed. An identification key to Sundaland taxa, species descriptions, notes and identification lists are provided. The genealogies produced showed that Sundaland lineages were largely distinct from mainland Asian ones, probably reflecting the biogeographic distinction of these regions. Limited introgression of the mainland lineage including *G. jasminoides* into the lineage with *G. chanii* was detected. There was evidence for reticulate evolution among Sundaland lineages indicated by discordant genealogies of chloroplast and nuclear regions. Introgression of the widespread Sundaland species *G. elata* into a lineage with the more locally restricted *G. beamanii* (Borneo) was probably enabled by increased chances of contact during Pleistocene sea-level minima, when lowland forest area was contiguous between present-day Peninsular Malaysia and Borneo. Local variation in genetic characteristics implies that current forest fragmentation in Sundaland could diminish the species variability of *G. elata*. A complex of rarer species mostly occurring in pockets in peat swamps (*G. chanii*, *G. griffithii*, *G. pterocalyx*, *G. tubifera*) and adjacent *kerangas* forests (*G. costulata*) would also be threatened by habitat disturbance and transformation.

ABSTRAK

P engetahuan terhadap pengkelasan genus *Gardenia* J.Ellis (Rubiaceae) di Asia Tenggara adalah amat kurang memuaskan. Ini disebabkan kekurangan kajian semakan yang menyeluruh, batasan spesies yang kurang jelas dan pengumpulan spesimen yang belum dapat dicamkan dalam pelbagai koleksi herbarium. Kajian ini mendokumentasikan sejarah taksonomi dan kedudukan taksonomi genus tersebut di wilayah Sunda (termasuk Sumatra, Semenanjung Melayu, Jawa, Borneo, Palawan dan pulau yang berdekatan). Kaedah kajian termasuk tinjauan dan analisa kladistik ke atas ciri morfologi dan juga analisa phylogenetik yang menggunakan dua bahagian gen kloroplas (*atpB-rbcL* dan *trnT-F*) dan bahagian gen nuklear (ITS) untuk spesies wilayah Sunda dan kawasan di sekitarnya. Sebanyak 12 spesies asli wilayah Sunda dan dua lagi spesies tanaman dari benua Asia dan wilayah Wallacea telah dikenal pasti. Ciri-ciri morfologi utama *Gardenia* yang dapat dikenalpasti termasuk sifat tumbuhan berkayu yang mempunyai model tumbesaran Leeuwenberg dan Scarrone; pucuk vegetatif yang dilindungi resin; pengasuh daun yang berbentuk tiub; bunga yang tunggal dan berkedudukan terminal; dan debunga yang berkumpulan tetrad. Ciri kaliks bunga didapati adalah yang paling berguna untuk mengecam spesies. Satu kajian morfologi bandingan telah dapat membezakan *G. elata* dan *G. tubifera*, iaitu dua spesies yang mempunyai batasan kurang cukup jelas selama ini; juga taraf *G. tubifera* var. *subcarinata* telah dikenalpasti pada tahap spesies dan *G. dolichantha* dapat disahkan sinonim dengan *G. griffithii*. Selain daripada itu, beberapa spesies baru telah dikenalpasti termasuk *G. beamanii* Y.W.Low, *G. chanii* Y.W.Low, *G. subcarinata* var. *sumatrana* Y.W.Low, dan *G. elata* var. *kinabaluensis* ined. Satu kekunci pengecaman serta pencirian spesies dibekalkan. Kajian ini juga telah menunjukkan satu perbezaan utama di antara keturunan-keturunan benua Asia dan wilayah Sunda. Walaubagaimanapun, introgressi yang terhad dikesani daripada keturunan benua Asia (yang termasuk *G. jasminoides*) telah memasuki keturunan wilayah Sunda (yang termasuk *G. chanii*). Juga, terdapat bukti evolusi yang berciri retikulat di antara keturunan wilayah Sunda. Introgressi juga dikesani daripada *G. elata* (spesies bersebaran luas) memasuki keturunan *G. beamanii* (spesies yang bertaburan terhad di Borneo). Ini mungkin berlaku apabila peluang untuk pertemuan spesies bertambah pada zaman Pleistocene semasa paras laut berada pada tahap yang rendah dan luas kawasan hutan tanah pamah ada pada maksima. Had variasi ciri genetik *G. elata* yang luas juga bermakna pemecahan kawasan hutan mungkin mengurangkan tahap variasi spesies tersebut. Selain daripada itu, satu kompleks spesies yang jarang ditemui yang terdapat di hutan tanah gambut (*G. chanii*, *G. griffithii*, *G. pterocalyx*, *G. tubifera*) serta hutan kerangas yang berdekatan (*G. costulata*) juga akan terancam akibat gangguan dan kemusnahan habitat.

ACKNOWLEDGEMENTS

I wish to extend my sincere thanks and appreciation to my supervisor, Professor Wong Khoon Meng for his constant guidance, encouragement and patience throughout the course of this study. I also thank Professor Datin Lim Ah Lan and Puan Sri Susan Jalaluddin for their constant encouragement and support.

The Keepers, Directors and Curators of various herbaria, namely, A, BO, BKF, BRUN, IBSC, K, KEP, KLU, L, MICH, NY, SAN, SAR, SING and US, are thanked for loans of specimens and permission to examine materials in their care.

Special thanks are due to Datuk C.L. Chan (Kota Kinabalu); Professor J.H. Beaman, J.J. Wood and M. Briggs (K); R. Pouwer and N. Sol (L); and Dr C. Anderson and Heather Huggins (MICH); for providing much needed help in obtaining literature and digital images of herbarium specimens. I also thank Dr. B.W. Eko, Dr. Irawati and H. Arief (BO), Dr. K. Chayamarit (formerly BKF); J. Hunnex and Dr. C. Jarvis (BM); A. Smith (E); Dr. A. Davis, Dr. R. Govaerts, S. Dawson and A. Bond (K); P. Frödén (LD); Dr. J.T. Pereira (SAN); J. Sang (SAR); Dr. B.C. Tan and S. Lee (SING); Dr. D.H. Nicolson (US) for their kind assistance with specimen loans and information.

I wish also to record my appreciation to Professor C. Puff of the Faculty Centre of Biodiversity (formerly Institute of Botany), University of Vienna, and Dr. J.F. Veldkamp of the Nationaal Herbarium Nederland for providing Latin translations of diagnoses of new *Gardenia* species used in this study.

Dr. A. Mouly, Dr. K. Kamiya, W.L. Goh, C.B. Fong, M. Sugumaran and D.K.P. Lee provided help in molecular work. Dr. A. Mouly, Dr. C. Sussman and Professor C. Puff provided DNA material of various taxa used in this study.

Field logistic support was provided by Dr. Y.F. Lee, J. Sugau, Dr. J.T. Pereira and M. Postar (Sabah); M. Sugumaran, I. Zulkapli, K.T. Yong and I.S. Shanmugaraj (Peninsular Malaysia); H.J. Jamilah, A.K. Muhd. Ariffin, E. Jangarun, P. Azlan and M. Jakaria (Brunei). Zainal Mustafa (Rimba Ilmu Botanic Garden, University of Malaya) prepared the botanical drawings.

Finally, financial support for this study was provided by the University of Malaya Postgraduate Research Funding (PPP) grants P0138-2006A and PS046-2007C.

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LIST OF ABBREVIATIONS

Place, units of measurement, collecting information

coll. = collector
compt. = compartment (i.e., division of a Forest Reserve)
F.R. = Forest Reserve
ft = foot (feet)
Kg = *Kampung* (Malay word for village)
km = kilometer
m = meter(s)
mm = millimeter
min. = minutes
ml. = mile(s)
Mt. = Mount
s.n. = *sine numero* (without number)
Sg = *Sungai* (Malay word for river)

Cardinal points and other positions

C = Central
E = East
N = North
NE = North-East
NW = North-West
S = South
SE = South-East
SW = South-West
W = West

Calendar months

Apr = April
Aug = August
Dec = December
Feb = February
Jan = January
Jul = July
Jun = June
Mar = March
May = May
Nov = November
Oct = October
Sept = September

Chapter One:

Background and Objectives

1.1 Background to the present work

The genus *Gardenia* J.Ellis was established in 1761 by John Ellis (c. 1710–1776), an eminent English merchant and naturalist (Cornelius & Wells 1988), to honour Dr. Alexander Garden (1730–1791), a physician and naturalist based in Charles Town, South Carolina (Ellis 1761). Currently, there are about 200 species of *Gardenia* recorded from the Old World tropics, extending from Africa to Hawaii (Mabberley 2008).

Only a small number of studies have been conducted for *Gardenia* outside of Southeast Asia. Keay (1958) has elucidated the genus in West Africa. St. John & Kuykendall (1949) and Smith (1974) have worked on the genus in the Pacific area, and Bremekamp (1957) and Tirvengadam (1983) have worked on selected mainland Asiatic species. Within Southeast Asia, a brief treatment of the genus has been given in Java (Backer & Bakhuizen van Den Brink Jr. 1965) prior to the partial treatments by Corner (1939) and Wong (1982), addressing, in particular, taxonomic distinctions for species in Peninsular Malaysia. There is, as yet, no large regional study undertaken for Southeast Asia, which is somewhat surprising considering that the genus is generally well known for its showy flowers and a number of species have been successfully utilised in horticulture (Holttum 1953; Macmillan 1991; Corner 1997).

The main problems surrounding *Gardenia* taxonomy have been alluded to by Wong (1982), who discussed the genus for Peninsular Malaysia, as well as by earlier authors such as Keay (1958) for tropical Africa and Tirvengadam (1982) for tropical

Asia. These include, in part, the classification of various taxa placed in *Gardenia* which are apparently aberrant in morphological characteristics (or, a taxonomically reasonable delimitation of *Gardenia* itself), as well as an acceptable framework for recognising species. In general, the definition of *Gardenia* as a genus has been streamlined for Southeast Asia following the work of Wong (1982, 1984, 1989) and Tirvengadam (1983), whose work has shown how a number of closely affiliated genera may be distinguished by suites of morphological characters. However, species delimitation, in Southeast Asia at least, has been somewhat contentious, as shown by the preferred (and different) species classifications adopted by Corner (1939) and Wong (1982).

As both of these authors mainly considered material pertinent to the Malay Peninsula, it is relevant to review their perspectives through a broader assessment of morphological variation and possible characters of taxonomic significance for a wider geographical region. The Sundaland region (or western portion) of the hot-wet botanical province of Malesia (van Steenis 1950; van Welzen *et al.* 2005) appears to be a coherent phytogeographical unit for the development of many plant lineages, as also shown by Ridder-Numan (1998) and other studies (Whitmore 1981, Ashton 1982). This is basically due to the fundamental distinction between the Sunda and Sahul continental shelves in the historical and structural evolution of Southeast Asia, where these are separated by a deep-water region between them known as Wallacea (including Lombok, the Lesser Sunda Islands, Sulawesi, Halmahera and the main part of the Philippine archipelago) (Morley 2000, 2003) (Fig. 1). This biogeographical barrier (Wallacea) has meant that characteristic lineages on either side have mainly developed within their individual confines, with fewer taxa able to disperse across (van Welzen *et al.* 2005). Thus, in order to understand *Gardenia* in Southeast Asia, a reasonable beginning might be made with the genus in a biogeographically defined region such as Sundaland.

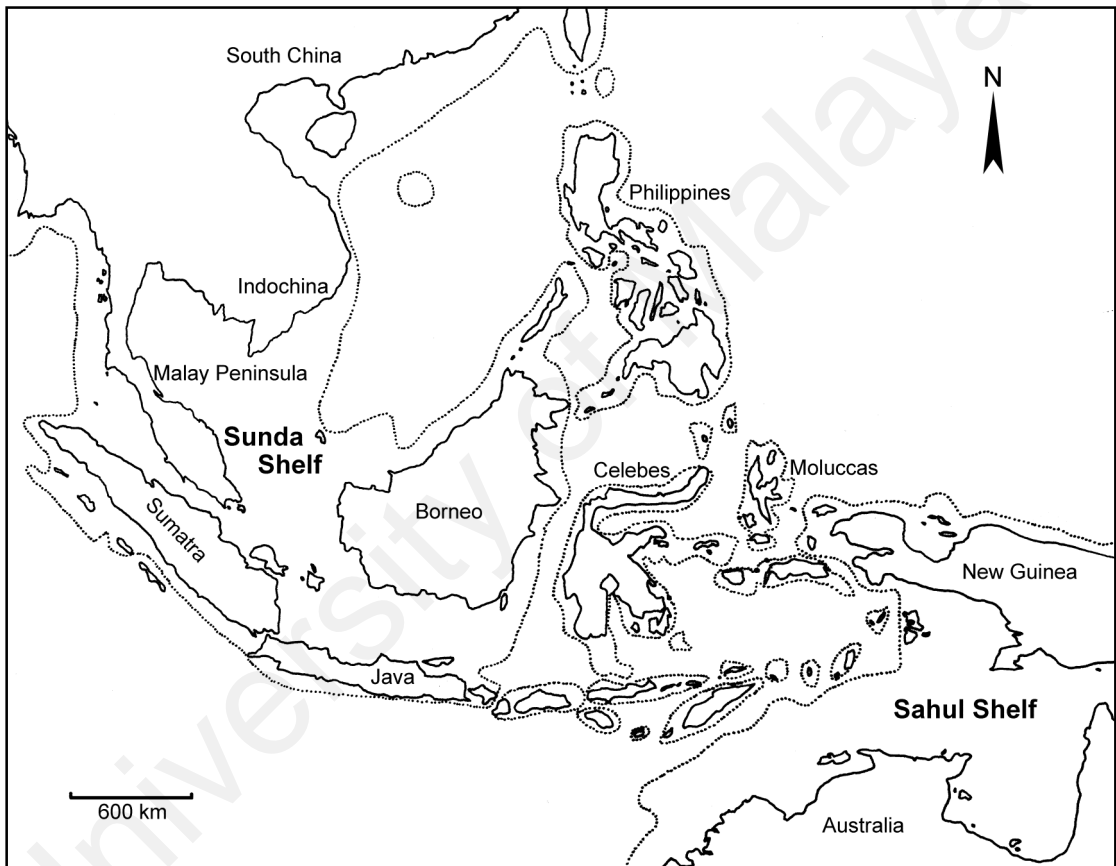


Fig. 1. Southeast Asia, showing Sunda and Sahul continental shelves separated by the deep-water region known as Wallacea. Solid line indicates extent of present day surface; dotted line indicates extent of land surface exposed during low sea level periods of glacial maxima. (after Primack & Corlett 2005.)

The present study therefore aims to produce a modern systematic revision of the genus *Gardenia* for the region phytogeographically known as West Malesia. This region includes Sumatra, the Malay Peninsula, Java, Borneo, Palawan, and some of the adjacent smaller islands, which are found on the Sunda continental shelf (or Sundaland).

1.2 Objectives

The beginning scenario for our study of *Gardenia* is therefore defined by a general difficulty with species definitions. This has been apparent through changes in species definitions in Peninsular Malaysia but would be similarly expected generally in Southeast Asia as both material and misinterpretations accumulate over time (such as in an overwhelming amount of herbarium material filed under *Gardenia tubifera*) since the last taxonomic commentaries for Southeast Asia in the 1980s. Thus, a study of plant characters, including both morphological as well as flower and fruit characters, would probably assist in determining the utility of characters used by various authors, as well as possible additional characters that could be taxonomically informative.

As the study would be carried out for the phytogeographical region of Sundaland or West Malesia, the phylogenetic relationships among the species would be of much interest. For instance, do all the Sundaland species fall into a single recognisable lineage derived from a particular ancestor (or ancestral group)? How are these related to mainland Southeast Asian species, or Pacific taxa farther east? Given the highly interesting geotectonic and climate-change fluctuations during the evolution of Southeast Asia (Morley 2000), are there any recognisable features among Sundaland *Gardenia* that reflect how such changes might have influenced the development of lineages? These questions depend on being able to assemble sufficient material toward a

phylogenetic analysis of molecular characters and ultimately on a sufficiently sound recognition of species (that serve as terminal taxa in such an analysis).

With these considerations, the main objectives of this study are categorised into four main components as listed below:

- 1) To assemble herbarium material and the relevant literature for the Sundaland region representing taxa hitherto recognised in the genus, for study and taxonomic assessment;
- 2) To conduct a survey of the morphology of vegetative parts, flowers and fruits, through both herbarium and field studies, in order to understand character variation better and identify taxonomically informative characters;
- 3) To employ molecular phylogenetic analyses to elucidate phylogenetic relationships among West Malesian (Sundaland) representatives of the genus *Gardenia*, and between these and congeners outside the region; and
- 4) To provide a taxonomic key, an updated enumeration including species descriptions, and a biogeographical interpretation for the genus *Gardenia* in West Malesia.

Chapter Two: Literature Review

2.1 Taxonomic History of *Gardenia*

The genus *Gardenia* J.Ellis was established in 1761 and is typified by *G. jasminoides* J.Ellis, a cultivated “double-flowered” specimen collected from the Cape of Good Hope in Africa. In his publication (Ellis 1761), a brief description was provided of the genus, accompanied by a drawing. *Gardenia* Ellis was first proposed for conservation by Sprague (1929), and confirmed as *nomen conservandum* since the 1952 Code (p. 135).

Some noteworthy discussion has appeared regarding the type species of *Gardenia*. The earliest name referring to *Gardenia* may well be *Catsjopiri* published in the *Herbarium Amboinense* of Rumphius (1755). Linnaeus (1759) published the name *Varneria augusta* L. in the *Amoenitates academicae* and referred to Rumphius's illustration and description of *Catsjopiri* in the *Herbarium Amboinense*. Merrill (1917) suggested that the correct species name for the type species was therefore to be found in the combination he made, *Gardenia augusta* (L.) Merr. as he regarded the name *Varneria augusta* L. as an earlier validly published name. Smith (1974), convinced that the Rumphius material was sufficiently unambiguous and validly published, accepted Merrill's interpretation. Tirvengadam (1978) decided to follow Smith (1974), but neither of these authors appeared to have been aware of a change of mind in Merrill (1935), where he agreed with Sprague (1929) that no genus description of *Varneria* had in fact been published by Linnaeus, so that Merrill also accepted *G. jasminoides* as the type. The *Herbarium Amboinense* is regarded as not validly published (it is listed in the Vienna Code of the *International Code of Botanical Nomenclature* (McNeill *et al.*

2006) as *opera utique oppressa* under Appendix VI). Thus, names of any rank listed in the publication are considered not validly published (Article 32.9). Rickett & Stafleu (1960), in their listing of conserved and rejected generic names, inserted a note under their entry for *Gardenia* Ellis thus: "*Warneria* or *Varneria* Linnaeus (a typographical variation) is not validly published in Amoen. Acad. 4: 136, 138 (1759). A simple reference to a Rumphius plate is not sufficient." Merrill's combination *Gardenia augusta* is thus rendered illegitimate. *G. florida* L., published in 1762 for the same species, is a synonym of *G. jasminoides*. Jarvis (2007), enumerating Linnaean plant names and their types, concurs.

Ever since the formalization of the genus, many species have been described under *Gardenia*, merely based on a few general characteristics (bisexual flowers with contorted corolla lobes, and unilocular or bilocular ovaries or fruits with many compressed and angular seeds) that were later considered as unspecific enough for generic recognition of genera within an alliance including *Gardenia*. For example, Roxburgh (1824) described the Malayan *G. anisophylla* Jack ex Roxb., which has a 2-loculate ovary and compressed seeds and so (in that feature) resembled *G. jasminoides*, although *G. anisophylla* was removed to *Randia* s.l. (Hooker 1873) and more subsequently to *Porterandia* Ridl. (Ridley 1939). Another example is the removal of a number of species from *Gardenia* s.l. (*G. campanulata* Roxb. and *G. turgida* Roxb. from the Indian-Burmese region, *G. mamillata* Craib and *G. sessiliflora* Wall. ex Kurz from the Burmese-Thai region) to *Ceriscoides* Tirveng. by Tirvengadum (1978). Also, *G. spinosa* Thunb. is the basis of *Catunaregam spinosa* (Thunb.) Tirveng., type species of the latter genus (Tirvengadum 1978). *G. pulcherrima* Kurz and *G. schoemanii* Teijs. & Binn. have also been transferred to *Rothmannia* Thunb. (Tirvengadum 1983). The

Fijian *G. pentagonoides* Seem. has been made the basis of the odd genus *Sukunia* A.C.Sm. (Darwin 1979).

A similar confusion had also characterized the naming of *Gardenia* spp. in Africa (Hutchinson & Dalziel 1931). In a revision of taxa formerly placed in *Randia* s.l. and *Gardenia* s.l., Keay (1958) recognized a number of monotypic genera from species previously placed in *Gardenia* s.l.: *Massularia* (K.Schum.) Hoyle based on *G. acuminata* G.Don; *Polycoryne* Keay based on *G. fernandensis* Hiern; *Oligocodon* Keay based on *G. cunliffeae* Wernham; *Pseudogardenia* Keay based on *G. kalbreyeri* Hiern. He also placed *G. abbeokutae* Hiern and others in *Didymosalpinx* Keay, and transferred a number of other *Gardenia* spp. to *Rothmannia* Thunb.

Perhaps the sectional classification for *Gardenia* also reflects this apparent earlier confusion. Authors who have offered such sectional classification include Hooker (1873, 1880), Ridley (1923) and Pitard (1923). Here is a summary of *Gardenia* sections that have been reassigned to other genera:

sect. *Ceriscoides* Hook.f. (Hooker 1873) = *Ceriscoides* (Tirvengadam 1978);

sect. *Rothmannia* Hook.f. (Hooker 1873) = *Rothmannia* Thunb. (Tirvengadam 1983);

sect. *Ceriscus* Hook.f. (Hooker 1880) = *Ceriscoides* (in most part) and *Dioecrescis* Tirveng. (based on *G. erythroclada* Kurz) (Tirvengadam 1983);

sect. *Rothmannia* Hook.f. (Hooker 1880) = *Kailarsenia* Tirveng. (Tirvengadam 1983);

sect. *Campanuloidea* Ridl. (Ridley 1923) = *Kailarsenia* (Tirvengadam 1983);

sect. *Gardeniella* Ridl. (Ridley 1923) = *Kailarsenia* Tirveng. (based on *G. tentaculata* Ridl.) (Tirvengadam 1983) and *Acranthera* Arn. ex Meisn. (Wong 1982);

sect. *Ceriscus* Pit. (Pitard 1923) = *Ceriscoides* (Tirvengadam 1978) and *Dioecrescis* Tirveng. (Tirvengadam 1983); and

sect. *Rothmannia* Pit. (Pitard 1923) = *Kailarsenia* (Tirvengadam 1983) and *Vidalasia* Tirveng. (based on *G. tonkinensis* Pit.) (Tirvengadam 1998).

It is notable that *Gardenia* sect. *Eugardenia* of these various authors (Hooker 1873, 1880; Ridley 1923; Pitard 1923) appears aligned in generic identity and there is still general acceptance of these species as part of *Gardenia*, i.e., in the same alliance as the type species, *G. jasminoides*. It is, however, uncertain what *Gardenia* sect. *Panduriformia* Pit., based on *G. panduriformis* Pierre ex Pit. (Pitard 1923), may refer to.

2.2 Systematic position and characters of *Gardenia*

Gardenia is the nomenclatural type for the tribe Gardenieae. Tribal characters listed by Robbrecht (1988) that are typical for *Gardenia* include the following: woody habit; interpetiolar, entire stipules; terminal flowers; left-contorted corolla lobes; 2-carpellate ovary; parietal placentation; large fruits with more-or-less dry wall; numerous lenticular or compressed seeds in a placental pulp; exotestal cells with thickenings typically found in the Gardenieae; pollen grains in tetrads; and stylar (or secondary) pollen presentation present.

Persson (2000) used chloroplast DNA sequences to investigate relationships in the Gardenieae and demonstrated that the tribe was polyphyletic. Robbrecht & Manen (2006), assessing the classification of the family by a supertree constructed from four plastid source trees, removed the Aulacocalyceae to a Vanguerieae alliance, and

maintained three other groups within a distinct Gardenieae alliance in the subfamily Cinchonoideae, one of only two subfamilies recognised in the classification. The Gardenieae were polyphyletic, but would be monophyletic if one of the four sub-groups that included *Schumanniphyton* Harms was removed. In this scheme, *Gardenia* emerged in the same (core) subgroup as *Kailarsenia*, *Porterandia*, *Randia* and *Trukia* Kaneh.

Genus characters summarized after the 1970s by various authors generally appear to be less variable compared to those used for older circumscriptions of the rather heterogeneous *Gardenia* s.l. Smith (1974) listed the following as genus characters: tree or shrub habit; stipules connate into a sheath and with yellowish exudate; domatia often present on lower leaf surface; 1-flowered terminal inflorescence; calyx infundibular or narrowly cupuliform, sometimes with lobe-like appendages; large conspicuous, white corollas; 6-9 left-contorted corolla lobes; 3-5 parietal placentas; numerous ovules immersed in a placental pulp; large subglobose-ellipsoid fruits with hard pericarp with bony endocarp; and numerous flattened seeds in an orange pulp. Darwin (1979) differentiated *Gardenia* from other Pacific members of the Gardenieae by its solitary flowers, calyx with persistent terminal or lateral spurs, conspicuous resinous exudate, and porate pollen in tetrads. Tirvengadam (1978) distinguished *Gardenia* among Sri Lankan genera by its tubular stipules that fall away leaving a persistent annular basal portion; resinous buds; lack of thorns; solitary, bisexual flowers; exerted anthers; tetrad 3-porate pollen; generally dehiscent fruits; and large, rounded, compressed seeds with areolate-foveate testa surface. Tirvengadam (1978) suggested that *Gardenia* is probably the only Asian genus with tetrad pollen.

Puttock & Quinn (1999) have carried out a cladistic study of morphological characters for some Australian Gardenieae and have identified, through taxa forming a *Gardenia* s.s. clade, the following genus synapomorphies: fusion of lateral branch to the stem for some distance above the node (they mean extra-axillary branching); subapical calyx spurs present; sticky paste-like placenta; placental tissue with sclereids; claret-reddish brown seed colour; tetrad pollen; and tectate-perforate pollen sexine.

A few character-states in several species still maintained in *Gardenia* seem highly unusual, given the recent characterization of *Gardenia* as described above. These include narrowly cylindrical, often curved fruits in the African *G. vogelii* Hook.f. and *G. leopoldiana* De Wild. & T.Durand, two little-known species that remain to be assessed more critically for other characters that support maintaining within the genus. Recently, Jongkind (2005) described *G. epiphytica* Jongkind from Gabon, which would appear to be highly unusual in being an epiphyte (all other accepted *Gardenia* spp. presently are terrestrial shrubs or trees), although in all other characteristics, including the possession of tetrad pollen, it fully corresponds to *Gardenia* as accepted by more recent authors.

2.3 *Gardenia* in the flora of Southeast Asia

2.3.1 Southeast Asia and Sundaland

Southeast Asia, including the Burmese-Thai-Indochinese area and the Malay Peninsula portion of Asia and the insular region that is botanically defined as Malesia (van Steenis 1950), has a largely tropical to subtropical climate with a lush vegetation climax and exceedingly rich flora (Whitmore 1986). The Malesian region includes two continental shelf regions, Sundaland to the west (comprising the Malay Peninsula, Sumatra, Java, Borneo and adjacent smaller islands; sometimes known as west Malesia), and Sahulland to the east (including New Guinea and northern Australia; also

called east Malesia); and a region of deeper seas and islands in between called Wallacea (Whitmore 1981), which includes the Philippines to the north, and Sulawesi, Maluku and other smaller Indonesian islands farther south.

The flora of this region is complex and has involved a number of regional and individual-country accounts of the 18th-20th centuries, and the principal accounts of Rubiaceae have appeared in the flora of "British India" (Hooker 1880), the flora of Indochina (Loureiro 1790, Pitard 1923), the flora of "Siam" (Craib 1932) and the flora of the Malay Peninsula (King & Gamble 1909, Ridley 1923), which were among the key primary floras that were the basis of much later taxonomic revisions and accounts. In the Sundaland region, here taken as west Malesia as defined above, together with Peninsular Thailand that links it with mainland Southeast Asia, the treatments the Rubiaceae in these historical works are particularly relevant to the documentation of *Gardenia*.

2.3.2 Current state of documentation of *Gardenia* relevant to Sundaland

Currently, the *World Checklist of Rubiaceae* (Govaerts *et al.* 2010) lists 11 species of *Gardenia* for the genus in the Sundaland territories, based on the documentation of Roxburgh (1824), Hooker (1880), Valetton (1912), Ridley (1923, 1934), Merrill (1923), and Tirvengadam (1983), as well as some results of the present work (Low & Wong 2007, 2009). Although substantial revisionary work still requires to be carried out for some areas, summaries of the current state of documentation for *Gardenia* in the various regions in or relevant to Sundaland are provided below.

Malay Peninsula

Early documentation of *Gardenia* in the Malay Peninsula began with the description of *G. carinata* from Penang and *G. tubifera* from Singapore (Roxburgh 1824). Hooker (1880) added *G. griffithii*, *G. speciosa* Hook.f., (a later homonym of *G. speciosa* Salisb.) and *G. tentaculata* (later made the basis of *Kailarsenia* by Tirvengadam 1983). King & Gamble (1909) added *G. godefroyana* Kuntz and *G. stenopetala* K. & G. but Ridley (1923) considered the former a synonym of *G. campanula* Ridl. and transferred the latter to *Randia*, which later Wong (1984) removed to *Kochummenia* K.M.Wong. Ridley (1923) also added *G. elata* (which was later confirmed an applicable name in place of *G. speciosa* Hook.f.), *G. resinifera* Korth. (later found to be a synonym of *G. tubifera*) and three aberrant species, *G. didymocarpus* Ridl., *G. pulchella* Ridl., and *G. virescens* Ridl., that were removed to *Acranthera* (Wong 1982, see above). Wong (1982) newly recorded *G. coronaria* and *G. pterocalyx* for the Malay Peninsula.

The relationship between *G. tubifera* and *G. elata* has been somewhat problematic. Corner (1939) considered them the same; Wong (1982) followed Corner but distinguished them as two forms of *G. tubifera* var. *tubifera*, while accepting *G. tubifera* var. *subcarinata* Corner. Later, Low & Wong (2009) considered evidence to separate *G. tubifera* and *G. elata* (also confirming *G. lobbii* Craib as a synonym of the latter), and elevated Corner's variety to *G. subcarinata* (Corner) Y.W.Low.

Thus, after consideration of ten *Gardenia* names as synonyms, misidentifications or new generic identities, only 7 spp. of *Gardenia* remain accepted as native to the Malay Peninsula: *G. carinata*, *G. coronaria*, *G. elata*, *G. griffithii*, *G. pterocalyx*, *G. subcarinata* and *G. tubifera*.

Borneo, including Brunei, Indonesia (Kalimantan) and Malaysia (Sabah and Sarawak)

Puff & Wong (1993) considered *Gardenia* as a poorly known genus in Borneo because of the lack of revisionary studies although much material had accumulated since the enumeration of Bornean plants by Merrill (1921) and the naming of some Bornean species by Ridley (1923, 1939). Masamune (1942) attempted to update Merrill's work and transferred three taxa previously placed as varieties of *G. anisophylla* to *Porterandia*, based on Ridley (1939), but overlooked the description of two *Gardenia* spp. by Ridley (1934). Among the 14 species so included by Merrill, 8 spp. have been reduced to synonymy or reassigned to other genera, such as *Porterandia* (Ridley 1939), *Ceriscoides* (Tirvengadam 1983; Reza 2003), and *Kailarsenia* (Tirvengadam 1983), or need to have their correct generic identities further verified in relation to *Rothmannia* (Pereira 2008). Recent local accounts in Borneo (Fox 1970 and Lee 2003 for Sabah; Anderson 1980 for Sarawak; Coode *et al.* 1996 for Brunei; Kessler *et al.* 2000 for Kalimantan) include few or doubtfully identified species.

Currently, the 7 spp. of *Gardenia* native to Borneo include only three of the ones originally listed by Merrill (1921), *G. elata* Ridl., *G. pterocalyx* Valetton and *G. tubifera* Wall. ex Roxb.; *G. costulata* Ridl. (Ridley 1934); and three species newly described or recorded by Low & Wong (2007), *G. beamanii* Y.W.Low, *G. chanii* Y.W.Low, *G. griffithii* Hook.f. Two other taxa listed by Merrill (1921), *G. acuminata* Korth. and *G. racemulosa* Korth., are suspect because of their descriptions recording axillary flowers (*Gardenia* as clarified by authors such as Keay (1958) and Tirvengadam (1978) has solitary terminal flowers).

Sumatra, Java and adjacent islands

For Sumatra, 5 spp. have been documented, *G. dolichantha* Merr., *G. elata*, *G. pterocalyx*, *G. subcarinata* (var. *sumatrana* Y.W.Low) and *G. tubifera* (Merrill 1938; Low & Wong 2007, 2009). Low & Wong (2009) also recorded *G. elata* for Bangka and Sumbawa.

An enumeration for Java by Backer & Bakhuizen van Den Brink Jr. (1965) recorded four taxa (*G. jasminoides*, *G. gjellerupii* Valetton, *G. siphonocalyx* Valetton and *G. tubifera*) introduced from other islands and being cultivated, but no native taxa were listed. Various *Gardenia* names applied to Javanese species have been found applicable to other genera: *G. blumeana* DC. and *G. campanulata* Roxb. are *Ceriscoides* (Tirvengadam 1978); *G. tomentosa* Blume is *Catunaregam* (Tirvengadam 1978); *G. curvata* Teijs & Binn. (also in Bantam) and *G. patula* Horsf. ex R. & S. (also in Bali and Sumba) are *Oxyceros* (Ridsdale 2007); and *G. schoemannii* Teijs. & Binn. (also in Sumatra) is *Rothmannia* (Tirvengadam 1983). *G. trichoclada* Miq. in the *Flora van Nederlandsch Indie* (Miquel 1857), from Sumbawa, has not been critically assessed.

More recent accounts by Sidiyasa *et al.* (1989a, 1989b, 1989c) for Bali, Maluku, Nusa Tenggara (Lombok, Sumba and Sumbawa), Sulawesi and Timor carried no entries for *Gardenia* in their enumeration, although earlier *G. mutabilis* Reinw. ex Bl. (Sulawesi) and *G. reinwardtiana* Bl. (Maluku) have been earlier recorded (Blume 1826).

Indochina (Cambodia, Laos, and Vietnam), Myanmar, Thailand

As many as 17 former *Gardenia* spp. have been reassigned or reduced to synonymy. This has largely been possible due to the work of Tirvengadam (1978, 1983,

1998), who diagnosed new generic identities (*Catunaregam* Wolf, *Ceriscoides*, *Dioecrescis*, *Kailarsenia*, and *Vidalasia*) or removed species to existing genera (*Rothmannia*). Merrill (1935), Jarvis (2007), and Low & Wong (2009) have reduced some species to synonymy, and Merrill (1922) has removed one to *Ichnocarpus* R.Br. (Apocynaceae).

There are 25 spp. currently accepted in *Gardenia*: *G. angkorensis* Pit., *G. annamensis* Pit., *G. cambodiana* Pit., *G. carinata* Wall. ex Roxb., *G. chevalieri* Pit., *G. collinsae* Craib, *G. coronaria* Buch.-Ham., *G. costata* Roxb., *G. cuneata* Kurz., *G. elata* Ridl., *G. griffithii* Hook.f., *G. ixoraefolia* R.Br., *G. jasminoides* Ellis, *G. lucida* Roxb., *G. magnifica* Geddes, *G. obtusifolia* Roxb., *G. panduriformis* Pierre ex Pit., *G. philasteri* Pierre ex Pit., *G. resinifera* Roth., *G. saxatilis* Geddes, *G. similis* Craib, *G. sootepensis* Hutch., *G. thailandica* Tirveng., *G. truncata* Craib and *G. tubifera* Wall. ex Roxb.

The Philippines

Blanco (1837) produced the first flora of the Philippines that consisted about 900 species, including *Sulipa pseudopsidium*, later recombined in Fernandez-Villar & Naves (1880) as *G. pseudopsidium* (Blanco) F.Villar. The latter authors listed five other species in *Gardenia* among the numerous names they enumerated, which Merrill (1915) explained was virtually impossible to assess as no reference material accompanied these records.

Among the older set of verifiable *Gardenia* names for Philippine plants are the following that have been transferred to *Villaria* Rolfe: *Gardenia acutifolia* Elmer (Merrill 1910); *Gardenia elliptica* Elmer (Merrill 1918); *Gardenia obscura* (Blanco)

S.Vidal and *Gardenia pinnata* (Blanco) Merr. (Mulyaningsih & Ridsdale 2004). *Gardenia whitfordii* Elmer (Elmer 1906) was later the basis of *Discospermum whitfordii* S.J.Ali & Robbrecht (Ali & Robbrecht 1991).

In his enumeration of Philippine plants, Merrill (1923) listed 11 native *Gardenia* spp.: *G. curranii* Merr. (transferred to *Ceriscoides*, Tirvengadam 1978); *G. longiflora* Vidal. (a synonym of *G. elata*, Low & Wong 2009); *G. morindaefolia* Elmer (transferred to *Vidalasia*, Tirvengadam 1998); *G. obscurinervia* Merr. (later the basis of *Sulitia* Ridsdale, Ridsdale 1979); *G. lagunensis* Merr., *G. merrillii* Elmer and *G. negrosensis* Merr. (aberrant and its suitability for transfer to *Rothmannia* being considered; Pereira 2008); *G. pubifolia* Merr. (aberrant from the axillary inflorescences noted); and *G. megalocarpa* Merr., *G. pseudopsidium*, and *G. segmenta* Elmer (these last three species not yet taxonomically assessed). Later, Merrill (1926) added a new taxa from Bohol island, *G. ramosii* Merr. After considering the above, it is still difficult to imagine that these islands would only have four *Gardenia* species, so a revision taking into account more recent collections is badly needed.

Chapter Three:

Materials and Methods

3.1 Herbarium studies

A total of 1,393 sheets of *Gardenia* specimens collected from Sundaland countries and adjacent areas were loaned from nine herbaria (BKF, BO, K, KEP, KLU, L, SAN, SAR, and SING) for the present study. Additionally, digitised images of herbarium specimens from seven herbaria, namely, A, IBSC, LINN, MICH, NY, P, and US were also obtained. Visits to three regional herbaria (BRUN, SAN, and SING) were made to study specimens curated there. Herbarium acronyms used follow Holmgren *et al.* (1990).

Morphological observations and dissections were carried out using an Olympus SZ 30 binocular microscope (magnification 9–40×) supported by a universal arm and an Olympus LG PS2 illuminator.

3.2 Field collections

Field collections were carried out in Brunei and Malaysia to obtain additional materials for morphological and molecular analysis. Listed below are the collection sites visited:

(a) Brunei

Andulau Forest Reserve; Badas Forest Reserve; Bukit Sawat, Ulu Sungai Mau; Sg. Liang Forest Recreational Park.

(b) Malaysia

(i) Peninsular Malaysia

Kedah: Nami; Pulau Dayang Bunting (Langkawi). Kuala Lumpur: Rimba Ilmu Botanic Garden, University of Malaya. Negeri Sembilan: Pasoh Forest Reserve. Pahang: MENCHALI Forest Reserve; Muazam Shah; Pulau Tioman; Sungai Bebar Forest Reserve; Tasik Bera. Perak: Gunung Bubu Forest Reserve (Kuala Kangsar). Pulau Pinang: Bukit Bendera (Penang Hill). Selangor: Sungai Tua Recreational Forest (Ulu Yam). Terengganu: Bukit Bauk Forest Reserve, (Dungun).

(ii) Sabah

Ranau: Poring; Tenompok Forest Reserve. Sandakan: Arboretum, Forest Research Centre (Sepilok). Tambunan: Rafflesia Forest Reserve.

(iii) Sarawak

Kuching: Matang.

Specimens collected from the field were trimmed and then pressed between newsprint and dried in a drying oven at 55°C. The Schweinfurth method was also used, in which specimens pressed between newsprint were bundled in polythene bags with alcohol (industrial methylated spirit) added, for longer preservation in the field (Bridson & Forman 1998).

Besides that, shoot apices with intact stipules at different stages, flowers and fruits were also preserved whenever possible in liquid preservative (21 water: 78 methyl alcohol: 1 glycerol) for further study in the lab. Fresh young leaves (free from fungus,

infection or dirt) were also collected in the field and preserved in silica-gel for subsequent DNA extraction following Chase & Hills (1991).

3.3 Plant architecture

Plant architecture was studied in the field, based on observations of young and adult plants of 13 *Gardenia* species. Throughout this study, attention was given to leaf arrangement on trunk and branches, branching sequences and position of inflorescences. Locations where tree architecture of *Gardenia* species were studied are listed below:

- G. beamanii* - Andulau Forest Reserve, Belait District, Brunei;
- G. carinata* - Rimba Ilmu Botanic Garden, University of Malaya, Kuala Lumpur, Peninsular Malaysia;
- G. chanii* - Bukit Sawat, Ulu Sungai Mau, Belait District, Brunei;
- G. costulata* - Matang, Kuching, Sarawak;
- G. elata* - Pasoh Forest Reserve, Negeri Sembilan, Peninsular Malaysia; Arboretum, Forest Research Centre, Sepilok, Sandakan, Sabah;
- G. griffithii* - Muazam Shah, Pahang, Peninsular Malaysia;
- G. jasminoides* - Rimba Ilmu Botanic Garden, University of Malaya, Kuala Lumpur, Peninsular Malaysia;
- G. mutabilis* - Rimba Ilmu Botanic Garden, University of Malaya, Kuala Lumpur, Peninsular Malaysia;
- G. pterocalyx* - Sungai Bebar Forest Reserve and Tasik Bera, Pahang, Peninsular Malaysia; Rimba Ilmu Botanic Garden, University of Malaya, Kuala Lumpur, Peninsular Malaysia;
- G. subcarinata* - Bukit Bauk Forest Reserve, Dungun, Terengganu, Peninsular Malaysia;

- G. thailandica* - Pulau Dayang Bunting, Langkawi, Kedah, Peninsular Malaysia;
- G. tubifera* - Menchali Forest Reserve and Sungai Bebar Forest Reserve, Pahang, Peninsular Malaysia; Rimba Ilmu Botanic Garden, University of Malaya, Kuala Lumpur, Peninsular Malaysia;
- G. sp. A* - Poring, Ranau, Sabah.

3.4 Photography

Field photography was made using a Nikon F80 camera with a 28–80 mm Nikon AF Nikkor Zoom lens and a 28–300 mm Sigma Zoom lens. Close-up photographs were taken using a 105 mm F2.8 EX Sigma lens supported by a Nikon SB-21 Macro Speedlight ringflash. The film used was Fujichrome Provia 100F (35 mm colour reversal film). Selected images were then digitised using a flatbed photo scanner (Hewlett-Packard Scanjet G4050), and edited with Adobe Photoshop in the Adobe Creative Suite 4 (CS4) Premium Student Edition package.

3.5 Cladistic analysis based on morphological characters

A total of 19 terminal taxa were included in the cladistic analysis, comprising:

- (a) an ingroup consisting of 17 terminal taxa of *Gardenia* (12 taxa recognised through the present study from Sundaland including an unidentified taxon, *G. sp. A*, from Sabah; four taxa from adjacent mainland Asia, namely, *G. hainanensis* Merr. (China, Hainan province), *G. jasminoides* J.Ellis (widely cultivated throughout Sundaland), *G. sootepensis* Hutch. (Myanmar and Thailand), and *G. stenophylla* Merr. (China, Hainan province; Vietnam); and one Wallacea taxon, *G. mutabilis*, from the Philippines and Sulawesi (cultivated in Indonesia, Malaysia, Singapore and Thailand); and

(b) two species of *Porterandia* Ridl., namely, *P. lambirensis* Zahid and *P. scortechinii* (King & Gamble) Ridl., forming the outgroup.

A total of 41 characters were identified and used (Table 1) based on herbarium specimens and also fresh materials obtained from the field for this analysis. Of these, one character (character 1 in Table 1) is related to plant architecture, 11 characters (characters 2–12 in Table 1) are related to vegetative parts and 29 (characters 13–41 in Table 1) are related to reproductive parts. Of the 29 characters pertaining to reproductive parts, 22 (characters 13–34 in Table 1) are related to flowers and seven (characters 35–41 in Table 1) are related to fruits. Character-states for *Porterandia* were obtained from Zahid (2004). Character-states were compiled using DELTA Editor (Dallwitz 1980; Dallwitz *et al.* 1999) and scored for the 19 terminal taxa.

For the cladistic analysis, the most parsimonious trees were obtained using PAUP* version 4.0b10 (Swofford 2002) with the full heuristic search option, 1000 replicates of random taxon sequence addition, retaining one tree at each step, with tree-bisection-reconnection (TBR) in effect, accelerated transformation (ACCTRAN) optimisation, and the MulTrees option in effect. Clade robustness was estimated using the bootstrap technique (Felsenstein 1985), with 1000 replicates, TBR branch swapping, and the MulTrees option in effect using PAUP*. Bremer support values or decay values (b) (Bremer 1988, 1994) were obtained using PAUP* in conjunction with PRAP 2.0b3 (Müller 2004) to supplement clade robustness inferred using the bootstrap technique (Felsenstein 1985) with values above 75% considered statistically supported.

Table 1. Characters and character states for a cladistic analysis of *Gardenia* J.Ellis and associated taxa.

1. Growth architecture:

- 1= Scarrone's model
- 2= Leeuwenberg's model

2. Branch position in relation to leaf axil:

- 1= axillary
- 2= extra-axillary

3. Resin exudate at shoot tips:

- 1= not present [*scoring this invalidates Character 4*]
- 2= present in minute traces, never congealing as blobs on the young shoot tips [*scoring this invalidates Character 4*]
- 3= present copiously

4. Resin exudate colour upon congealing:

- 1= yellowish amber-brown
- 2= black

5. Leaf width (on flowering branches):

- 1= medium to broad (>1 cm wide)
- 2= narrow (0.4–1 cm wide)

6. Leaf apex:

- 1= acute to rounded
- 2= cuspidate

7. Leaf texture:

- 1= chartaceous to thin-coriaceous
- 2= stiffly thick-coriaceous

8. Lower leaf surface hairiness:

- 1= glabrous or glabrescent (the latter with very few minute-powdery hairs on the midrib only)
- 2= sparsely to densely hairy (hairs always distinct, at least on veins on the lower leaf surface)

9. Lower leaf surface domatia in vein axils:

- 1= absent
- 2= present

10. Stipule form:

- 1= cupular (forming a cup-like structure)
- 2= sheathing (forming a tubular sheath with an oblique mouth)

11. Stipule margin:

- 1= with 2-several subequal lobes
- 2= with a single triangular apex
- 3= subtruncate

12. Stipule persistence:

- 1= stipule detaching whole from the node
- 2= detached stipule bases often persistent as annular rings around twig internodes

Table 1 continued next page

13. Flower number:

- 1= several in an inflorescence (at least in bisexual flowers)
- 2= always solitary

14. Flower size:

- 1= small (corolla span less than 1 cm in open flower)
- 2= large (corolla span more than 2 cm in open flower)

15. Flower sexuality:

- 1= bisexual or female (in separate inflorescences)
- 2= bisexual

16. Floral mid-hypanthium width (open flowers):

- 1= less than 3–4 mm (flowers generally small)
- 2= 6 mm or more (flowers generally large)

17. Calyx tube general shape:

- 1= distally broadened, obconical or trumpet-like
- 2= cylindric-tubular-sheathing

18. Calyx tube length in relation to mature corolla tube length:

- 1= almost a third the corolla tube length or shorter
- 2= nearly half the corolla tube length or longer

19. Calyx tube texture:

- 1= firm, at least for the most part below the margin
- 2= membranaceous throughout

20. Calyx outer surface pubescence:

- 1= sparsely pubescent
- 2= glabrous

21. Calyx tube ridges/keels:

- 1= absent
- 2= with longitudinal ridges or ribs (appearing as sharp ridges or vein-like protrusions above the calyx surface)
- 3= with longitudinal low keels not or only very slightly continuing as short apical spurs or lobes exceeding the calyx mouth

22. Calyx wings/spurs:

- 1= absent
- 2= with conspicuous triangular wings expanded at the distal-most ends of longitudinal ribs or keels on the calyx
- 3= with long, linear, bilaterally flattened spurs extending beyond the calyx margin

23. Calyx tube margin:

- 1= mouth more-or-less evenly level, with a subtruncate, wavy or several-lobed margin
- 2= mouth oblique-entire with an acute to minutely toothed apex

24. Calyx mouth width compared to corolla tube thickness:

- 1= calyx mouth as wide as to twice as wide as the corolla tube
- 2= calyx mouth 3 times as wide as the corolla tube, or wider

Table 1 continued next page

25. Calyx tube hairiness on inner tube surface:

- 1= densely hairy (calyx tube surface completely hidden by hair covering)
- 2= sparsely hairy (much of the calyx tube surface not hidden by hairs)
- 3= totally glabrous

26. Colleters on inner calyx surface:

- 1= colleters absent to scarce and restricted to area between calyx lobes
- 2= dense colleters along the basal part of the calyx inner surface

27. Corolla colour:

- 1= greenish cream
- 2= white turning yellow to orange

28. Corolla mid-tube width:

- 1= variably thin to medium width (3–5 mm thick)
- 2= consistently very slender (2–3 mm thick)
- 3= very wide (6–10 mm or more)

29. Corolla tube hairiness on outer surface:

- 1= wholly covered by thick, stiff bristle-like hairs that are individually discernible without a lens
- 2= glabrous or with scattered fine, short flexuous or minute hairs, not obscuring the tube surface

30. Corolla tube hairiness on inner surface and throat:

- 1= hairs sparse to dense but not covering the mouth and base of corolla lobes
- 2= hairs dense and covering the mouth and base of corolla lobes

31. Corolla lobe number:

- 1= consistently five lobes
- 2= 6–9 or more lobes

32. Style hairiness:

- 1= short-hairy at lower part
- 2= glabrous throughout

33. Anther apices:

- 1= connective not conspicuously to only very slightly prolonged (about 0.2–0.4 mm) beyond the apices of anther sacs
- 2= connective conspicuously prolonged 0.8–1 mm beyond the apices of anther sacs

34. Pollen type:

- 1= issued as monads
- 2= issued as tetrads

35. Calyx tube persistence after fertilisation:

- 1= persistent
- 2= caducous

36. Fruit attachment:

- 1= distinctly pedicellate (pedicel at least 5 mm long)
- 2= sessile-subsessile

37. Fruit shape at maturity:

- 1= variably ovoid or globose
- 2= consistently obovoid
- 3= ellipsoid

38. Fruit surface appendages:

- 1= none (smooth)
- 2= with longitudinal ridges or ribs
- 3= with longitudinal keels

39. Fruit epidermal texture at maturity:

- 1= smooth (non-flaky), generally brown
- 2= minutely grey-flaky and lenticellate

40. Fruit dehiscence:

- 1= indehiscent
- 2= dehiscent upon maturity

41. Placental mass colour in ripe fruit:

- 1= translucent creamy brown
 - 2= orange-red
-

Finally, a consensus tree (produced from resulting trees) produced from PAUP* was viewed using TreeView (Win32) according to Page (1996). The programme MacClade 4.08 (Maddison & Maddison 2005) was also used for character exploration.

3.6 Phylogenetic analyses based on molecular data sets

3.6.1 Experimental design and sampling

An attempt to investigate the phylogenetic relationships among Sundaland *Gardenia* using DNA sequencing data from two chloroplast (*atpB-rbcL* and *trnT-F*) and a nuclear (ITS) gene region, based on 16 taxa representing three Gardenieae genera (*Aidia* Lour., *Gardenia* and *Porterandia* Ridl.) were performed in this study. These selected taxa are *A. wallichiana* Tirveng., *G. beamanii*, *G. chanii*, *G. elata*, *G. griffithii*, *G. hainanensis*, *G. mutabilis*, *G. pterocalyx*, *G. saxatilis* Geddes, *G. stenophylla*, *G. sootepensis*, *G. sp. A*, *G. thailandica*, *G. tubifera*, *P. lambirensis* and *P. scortechinii*. Every taxon is represented by a terminal taxon except for *G. elata*, which is the most widespread taxon in Sundaland (Low & Wong 2009), represented by four terminal taxa from four different provenances: Peninsular Malaysia-East (PME), Peninsular Malaysia-West (PMW), Sabah (SAB) and Sarawak (SAR). *Aidia wallichiana* is the sole outgroup terminal, while *Porterandia*, a well-revised genus (Zahid 2004; Zahid & Wong in press) and *Gardenia* were placed as ingroup taxa.

Of the 13 *Gardenia* species enumerated for Sundaland, including two unidentified taxa, listed here as *G. sp. A* and *G. sp. B*, from Borneo, only eight (*G. beamanii*, *G. chanii*, *G. elata*, *G. griffithii*, *G. pterocalyx*, *G. sp. A*, *G. thailandica* and *G. tubifera*) were possible to include in this study. Complete sampling for the analysis was not possible due to lack of leaf material available or failure to obtain optimum DNA sequences for some taxa. Additionally, four mainland Asiatic *Gardenia* taxa, namely, *G.*

hainanensis, *G. saxatilis* (Thailand), *G. sootepensis* and *G. stenophylla*; and a Wallacea taxon, *G. mutabilis*; were included in this study with the objective of elucidating the relationship of the mainland Asian and Wallacea taxa with the Sundaland taxa. All samples used in the molecular analyses are listed in Appendix 1.

3.6.2 Extraction, amplification and sequencing

Most of the DNA samples extracted were from silica-dried leaf material collected from the field (Chase & Hills 1991) except for a few species (*Aidia wallichiana*, *G. hainanensis*, *G. mutabilis*, *G. sootepensis*, *G. stenophylla*, and *P. scortechinii*), for which fresh material was obtained.

DNA extraction was performed using QIAGEN DNeasy™ plant mini kits, following the manufacturer's protocol. To avoid polymerase chain reaction (PCR) inhibition, extracted DNA samples were purified using QIAGEN QIAquick™ PCR purification kits as described in the manufacturer's protocol before storing in a -20°C freezer.

Two chloroplast regions (*atpB-rbcL* and *trnT-F*) and a nuclear region (ITS) were amplified in the present work. The volume of each PCR reaction was 50 µl and contained 2.5 µl each of the 10 mM primers, 25 µl GoTaq® polymerase (5 U/µl) (Promega, Madison, WI, USA) and 15 µl ddH₂O. Amplification of *atpB-rbcL* was carried out using primers *rbcL5'R^c* and *atpB5'R^d* of Rydin *et al.* (2008). Primers *a* and *f* of Taberlet *et al.* (1991) were used for amplification of *trnT-F*. For ITS amplification, primer ITS4R of White *et al.* (1990) was utilised. In all PCR executions, a negative control was performed to check for possible contamination. The negative control

samples used 5 µl of nucleus free water to replace DNA samples in the 50 µl PCR reaction.

PCR was conducted using a Biometra[®] thermocycler. The programmed PCR parameters were 2 min at 94°C (activation of the GoTaq[®] polymerase), followed by 35 cycles of 30 sec at 94°C (denaturation), 45 sec at 52°C (annealing), and 1 min at 72°C (extension); and then a final 5 min extension at 72°C. Amplified PCR products were further purified using QIAGEN QIAquick[™] PCR purification kits according to the manufacturer's protocol.

For sequencing, amplified PCR products that have been purified were sent to First BASE Laboratories Sdn. Bhd. (Seri Kembangan, Selangor, Malaysia) with the same primers used for PCR amplifications.

3.6.3 Sequence alignment

The *atpB-rbcL*, *trnT-F* and ITS sequences were assembled manually after base-calling was verified. All sequences were preliminarily aligned using ClustalX (Thompson *et al.* 1997) and then manually adjusted with the programme Bioedit (Hall, 1999) based on the similarity criterion (Morrison 2006).

3.6.4 Phylogenetic analyses

Two analyses were performed, namely, the Bayesian Markov chain Monte Carlo (MCMC) (Yang & Rannala 1997) as implemented in the programme MrBayes version 3.0B (Huelsenbeck & Ronquist 2001) and Maximum Parsimony (MP) as implemented in the programme PAUP* version 4.0b10 (Swofford 2002) for two chloroplast regions and a nuclear gene region, viz., (i) *atpB-rbcL*, (ii) *trnT-F*, (iii) ITS, respectively; and (iv)

the combined plastid data, and (v) the combined plastid and nuclear data. The Bayesian approach estimates the posterior probability (PP) of a tree generated being accurate based on the character matrix provided, while the Maximum Parsimony approach evaluates the bootstrap support values (BP).

3.6.4.1 Bayesian analyses

Partitioned Bayesian analyses were conducted for (i) *atpB-rbcL*, (ii) *trnT-F*, (iii) ITS, (iv) combined plastid data, and (v) combined plastid and nuclear data. For each partition, the programme MrModeltest 2.0 (Nylander 2004) was executed to select a suitable model of nucleotide substitution that best fits each data set, following Akaike's Information Criterion Calculation Method (Akaike 1974). The selected models in this study were: GTR (General Time Reversible) for *trnT-F*; GTR+I (General Time Reversible with a fraction of invariant site constraint) for the *atpB-rbcL* and combined plastid analyses; GTR+I+G (General Time Reversible with a fraction of invariant site constraint and among-site substitution rate heterogeneity described by a gamma distribution) for the combined plastid and nuclear analysis; and HKY+I (Hasegawa-Kishino-Yano with a fraction of invariant site constraint) for ITS.

All analyses were conducted with four independent Markov chains that run for 2×10^6 metropolis-coupled MCMC generations, with tree sampling at every 1×10^3 generations, and burn-in after 500 trees.

The analyses included three cycles using different random starting trees to evaluate the convergences of the likelihood values and posterior clade probabilities (Huelsenbeck *et al.* 2002). The consensus tree was generated using selected trees from each cycle. In the Bayesian analyses, clade robustness is indicated by posterior

probability (PP) values above 0.95, a commonly used statistical significance (Mouly *et al.* 2009a; Wurdack *et al.* 2005; Eriksson *et al.* 2003; Kauff & Lutzoni 2002).

3.6.4.2 Maximum parsimony analyses

For parsimony analyses conducted in the present work, gaps were treated as missing data and characters were equally weighted and unordered (Fitch 1971). The consistency index (CI) (Kluge & Farris 1969) and the retention index (RI) (Farris 1989) were calculated to estimate homoplasy.

The most parsimonious trees were calculated using the heuristic search option, 1×10^4 replicates of random taxon sequence addition, retaining one tree at each step, with tree-bisection-reconnection (TBR) branch swapping, accelerated transformation (ACCTRAN) optimisation, and the MulTrees option in effect. Bootstrap support values for each node were estimated from 1000 replicates, with TBR branch swapping and MulTrees option in effect (Felsenstein 1985).

A majority rule consensus tree was produced from the resulting trees, in which nodes with bootstrap support less than 50% were collapsed. Branches with bootstrap support (BP) above 70% were considered as statistically supported, and equivalent to 95% (or 0.95) Bayesian support in trees (Eriksson *et al.* 2003).

Chapter Four:

Survey of morphological characters of possible taxonomic utility

This chapter surveys morphological characters of the species included in the current revision of *Gardenia* in Sundaland, as well as several related ones from adjacent mainland Asia and Wallacea. It precedes an attempt to examine possible relationships by analysis of morphological character-states using a phylogenetic programme. It focuses on the structure of the calyx, corolla and fruit that has been much used for species diagnosis in previous accounts of the genus (St. John & Kuykendall 1949; Keay 1958; Smith 1974; Wong 1982, 1989) and also examines a number of other characters, such as plant architecture, leaf features, stipule form and bud resin for possible variation that may be useful in recognising and grouping species.

4.1 Habit and plant architecture

Of the *Gardenia* spp. included in this study, 14 species (including 13 Sundaland *Gardenia* taxa: *G. barnesii*, *G. beamanii*, *G. carinata*, *G. chanii*, *G. costulata*, *G. elata*, *G. griffithii*, *G. pterocalyx*, *G. sp. A*, *G. sp. B*, *G. subcarinata*, *G. thailandica*, and *G. tubifera*; and the mainland Asian *G. sootepensis*) have solitary stems or trunks that branch, with no buttresses. The tallest *Gardenia* specimen recorded from Sundaland based on herbarium specimens examined is *G. elata* at 30 m (100 ft) high from Bukit Timah, Singapore (Ridley 11332) (Low & Wong 2009). The mainland Asian *G. hainanensis*, *G. jasminoides* and *G. stenophylla*, and the Wallacean *G. mutabilis* are treelets or shrubs (multi-stemmed) 1-few m in height. All taxa examined have smooth to slightly scaly or fissured bark and bark colour ranges from pale yellowish grey brown to dark brown.

These species of *Gardenia* can be grouped into either Leeuwenberg's model or Scarrone's model (Hallé, Oldeman & Tomlinson 1978). All Sundaland taxa, and mainland Asian tree taxa such as *G. sootepensis*, conform to Scarrone's model (Fig. 2), whereas the 'shrub' taxa *G. hainanensis*, *G. jasminoides* and *G. stenophylla* (mainland Asia), and *G. mutabilis* (Wallacea) conform to Leeuwenberg's model (Fig. 3).

Several key characters distinguish these two models, where all axes are orthotropic. In Leeuwenberg's model, height growth is sympodial, by sequential development of modular units developing on the primary trunk, which has limited growth. In Scarrone's model, height growth is by monopodial stem growth, and is rhythmic (episodic, i.e., extension growth is interrupted by periods of slower growth that coincide with branch development). In Leeuwenberg's model, the vegetative axes (trunk and branches) are homogeneous and cannot be differentiated, and the whole architecture develops into an obpyramidal structure with repeating orthotropic modules (each module ceases growth after a short length and distally produces 2-3 branches that are homologous in form and growth behaviour). In Scarrone's model, the vegetative axes are heterogeneous (trunk and branches clearly differentiated), and the branches are closely clustered in distinct tiers. Terminal bud cessation in each branch is associated with terminal flowering, although this is often delayed in the early stages of growth.



Fig. 2. A mature specimen of *Gardenia thailandica*, showing heterogeneous vegetative axes (trunk and branches clearly differentiated); the trunk is monopodial and elongation is interrupted by episodes of slower growth that coincide with branch development.



Fig. 3. A cultivated specimen of *Gardenia jasminoides*, showing stems and branches that are homogeneous in orientation (both orthotropic) and form (similar size and morphology). The whole architecture develops into an obpyramidal structure with repeating modules.

4.2 Stipules, colleters and resin

All *Gardenia* spp. examined have interpetiolar stipules that are connate into a tube and stipule bases are often persistent as annular rings around twig internodes. Two types of stipules are recognised for the *Gardenia* spp. examined in this study, namely, (i) cupular stipules with level margin (whether or not with small lobes or teeth) (Fig. 4) and (ii) sheathing tubular stipules with an oblique mouth (and no distinct teeth, the whole apical portion resembling an acute triangle) (Fig. 5).

Ten taxa, i.e., *G. beamanii*, *G. chanii*, *G. costulata*, *G. elata*, *G. griffithii*, *G. pterocalyx*, *G. sp. A*, *G. sp. B*, *G. subcarinata*, and *G. tubifera*, have cupular stipules that are variable in length, 0.2–1.7 cm long. Three of the 10 taxa with cupular-shaped stipules, i.e., *G. chanii*, *G. costulata*, and *G. pterocalyx*, have a subtruncate stipule margin, whereas the others have 2-several teeth or lobes on the stipular margin. Cupular stipules vary from being loose-fitting or tight-fitting around the internodes where they occur. In contrast, sheathing stipules are invariably tightly sheathing around young shoots or even (terminal) flower buds. Taxa that have sheathing stipules of variable length, 0.5–2 cm long include *G. barnesii*, *G. carinata*, *G. hainanensis*, *G. jasminoides*, *G. mutabilis*, *G. sootepensis*, *G. stenophylla* and *G. thailandica*.

The stipule outer surface is generally glabrous to minutely puberulent, to densely covered with short erect hairs. In contrast, the stipule inner surface is generally covered with a mixture of dark colleters and translucent trichomes that are found (i) as a narrow fringe just along the base; or (ii) covering the basal quarter; or (iii) covering the basal half; or (iv) covering as much as three-quarters of the surface from the base. However, there appeared to be variation between these distribution types within species, so this character seems difficult to use for certain species recognition or grouping.



Fig. 4. An example of cupular stipules with level margin in *Gardenia costulata* (the stipule margin in this case is subtruncate).



Fig. 5. An example of sheathing tubular stipule with an oblique mouth (the whole apical portion resembling an acute triangle), *Gardenia thailandica*.

Among the *Gardenia* spp. examined, resin is present and congeals as a thin coating over the surface of young leaves or flower buds, and also sometimes the outer surface of the stipules. At the shoot tips, resin exudate may not be very conspicuous, present only in minute traces that do not form conspicuous blobs (as in *G. hainanensis*, *G. jasminoides*, *G. mutabilis* and *G. stenophylla*), or it may be present copiously (as in the remaining species; Fig. 6). When copiously present, the resin is generally yellowish amber-brown, except for *G. beamanii* that has black resin, an extremely unusual condition verified with both herbarium and fresh material.

4.3 Leaves

Gardenia spp. have an opposite and decussate leaf arrangement on both trunk and branches, except in the 'shrub' species (*G. hainanensis*, *G. jasminoides*, *G. mutabilis*, *G. stenophylla*), which have opposite to verticillate leaves (the latter usually with three leaves per node). The leaf shape for all taxa is generally obovate. However, leaf shape in some taxa, such as *G. barnesii*, *G. chanii*, *G. elata*, *G. griffithii*, *G. jasminoides* and *G. mutabilis*, can vary to broad-elliptic. *G. stenophylla*, a rheophyte, is the only taxon that has linear leaves.

The leaf bases are cuneate in all *Gardenia* spp. examined, and generally symmetric. However, the leaf base in *G. mutabilis* and *G. thailandica* is often asymmetric (with the two sides at different levels). Leaf apices generally vary from acute to acuminate to obtuse with pointed, short-cuspidate or long-cuspidate tips. However, *G. chanii* and *G. pterocalyx* consistently have obtuse leaf apices, with rounded or pointed to short-cuspidate leaf tips, respectively. Most *Gardenia* spp. examined have thin-coriaceous leaves, except for *G. chanii* and *G. pterocalyx*, which have coriaceous leaves.



Fig. 6. All Sundaland *Gardenia* spp. have vegetative buds covered by resin, just as shown here for *Gardenia subcarinata*, with yellow resin.

Leaf lamina size is generally variable among species, 3.2–28.5 cm long and 1.4–13 cm wide. *G. stenophylla*, as pointed out earlier, has very narrow leaves (0.4–1 cm wide). Anisophylly is observed in all *Gardenia* spp. examined; this involves development of unequal leaf sizes among a ternate cluster (in taxa with Leeuwenberg's model: see above) or between a leaf pair (in taxa with Scarrone's model). Apparently, anisophylly is a common feature of the Gardenieae (Robbrecht & Puff 1986; Robbrecht 1988).

Petiole dimensions are variable, 0.1–3.8 cm long and 1–5 mm wide. The leaf midrib is typically flattened to slightly raised on the upper leaf surface, but always prominent on the lower leaf surface. Generally, the number of leaf secondary veins varies, 6–22 pairs, but *G. jasminoides*, *G. stenophylla* and *G. sp. B* consistently have 6–9 pairs, the least number among all species surveyed for this study. All taxa studied have a scalariform tertiary venation.

Domatia are generally present in all *Gardenia* spp. examined, but this character appears to be unreliable for species distinction. Three common types of domatia (Robbrecht 1988, with minor modifications) were recognised: (i) ciliate pit-domatia (with deep pin-hole form), (ii) tuft-domatia (without any significant depression of the surface), and (iii) glabrous to sparsely hairy pocket-domatia (with shallow depressions).

The upper and lower leaf surfaces are either glabrous or pubescent (puberulent or sparsely to densely hairy). Upper leaf surface hairiness is generally very variable and unreliable for species distinction. However, lower leaf surface hairiness is sometimes useful for distinguishing between closely related taxa, such as (i) *G. beamanii* (glabrous) and *G. griffithii* (glabrescent); (ii) *G. elata* (sparsely hairy) and *G. tubifera*

(glabrous to rarely minute puberulent); and (iii) *G. thailandica* (sparsely hairy) and *G. sootepensis* (densely hairy).

4.4 Flower number and flowering position

All *Gardenia* spp. examined (including *G. sp. B* based on a fruiting branch available for close examination) have terminal solitary flowers.

4.5 Flower pedicels

All taxa examined have variable flower pedicel length (0.1–1.8 cm long) and width (1–4 mm wide). However, this character is useful for distinguishing between some closely related taxa, such as (i) *G. chanii* (0.4–0.6 cm long) and *G. pterocalyx* (1–2.5 cm long); and (ii) *G. elata* var. *elata* (0.1–0.4 cm long) and *G. elata* var. *longipedicellata* (0.7–1 cm long) (Low & Wong 2009).

In fruiting state, pedicel length and width were observed to have slightly increased from the flowering state. However, these changes are insignificant for species distinction.

4.6 Calyx

The *Gardenia* spp. examined have calyx shapes that can be categorised as two groups, namely, (i) calyx distally broadened into obconical or trumpet-like structures (i.e., apex broader than middle or base), and (ii) calyx cylindrical to tubular, sheathing structures (i.e., apex equal to, or narrower than, middle or base). Nine taxa (*G. costulata*, *G. elata*, *G. hainanensis*, *G. jasminoides*, *G. stenophylla*, *G. sp. A*, *G. sp. B*, *G. subcarinata*, and *G. tubifera*) have calyces distally broadened into cuplike obconical



Fig. 7. *Gardenia griffithii* showing terminal solitary flowers that are a constant character of the genus.

structures and three taxa (*G. beamanii*, *G. chanii*, and *G. griffithii*) have calyces distally broadened into trumpet-like structures. Six taxa (*G. barnesii*, *G. carinata*, *G. mutabilis*, *G. pterocalyx*, *G. sootepensis* and *G. thailandica*) have cylindrical to tubular, sheathing calyces.

Generally, the calyx mouth is more-or-less level with a subtruncate to wavy margin (with or without small lobes or teeth); or it is oblique with an acute triangular apex. *G. barnesii*, *G. sootepensis* and *G. thailandica* are the only taxa with the oblique-type calyx margin; the rest of the species surveyed here have level calyx mouths.

Calyx tube length is variable among species, 0.4–10 cm long, but it is the relative length compared with that of the corolla tube that may make the calyx conspicuous. Only three taxa, *G. beamanii*, *G. chanii* and *G. griffithii*, have significantly long calyx tubes that sheath about half or more of the corolla tube length. Only *G. beamanii*, *G. chanii* and *G. griffithii* have broad calyx tube bases (5–10 mm) compared to the others (calyx tube base less than 5 mm across). The calyx tube mouth in four taxa, namely, *G. beamanii*, *G. chanii*, *G. griffithii* and *G. sp. A*, are conspicuously wider than the corolla tube; in the other species, the calyx tube mouth fits the corolla tube tightly.

In texture, the calyx tube is somewhat coriaceous and firm (for the most part) or (in *G. mutabilis*, *G. sootepensis* and *G. thailandica*) it is membranaceous. Only three taxa, *G. beamanii*, *G. chanii* and *G. pterocalyx*, have a glabrous outer calyx surface; in the other species, it is pubescent (puberulent to covered with short erect hairs). The inner calyx tube surface is generally covered with a mixture of dark colleters and translucent trichomes.

4.7 Corolla

All *Gardenia* spp. studied have a hypocrateriform corolla, with a funnel-shaped tube that flares slightly upward at the throat, and 5–13 lobes. The corolla lobes are contorted and overlap to the left in the bud stage, and oblanceolate to obovate or even rounded. Corolla lobe length is very variable among species, 12–53 mm long, but is difficult to use for the distinction of even closely related species pairs because of overlap in dimensions.

Corolla tubes are 2–15 mm long and corolla throats are 3.5–17 mm wide. The mid-tube width is 1.5–8 mm. Among the *Gardenia* spp. examined in this study, *G. chanii* has the thickest corolla tubes, 6–8 mm wide at mid-tube. The outer corolla tube surface is generally glabrous to finely hairy for all *Gardenia* spp. surveyed. The inner corolla tube surface is largely glabrous, except for a sparsely or densely hairy region from just below the throat to slightly below the stamens or sometimes even lower (to mid-tube), in most of the species. Only in *G. elata*, *G. mutabilis* and *G. tubifera* does the hairy region extend to densely cover the corolla mouth and even the base of the corolla lobes.

4.8 Androecium and pollen

The number of stamens among the species ranges from 5 to 13, and corresponds to the number of corolla lobes present. Stamen length ranges 5–18 mm long and is a quarter exerted in an open flower. Anthers are dorsifixed, sessile to subsessile, attached between corolla lobes, and dehisce longitudinally. All taxa examined have pollen grains issued in tetrads.

4.9 Gynoecium, disk and secondary pollen presentation

All *Gardenia* spp. examined have a club-like stigma with 2–7 lobes. Stigmas are 2–12 mm long and 1–8 mm wide. The consistency of stigma lobe number for a particular species is difficult to determine because of few specimens available or the poor condition of the material that does not permit precise determinations. In an open flower, the stigma is fully exerted. For all *Gardenia* species, the style is cylindrical and columnar, 2.5–15.5 cm long. The surface of the style is generally glabrous except for *G. carinata*, *G. sootepensis* and *G. thailandica*, which have pubescent styles.

Secondary pollen presentation (Robbrecht & Puff 1986; Puff *et al.* 1996), also known as the “ixoroid pollination mechanism” (Bremekamp 1966), has been observed for all *Gardenia* flowers examined in the field, and adduced in specimens with an adequate representation of various floral stages (Fig. 8). The impression gained is that it is generally present in the genus. The mechanism for secondary pollen presentation involves the following sequence of events:

- i. anthers dehisce in the flower bud just before flower opens;
- ii. pollen is deposited onto the immature (unreceptive) stigmatic surface;
- iii. flower opens and pollen is presented on the stigmatic head (at this stage, the flower is in the male phase and the stigma has tightly appressed lobes and is still not receptive) (Fig. 9); and
- vi. stigma lobes become receptive and part slightly (the flower enters the female phase).

The number of locules in an ovary has not been possible to study properly for all *Gardenia* spp., because of paucity of material of different stages of development. It is possible that locule number may correlate with the number of stigma lobes, or even with



Fig. 8. A series of colour changes from the floral bud stage to post floral opening and just before flower deterioration in *Gardenia carinata*.



Fig. 9. Secondary pollen presentation in the advanced flower bud stage of *Gardenia jasminoides* (specimen on the right with some corolla lobes removed, showing pollen already deposited on the stigmatic head).

the number of corolla lobes. Generally, the ovary has many ovules with parietal placentation. Besides that, all taxa examined have a glabrous annular disk seated upon the receptacle, as was also reported for *G. imperialis* (Robbrecht 1988).

4.10 Fruits and seeds

Most *Gardenia* spp. examined have fruits with thick pericarp, including a hardened or bony endocarp (which is also known as a stone), except the mainland Asian 'shrub' species *G. hainanensis*, *G. jasminoides* and *G. stenophylla*, which have fruits with thin mesocarp and papery endocarp. The *Gardenia* fruit types recognised in the present study and which could be reconciled with the classification of Rubiaceae fruits offered by Puff (2001) include:

- (i) capsules that dehisce irregularly (neither just loculicidal or septicidal) (found in all Sundaland and mainland Asian tree species, and also *G. mutabilis*, which have thick pericarp and hard endocarp); and
- (ii) drupes (found in the mainland Asian 'shrub' species *G. hainanensis*, *G. jasminoides* and *G. stenophylla*, which have indehiscent fruits with thin-fleshy mesocarp and thin-hard endocarp).

When the fruits are naturally dehiscent, the inside of the fruit is exposed, with the seeds embedded in an orange-red pulp (observed in the field for *G. carinata*, *G. elata* and *G. tubifera*; also noted on specimen labels for *G. pterocalyx* and *G. thailandica*) (Fig. 10).

Most species of *Gardenia* studied have fruit shapes ranging from globose to subglobose, or even ellipsoid. The only taxon that consistently has obovoid fruits is *G. thailandica*. The range of fruit sizes recorded is 0.6–6.5 cm long and 0.6–6 cm wide. The smallest fruit size known in Sundaland (0.6 × 0.6 cm) is found in *G. sp. B*. The

calyx tube is persistent in most *Gardenia* spp. examined at fruiting state; only *G. mutabilis*, *G. sootepensis* and *G. thailandica* have a caducous calyx tube (i.e., the calyx tube detaches very soon from the young fruit stage) so that fruits of these taxa are not persistently crowned with a calyx tube.

The outer fruit surface is smooth in *G. beamanii*, *G. elata*, *G. griffithii*, *G. sp. A*, *G. subcarinata* and *G. tubifera*; lenticellate to rugose in *G. mutabilis*; clearly ridged in *G. chanii*; keeled in *G. pterocalyx*; and ribbed in *G. carinata*, *G. thailandica* and *G. sp. B*. There is a large variation in the way some of these terms are defined or used in different works, so some standardisation for present purposes is required. Here, a ridge is taken to be a slight to pronounced angular prominence on the general surface, usually presenting a sharp angle (such as the junction between two sloping or slightly concave surfaces). A keel is a raised, plate-like or fin-like, elongate structure along a surface. A rib is a slightly prominent vein-like structure on the general surface, rounded in cross-section. However, some taxa may have a combination of two conditions, such as *G. costulata* (smooth to keeled fruit surfaces); and *G. barnesii* (ridged to ribbed fruit surfaces).

All *Gardenia* spp. examined have fruits with many seeds. The seeds are flattened and irregularly angular to rounded and sometimes elliptic, 1–10 mm × 1–8 mm. Seed sizes are difficult to use for characterising species because the precise state of fruit ripeness is often difficult to determine. The testa surface is generally fine-areolate.



Fig. 10. A dehiscent fruit of *Gardenia tubifera* showing seeds embedded in bright red pulp. The split fruit wall portions show a thick pericarp and hard (bony) endocarp.

Chapter Five:

Cladistic Studies and Phylogenetic Relationships

5.1 Cladistic analysis of Sundaland *Gardenia* based on morphological characters

Four most parsimonious trees were retrieved from analysis of the morphological data set (Table 2) and the strict consensus tree (CI = 0.66, RI = 0.77) generated is shown in Fig. 11. The analysis shows that *Gardenia* as represented by the taxa included here is a monophyletic group with overall strong support (BP = 100, $b = 16$). However, resolution within the *Gardenia* clade appears to be very incomplete.

5.1.1 Characterisation of *Gardenia*

Gardenia is distinct from *Porterandia* based on 11 synapomorphic character-states: extra-axillary branches (character 2, character-state 2); domatia present in vein axils on the lower leaf surface (character 9, character-state 2); detached stipule bases often persistent as annular rings around twig internodes (character 12, character-state 2); flowers always solitary (character 13, character-state 2); flowers large (corolla span more than 2 cm in open flower) (character 14, character-state 2); flowers bisexual (character 15, character-state 2); colleters densely covering the basal part of the inner calyx surface (character 26, character-state 2); corolla white turning yellow to orange (character 27, character-state 2); outer surface of corolla tubes glabrous or with scattered fine, short flexuous or minute hairs (character 29, character-state 2); pollen issued as tetrads (character 34, character-state 2); and placental mass orange-red in ripe fruits (character 41, character-state 2).

Table 2. Data matrix of 41 character values scored for a cladistic analysis of *Gardenia* spp. and associated taxa.

Characters are numbered 1–41 following the list provided by Table 1 and taxa are marked **G1–G17** (as listed below for *Gardenia*) and **P1–P2** (as listed below for *Porterandia*). A dash (-) under Character 4 (resin exudate colour upon congealing) indicates absence of colour (i.e., clear resin).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>G1</i>	1	2	3	1	1	2	1	2	2	2	2	2	2	2	2	1	2	1	1	1
<i>G2</i>	1	2	3	2	1	2	1	1	2	1	1	2	2	2	2	2	1	2	1	2
<i>G3</i>	1	2	3	1	1	2	1	2	2	2	2	2	2	2	2	1	2	1	1	1
<i>G4</i>	1	2	3	1	1	1	2	1	2	1	3	2	2	2	2	2	1	2	1	2
<i>G5</i>	1	2	3	1	1	2	1	1	2	1	3	2	2	2	2	1	1	2	1	1
<i>G6</i>	1	2	3	1	1	2	1	2	2	1	1	2	2	2	2	1	1	1	1	1
<i>G7</i>	1	2	3	1	1	2	1	2	2	1	1	2	2	2	2	2	1	2	1	1
<i>G8</i>	2	2	2	-	1	2	1	1	2	2	2	2	2	2	2	1	1	1	1	2
<i>G9</i>	2	2	2	-	1	2	1	1	2	2	2	2	2	2	2	1	1	1	1	1
<i>G10</i>	2	2	2	-	1	2	1	1	2	2	2	2	2	2	2	1	2	1	2	1
<i>G11</i>	1	2	3	1	1	1	2	1	2	1	3	2	2	2	2	1	2	2	1	2
<i>G12</i>	1	2	3	1	1	2	1	2	2	2	2	2	2	2	2	1	2	1	2	1
<i>G13</i>	1	2	3	1	1	2	1	1	2	1	1	2	2	2	2	1	1	1	1	1
<i>G14</i>	2	2	2	-	2	2	1	1	2	2	2	2	2	2	2	1	1	1	1	2
<i>G15</i>	1	2	3	1	1	2	1	1	2	1	1	2	2	2	2	1	1	1	1	1
<i>G16</i>	1	2	3	1	1	2	1	2	2	2	2	2	2	2	2	1	2	1	2	1
<i>G17</i>	1	2	3	1	1	2	1	1	2	1	1	2	2	2	2	1	1	1	1	1
<i>P1</i>	1	1	1	-	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>P2</i>	1	1	1	-	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Table 2 continued next page

21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41
3	3	1	1	2	2	2	1,2	2	1	2	2	1	2	1	1	1,3	2	1	2	2
1	1	1	2	2	2	2	1	2	1	2	2	1	2	1	1	1	1	1	2	2
3	2	1	1	2	2	2	1,2,3	2	1	2	1	2	2	1	1	1,3	2	1	2	2
3	1	1	2	2	2	2	3	2	1	2	2	1	2	1	1	1	2	1	2	2
3	1	1	1	2	2	2	1,2	2	1	2	2	1	2	1	1	1	1,3	1	2	2
1	1	1	1	2	2	2	1,2	2	2	2	2	1	2	1	1,2	1	1	1	2	2
1	1	1	2	2	2	2	1,3	2	1	2	2	1	2	1	1,2	1	1	1	2	2
3	3	1	1	3	2	2	1,2	2	1	2	2	1	2	1	-	1	2	1	1	2
3	3	1	1	3	2	2	1,2,3	2	1	2	2	1	2	1	1	1,3	3	1	1	2
2	1	1	1	3	2	2	1	2	2	2	2	1	2	2	2	1	1	2	2	2
3	1	1	1	2	2	2	1,2	2	1	2	2	1	2	1	1	1	3	1	2	2
2	1	2	1	1	2	2	1,2	2	1	1	1	1	2	2	1	2	2	1	2	2
1	1	1	2	2	2	2	1,2	2	1	2	2	2	2	1	1	1	1	1	2	2
3	3	1	1	3	2	2	1	2	1	2	2	1	2	1	1	3	3	1	1	2
3	1	1	1	2	2	2	1,2	2	1	2	2	1	2	1	2	1	1	1	2	2
2	1	2	1	1	2	2	1,2	2	1	1	1	1	2	2	1	2	2	1	2	2
1	1	1	1	2	2	2	1,2	2	2	2	2	1	2	1	1,2	1	1	1	2	2
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

***Gardenia* (ingroup)**

G1 = barnesii G5 = costulata

G2 = beamanii G6 = elata

G3 = carinata G7 = griffithii

G4 = chanii G8 = hainanensis

G9 = jasminoides

G10 = mutabilis

G11 = pterocalyx

G12 = sootepensis

G13 = sp. A

G14 = stenophylla

G15 = subcarinata

G16 = thailandica

G17 = tubifera

***Porterandia* (outgroup)**

P1 = lambirensis

P2 = scortechinii

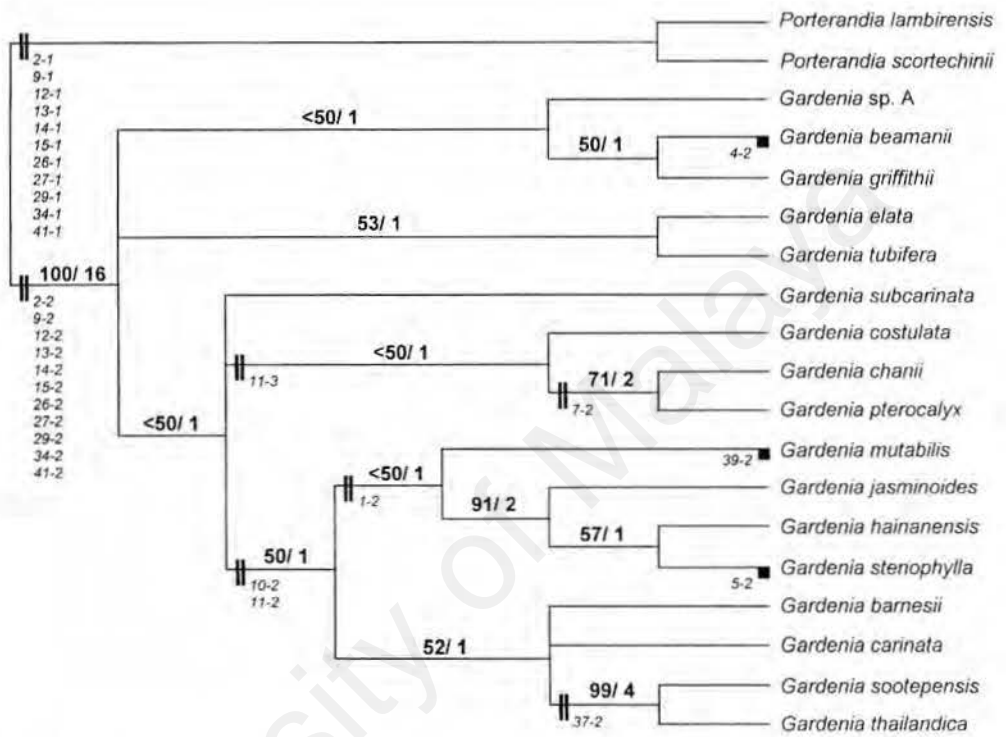


Fig. 11. Strict consensus tree of four most parsimonious trees generated by a morphological data set for 19 taxa (tree length = 73). Bootstrap values (BP), followed by Bremer support values or decay values (*b*), are mapped onto the tree and placed above branches. Selected characters (based on the list provided in Table 1) that are synapomorphic (present for entire lineages) with consistency index = 1 and retention index = 1 are indicated as double bars and given below branches. The number of each mapped character from Table 1 is followed by the character-state, e.g., 2-1 (character 2, character-state 1). Characters with consistency index = 1 and retention index = 0 (autapomorphies for terminal taxa) are indicated by a black flag.

5.1.2 Resolution within the *Gardenia* clade

Generally, the 17 *Gardenia* taxa were poorly resolved, with only three statistically well-supported groups (bootstrap support (BP) value above 70), namely, the *G. chanii-pterocalyx* group (BP = 71, $b = 2$); the *G. hainanensis-jasminoides-stenophylla* group (BP = 91, $b = 2$); and the *G. sootepensis-thailandica* group (BP = 99, $b = 4$).

The ***G. chanii-pterocalyx* group** (BP = 71, $b = 2$) includes two Sundaland taxa based on a single synapomorphic character-state (unique character-states that appear only in a lineage), i.e., leaf texture stiffly thick-coriaceous (character 7, character-state 2). Besides that, these two taxa also have a common ecological preference, occurring in peat-swamp forest, but geographically, they are distinct. *G. chanii* is restricted to Southwest Borneo (west coast of Sabah, Brunei, west coast of Sarawak), whereas *G. pterocalyx* occurs in the Malay Peninsula, Sumatra and south Borneo (Low & Wong 2007). *G. costulata* was resolved basally to this pair, but the relationship was weakly supported (BP = <50, $b = 1$). Notwithstanding, these three taxa share a potential synapomorphic character-state, i.e., stipule margins subtruncate (character 11, character-state 3) (CI = 1, RI = 1). These three taxa have longitudinal low keels present along their calyx tube that do not form wings or spurs at the distal part of the calyx, and so appear distinct as a potentially related group, although presently there is not enough statistical support through the analysis. Calyx characters have been much used for species distinction (St. John & Kuykendall 1949; Smith 1974; Jongkind 2005; Wong 1982, 1989; Low & Wong 2007, 2009).

The ***G. hainanensis-jasminoides-stenophylla* group** (BP = 91, $b = 2$) includes three mainland Asian taxa and had no morphological synapomorphy in the present

analysis. Although they have a calyx with long, linear, bilaterally flattened spurs extending beyond the calyx margin (character 22, character-state 3), this feature is also found in *G. barnesii* that was resolved in a different clade. Resolved basally to the *G. hainanensis-jasminoides-stenophylla* group was *G. mutabilis*, a Wallacea taxon (the Philippines and Sulawesi), with weak association (BP = <50, $b = 1$). The *G. hainanensis-jasminoides-stenophylla* group and *G. mutabilis* were clustered together based on two potential synapomorphic character-states, namely, Leeuwenberg's model of growth architecture (character 1, character-state 2); and resin exudate present in minute traces, never congealing as blobs on the young shoot tips (character 3, character-state 2). *G. mutabilis* is distinct from the *G. hainanensis-jasminoides-stenophylla* group by its calyx lacking long spurs

The ***G. sootepensis-thailandica* group** (BP = 99, $b = 4$) includes two mainland Asian taxa that clustered together based on a single synapomorphic character-state, i.e., obovoid fruit shape (character 37, character-state 2). *G. barnesii* and *G. carinata* formed a polytomy with the *G. sootepensis-thailandica* group, but this relationship was weakly supported (BP = 52, $b = 1$).

These three well-supported groups, namely, the *G. chanii-pterocalyx* group, the *G. hainanensis-jasminoides-stenophylla* group and the *G. sootepensis-thailandica* group, were part of a larger but weakly supported primary clade (BP = 50, $b = 1$). This clade consists of mostly mainland Asian and Wallacea taxa, with the exception of *G. barnesii* that also occurs in the northern fringe of Sundaland (Philippines: Palawan). These taxa share two potential synapomorphic character-states, namely, sheathing stipule (character 10, character-state 2) and stipule margin with a single triangular apex (character 11, character-state 2). There appears to be little significance in this

relationship except for the weak separation between the mainland Asian-Wallacean group of taxa from the predominantly Sundaland group.

5.1.3 Summary

As a whole, the cladistic analysis based on morphological characters was generally uninformative. It is possible that addition of further characters, such as palynological or micro-morphological (including stomatal and epidermal) characters, and more taxa could enhance resolution within similar analyses. Alternatively, the lack of autapomorphic character-states defining individual taxa, which are defined by combinations of character-states, could also imply complex lineage development, so that straightforward analysis of morphological states returns little clear resolution.

5.2 Phylogenetic analyses of *Gardenia* and associated taxa based on chloroplast (*atpB-rbcL* and *trnT-F*) and nuclear (ITS) gene regions

5.2.1 Analysis of the *atpB-rbcL* data set

A total of 788 nucleotide positions were obtained from this region. Of these, 32 (4.06%) nucleotide positions were variable, including 23 (2.92%) that were informative (see Table 3). The results from the Maximum Parsimony and Bayesian analyses were congruent. Resolution at generic level was highly supported but resolution at specific level (within *Gardenia*) was poor. This could probably be due to a high level of conservation of this gene within the genus. Fig. 12 shows the topology obtained with both Maximum Parsimony and Bayesian analyses, with the corresponding support for, or confidence levels of, branch robustness indicated.

Table 3. Key parameters relevant to phylogenetic analyses of chloroplast regions *atpB-rbcL* and *trnT-F*, nuclear region (ITS), the combined chloroplast regions, and the combined chloroplast and nuclear regions.

Characteristic	Chloroplast region		Combined Chloroplast regions	Nuclear region	Combined Chloroplast and Nuclear regions
	<i>atpB-rbcL</i>	<i>trnT-F</i>		<i>ITS</i>	
No. of terminals	19	19	19	19	19
No. of taxa	16	16	16	16	16
Total no. of characters	788	893	1681	651	2332
Invariable characters	756	877	1633	351	1984
Parsimony uninformative characters	9	3	12	115	127
Parsimony informative characters (%)	23 (2.92%)	13 (1.46%)	36 (2.14%)	185 (28.42%)	221 (9.48%)
Tree length	37	17	54	484	557
Consistency index (CI)	0.8919	0.9412	0.9074	0.7355	0.7271
Retention index (RI)	0.9259	0.9583	0.7311	0.9359	0.7256
Score of best tree(s) found	37	17	54	484	557
No. of tree(s) retained	4	1	2	14	6

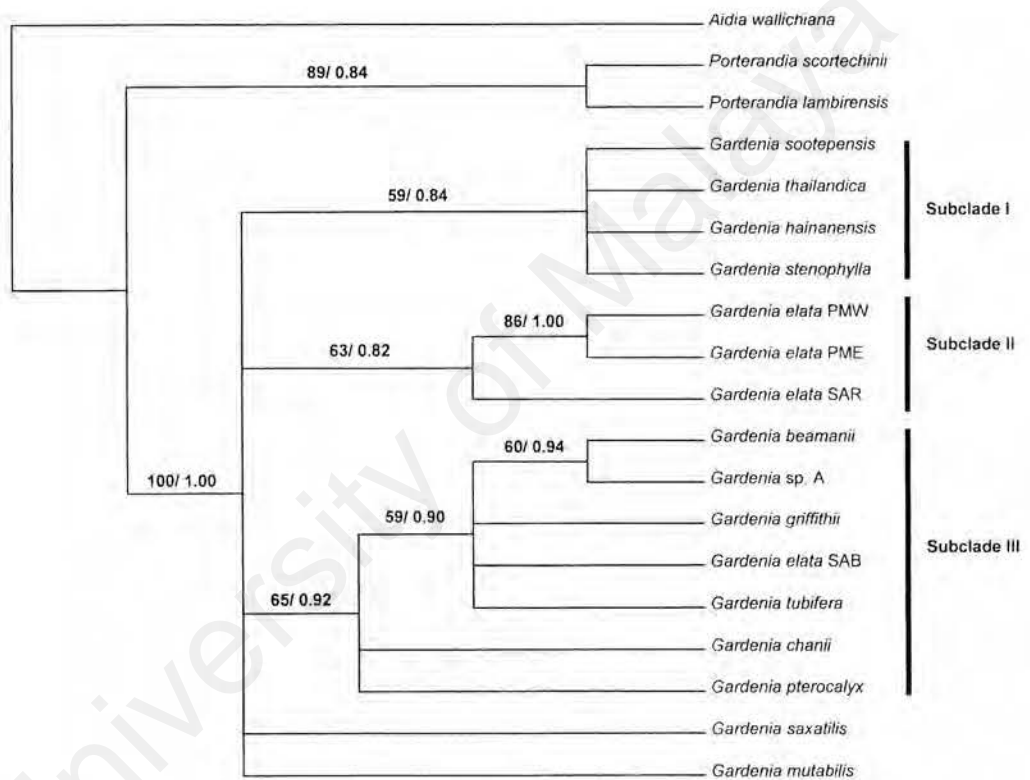


Fig. 12. Majority rule consensus tree generated by Maximum Parsimony analysis of the chloroplast DNA region, *atpB-rbcL*, for 19 terminal taxa. Bootstrap values (BP) mapped onto this tree are placed above branches, followed by Posterior Probability values (PP) calculated from a separate Bayesian analysis yielding congruent topology.

The ingroup (*Gardenia* and *Porterandia*) was adequately polarised by the outgroup (*Aidia*). Within the ingroup, two well-supported monophyletic clades, namely, the *Gardenia* clade and the *Porterandia* clade, were formed. The *Gardenia* clade was highly supported overall (BP = 100 and PP = 1.00), while the *Porterandia* clade was only highly supported based on BP (89).

Within the *Gardenia* clade, a polytomy was formed, consisting of subclades I, II, and III (all weakly supported), and *G. saxatilis* and *G. mutabilis*. Subclade I is a polytomy of *G. hainanensis*, *G. sootepensis*, *G. stenophylla* and *G. thailandica* (BP = 59, PP = 0.84). Subclade II consists of three *G. elata* terminals, namely, *G. elata* PME, *G. elata* PMW and *G. elata* SAR (BP = 63, PP = 0.82). *G. elata* PME and *G. elata* PMW associated with strong support (BP = 86, PP = 1.00). The fourth *G. elata* terminal, *G. elata* SAB, resolved within Subclade III rather than with the other *G. elata* terminals in Subclade II. Subclade III (seven terminals) is the largest subclade formed (BP = 65, PP = 0.92). In this subclade, only the weak clustering of *G. beamanii* and *G. sp. A* (BP = 60, PP = 0.94) was noticeable, otherwise there was hardly any special clustering of the species. *G. elata* SAB, *G. griffithii* and *G. tubifera* resolved as a polytomy together with the *G. beamanii* - *G. sp. A* cluster.

5.2.2 Analysis of the *trnT-F* data set

This region has the longest DNA sequence compared to the other two regions, with a total of 893 nucleotide positions. However, only 16 (1.79%) nucleotide positions were variable, with 13 (1.46%) parsimoniously informative, i.e., this region has the lowest number of variable nucleotide positions compared to the other regions (Table 3). The results obtained from the Maximum Parsimony and Bayesian analyses were congruent. Resolution at generic level was well supported but species-level resolution

(within *Gardenia*) was poor. Again, this is probably due to a high degree of conservation of this gene. Fig. 13 shows the cladogram obtained with both Maximum Parsimony and Bayesian analyses.

The outgroup (*Aidia*) adequately polarised the ingroup (*Gardenia* and *Porterandia*). Within the ingroup, two monophyletic clades with high statistical support were formed, namely the *Gardenia* clade (BP = 100, PP = 1.00) and the *Porterandia* clade (BP = 97, PP = 1.00).

In the *Gardenia* clade, *G. saxatilis* was basally resolved. Its sister clade (weakly supported; BP = 63, PP = 0.91) was an extensive polytomy of individual species, except for two discernible subclades (I and II), of two terminals each. Subclade I consists of *G. elata* PME and *G. elata* PMW, with poor bootstrap (BP = 61) but significant Bayesian support (PP = 0.97). Subclade II includes *G. hainanensis* and *G. stenophylla*, weakly supported by BP (55) but highly supported by PP (0.98).

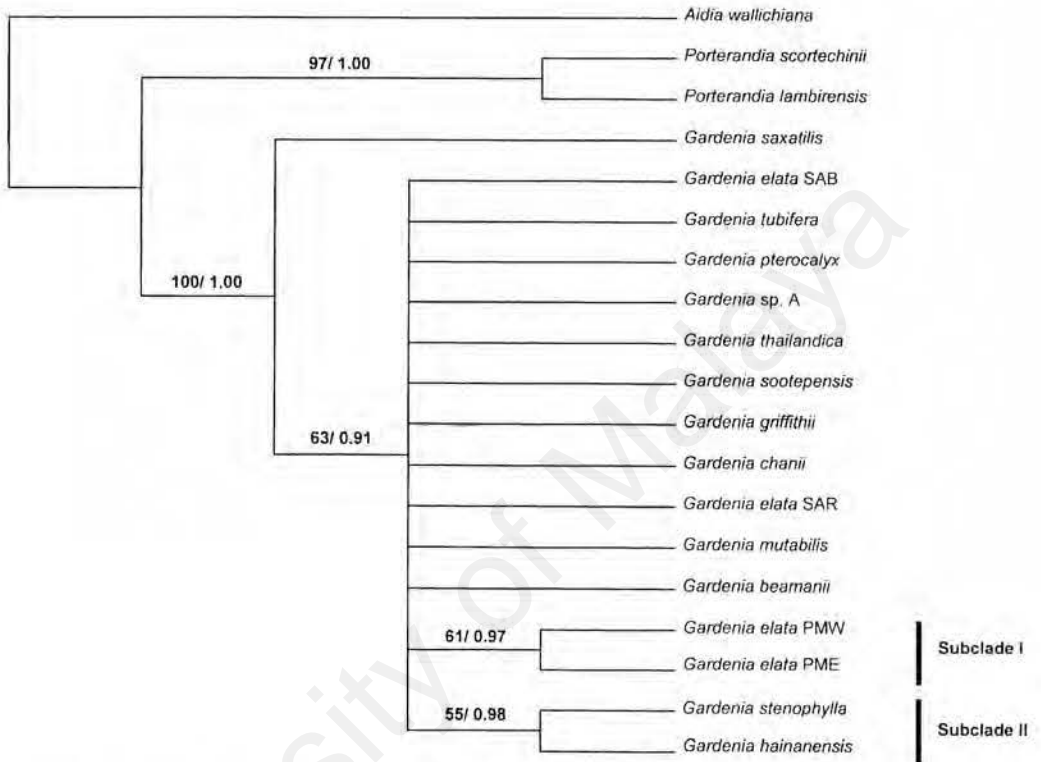


Fig. 13. Majority rule consensus tree generated by Maximum Parsimony analysis of the chloroplast DNA region, *trnT-F*, for 19 terminal taxa. Bootstrap values (BP) mapped onto this tree are placed above branches, followed by Posterior Probability values (PP) calculated from a separate Bayesian analysis yielding congruent topology.

5.2.3 Analysis of the combined chloroplast (*atpB-rbcL* + *trnT-F*) data

sets

In this data set, a total of 1,681 nucleotide positions were assembled, with 48 (2.9%) variable and 36 (2.1%) parsimoniously informative. The results from both Maximum Parsimony and Bayesian analyses were congruent. Support for generic resolution was improved with higher BP and PP support values, compared to the individual plastid analyses. However, support for species associations in *Gardenia* was still weak. Topology produced for this data set (Fig. 14) was very much influenced by the *atpB-rbcL* region (by comparison with Fig. 12). This appears to be due to the *atpB-rbcL* region having twice the number of variable nucleotide positions as in the *trnT-F* region (see Table 3).

Within the ingroup, two well-supported clades were formed, namely the *Gardenia* clade (BP = 100, PP = 1.00) and the *Porterandia* clade (BP = 100, PP = 1.00). In the *Gardenia* clade, *G. saxatilis* resolved in the most basal position and sister to a polytomy of reasonable support (BP = 70, PP = 0.97), formed by *G. mutabilis* and subclades I, II and III (with numbering adopted from Fig. 12, where the same subclades are found). This appears to consolidate the basal position of the mainland Asiatic *G. saxatilis*.

In Subclade I (BP = 61, PP = 0.92), of four terminals, only *G. stenophylla* and *G. hainanensis* indicated weak association (BP = 63, PP = 0.94), which was not displayed in the individual *atpB-rbcL* analysis (Fig. 12). Subclade II (BP = 64, PP = 0.87) is identical to that in the individual *atpB-rbcL* analysis (Fig. 12). As in that analysis, the pair of *G. elata* PME and *G. elata* PMW formed a well-supported association (BP = 95, PP = 1.00). Subclade III, the largest clade with seven terminals,

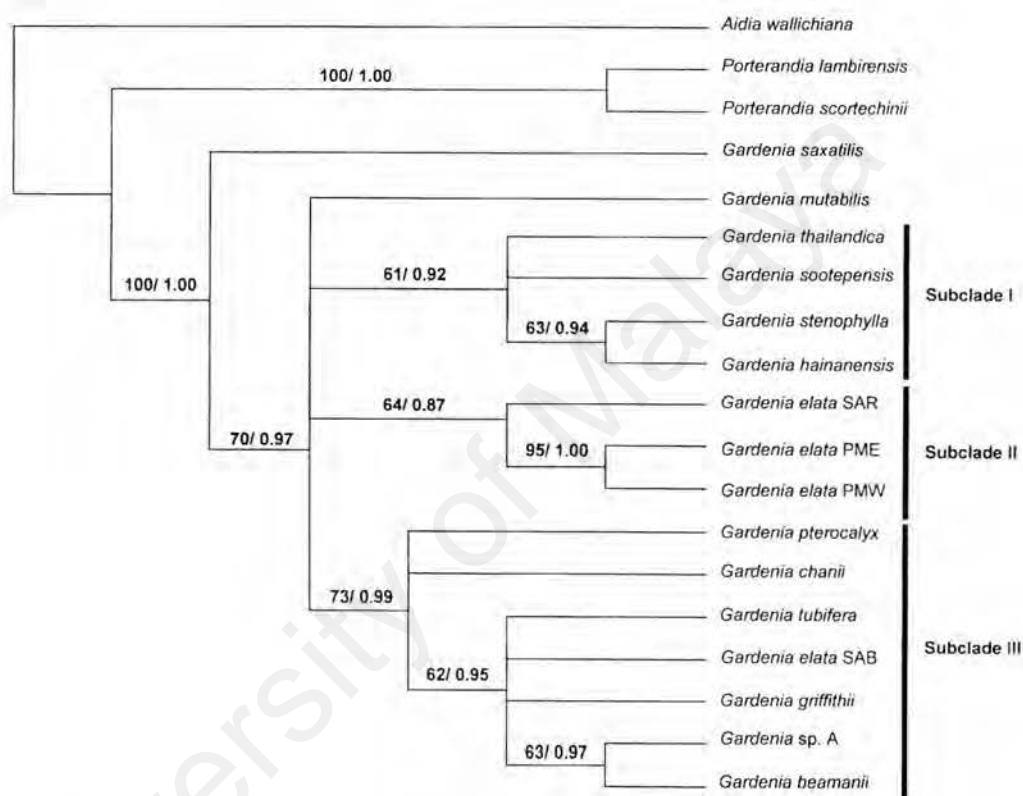


Fig. 14. Majority rule consensus tree generated by Maximum Parsimony analysis of the combined chloroplast DNA regions, namely, *atpB-rbcL* and *trnT-F*, for 19 terminal taxa. Bootstrap values (BP) mapped onto this tree are placed above branches, followed by Posterior Probability values (PP) calculated from a separate Bayesian analysis yielding congruent topology.

again had somewhat uncertain support (BP = 73, PP = 0.99) as in the individual *atpB-rbcL* analysis (Fig. 12). The pair of *G. beamanii* and *G. sp. A* again clustered with weak bootstrap support (BP = 63) but acceptable Bayesian support (PP = 0.97).

5.2.4 Phylogenetic analysis of the nuclear (ITS) region

The DNA sequence obtained for this region (651 nucleotide positions) is shorter than the other two regions (*atpB-rbcL* & *trnT-F*), but yielded the highest number of variable nucleotide positions. There were a total of 300 (46.08%) variable nucleotide positions, with 185 (28.42%) that were parsimoniously informative. The topologies obtained from both Maximum Parsimony and Bayesian analyses were congruent. The overall better resolution suggested that this region is highly informative at both generic and specific levels. Figure 15 represents the combined results for this data set based on Maximum Parsimony and Bayesian analyses. The outgroup (*Aidia*) neatly polarised the ingroup (*Gardenia* and *Porterandia*). Within the ingroup, two well-supported clades were formed, representing *Gardenia* (BP = 100, PP = 1.00) and *Porterandia* (BP = 87, PP = 1.00).

Within the *Gardenia* clade, the primary resolution was a polytomy of five subclades (numbered I to V in the cladogram). Subclade I (BP = 68, PP = 0.96) is a cluster of three terminals, with *G. chunii* basal to the strongly associated pair of *G. hainanensis* and *G. stenophylla* (BP = 89, PP = 1.00). Subclade II is formed of *G. pterocalyx* and *G. tubifera* (with good support; BP = 93, PP = 1.00).

Subclade III is the largest subclade within *Gardenia*, in which its seven terminals were grouped together with high statistical support (BP = 92, PP = 0.98). In this subclade, two strongly supported major groupings resolved, viz., Group IIIA with

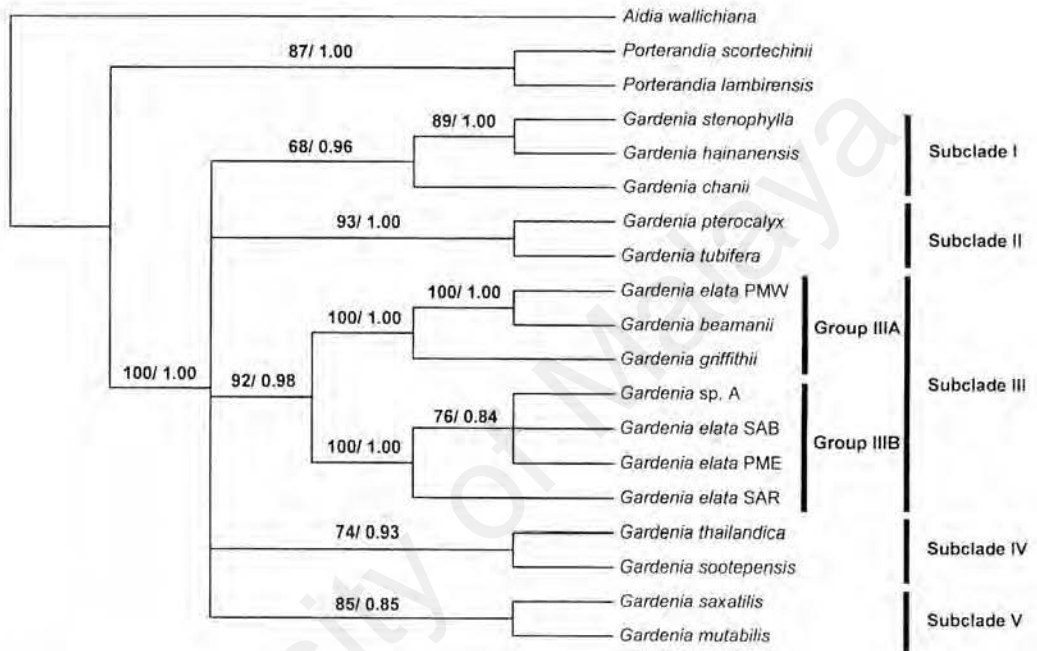


Fig. 15. Majority rule consensus tree generated by Maximum Parsimony analysis of the nuclear ITS region, for 19 terminal taxa. Bootstrap values (BP) mapped onto this tree are placed above branches, followed by Posterior Probability values (PP) calculated from a separate Bayesian analysis yielding congruent topology.

three terminals (BP = 100, PP = 1.00), and Group IIIB with four terminals (BP = 100, PP = 1.00). In Group IIIA, *G. griffithii* resolved basal to the well-supported pair of *G. beamanii* and *G. elata* PMW (BP = 100, PP = 1.00). Group IIIB consisted of the *G. elata* provenances SAR (basal to the others), PME and SAB together with *G. sp. A*; The latter three had good bootstrap support (BP = 76) but poor Bayesian support (PP = 0.84).

Subclade IV is made of *G. thailandica* and *G. sootepensis* clustering with weak support (BP = 74, PP = 0.93). *G. saxatilis* and *G. mutabilis* formed Subclade V, highly supported with BP (85) but only weakly by PP (0.85).

5.2.5 Phylogenetic analysis based on the combined chloroplast DNA (*atpB-rbcL* + *trnT-F*) and nuclear DNA (ITS) data sets

Overall, the topology from this combined analysis was very much influenced by (similar to) the ITS region, which had the most number of variable parsimonious sites among the regions used (see Table 3). Fig. 16 shows the topology obtained from this combined analysis, based on the Maximum Parsimony and Bayesian analyses giving congruent topologies. Both ingroup genera (*Gardenia* and *Porterandia*) were fully supported monophyletic groups, as in the combined cpDNA analysis.

Within the *Gardenia* clade, a polytomy was formed that includes *G. chanii* and subclades I, II, III, IV and V (these are numbered as in the ITS analysis in Fig. 15, with identical subclade composition, except that *G. chanii* associated uncertainly with Subclade I in the ITS analysis). Associations obtained from this combined cpDNA-nrITS analysis which have substantially the same composition as those from the ITS analysis, and with similarly high or improved levels of support, include Subclade I (*G.*

hainanensis and *G. stenophylla*) (BP = 96, PP = 1.00); Subclade II (*G. tubifera* and *G. pterocalyx*) (BP = 91, PP = 1.00); Subclade IV (*G. sootepensis* and *G. thailandica*) (BP = 86, PP = 0.99); and Subclade V (*G. mutabilis* and *G. saxatilis*) (BP = 75, PP = 0.96).

Subclade III is well-supported (BP = 87, PP = 97) with the same seven terminals as in the ITS analysis (Fig. 15), namely *G. beamanii*, *G. elata* PME, *G. elata* PMW, *G. elata* SAB, *G. elata* SAR, *G. griffithii* and *G. sp. A*. This subclade III further resolved as two fully supported groups (IIIA and IIIB). In Group IIIA, *G. elata* PMW and *G. beamanii* associated as a pair with nearly complete support (BP = 99, PP = 1.00), and sister to *G. griffithii*. Group IIIB shows weak clustering of *G. elata* SAR and *G. elata* PME (BP = 61, PP = 0.73), and of *G. elata* SAB and *G. sp. A* (BP = 53, PP = 0.71).

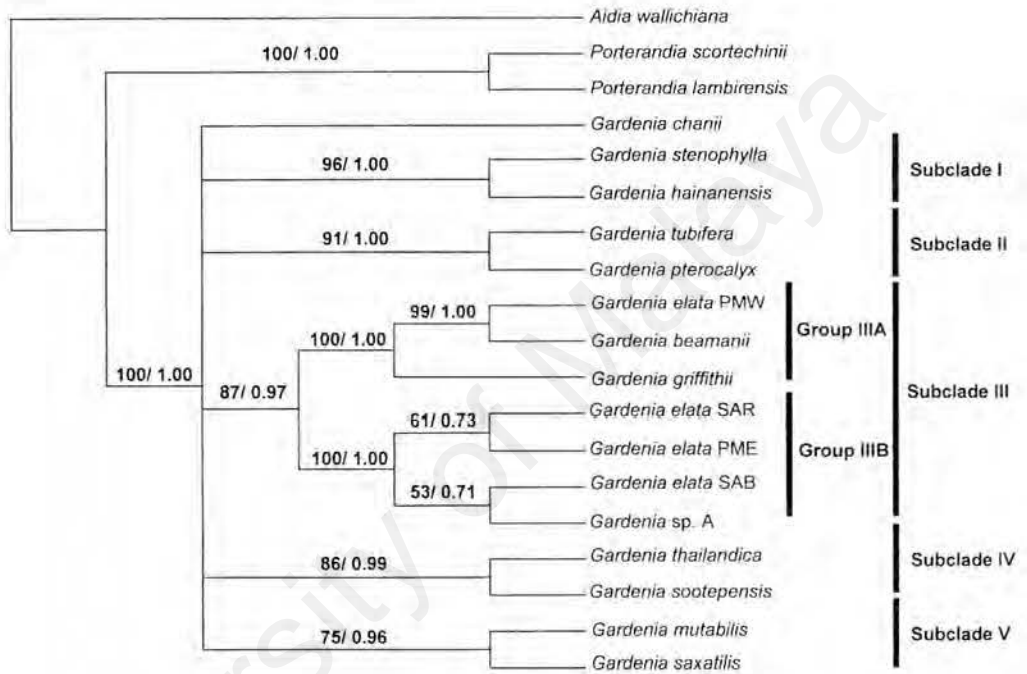


Fig. 16. Majority rule consensus tree generated by Maximum Parsimony analysis of the combined chloroplast DNA regions (*atpB-rbcL* and *trnT-F*) and nuclear DNA (ITS) region, for 19 terminal taxa. Bootstrap values (BP) mapped onto this tree are placed above branches, followed by Posterior Probability values (PP) calculated from a separate Bayesian analysis yielding congruent topology.

5.2.6 Interpretation of phylogenetic relationships of Sundaland

Gardenia

The phylogenetic relationships of Sundaland and mainland Asiatic *Gardenia* are mainly interpreted based on the combined cpDNA-nrITS analysis (Fig. 16), which shows the best resolution with well-supported nodes from both Maximum Parsimony and Bayesian analyses. Reference is also made, at relevant points, to the combined chloroplast genealogy obtained (Fig. 14) and the nuclear DNA genealogy (ITS, Fig. 15).

All species of the genus *Gardenia* in this analysis form a fully supported clade, and distinct from *Porterandia*, a sister clade of its own (this was also reflected in the individual *atpB-rbcL*, *trnT-F* and ITS analyses, as well as the combined cpDNA analysis). This provides basic indication that we are dealing with a coherent generic group represented by the species of *Gardenia* sampled.

Within *Gardenia*, five main subclades can be identified (subclades I to V in Fig. 16), based on strong branch support values: the *G. hainanensis-stenophylla* subclade (Subclade I); the *G. tubifera-pterocalyx* subclade (Subclade II); the *G. beamanii-elata-griffithii* subclade (Subclade III); the *G. sootepensis-thailandica* subclade (Subclade IV); and the *G. mutabilis-saxatilis* subclade (Subclade V). However, only two, namely, the *G. hainanensis-stenophylla* and *G. sootepensis-thailandica* subclades (i.e., Subclades I and IV), are each characterized by conspicuous calyx morphological character-states unique to subclade members.

5.2.6.1 Groups distinguished by unique morphological characters

The *G. hainanensis-stenophylla* subclade (Subclade I in Fig. 16) includes two mainland Asian taxa, *G. hainanensis* and *G. stenophylla*. They share a common calyx

morphological character-state unique to the subclade and which distinguishes them from other taxa (i.e., a likely synapomorphy in cladistic terminology): long narrow spurs (extending from the calyx keels) that protrude beyond the calyx tube margin. Their association is also well-supported in the individual *trnT-F* and ITS analyses.

The *G. sootepensis-thailandica* subclade (Subclade IV in Fig. 16) also includes two mainland Asian taxa, namely, *G. thailandica* and *G. sootepensis*. Several morphological character-states unique to this subclade, and not found in other SE Asian-Sundaland species, include (1) the tightly sheathing calyx tube with an oblique margin, (2) obovoid mature fruit shape, and (3) five corolla lobes. As (3) is also known in other species, such as *G. subacaulis* Stapf & Hutch. from Africa, it is an unlikely synapomorphy (although within the SE Asian - Sundaland analysis it is a meaningful supporting character for group distinction). On the other hand, (1) and (2) are possible synapomorphies, as judged from a general survey of the literature and material of extra-Asiatic taxa. However, it is to be noted that a full morphological study of other *Gardenia* species outside SE Asia has not yet received recent attention.

The distinction of these two subclades by both molecular and morphological characteristics suggests possibly fundamental divergences between these mainland Asiatic groups from other Sundaland taxa.

5.2.6.2 Groups apparently without shared morphological characters

Subclade II: the *G. tubifera-pterocalyx* alliance

The *G. tubifera-pterocalyx* subclade (Subclade II of Fig. 16) includes *G. tubifera* and *G. pterocalyx*. These two endemic Sundaland *Gardenia* taxa have rather different calyx morphology (*G. tubifera* has cupular-obconical calyx and the outer calyx tube

surface smooth, whereas *G. pterocalyx* has broad-tubular calyx and the outer calyx tube surface with keels). There also appears to be no obvious morphological similarities unique to the subclade. However, these two taxa have a common habitat preference, as they are sympatric congeners, occurring together in coastal-peatswamp forests on both sides of the South China Sea.

The association of this pair of species is not consistent. In the combined chloroplast genealogy (Fig. 14), *G. tubifera* shows equivocal association (indicated by weak bootstrap and acceptable Bayesian support) with the group containing *G. beamanii*, *G. elata* SAB, *G. griffithii* and *G. sp. A*; whereas *G. pterocalyx* is an unresolved branch basal to this. On the other hand, in the nuclear (ITS) genealogy (Fig. 15), *G. tubifera* strongly associates with *G. pterocalyx*, as is shown in the combined cpDNA-nrITS analysis (Fig. 16).

Thus, *G. pterocalyx* and *G. tubifera* associate differently in the chloroplast and nuclear DNA genealogies. It has been shown in a number of studies (e.g., Mouly *et al.* 2009b; Kim & Donoghue 2008; Maurin *et al.* 2007) that incongruency between chloroplast and nuclear genealogies may reflect complex speciation processes such as paralogy, incomplete lineage sorting, or hybridisation.

Sang & Zhong (2000) demonstrated that when multiple gene lineages can be considered, the time of divergence of each gene in an 'intermediate' taxon (one showing discordant genealogies) is nearly equal (or not different) between the putative 'parental' or 'extreme' taxa in the case of hybridisation, but differs significantly with differential lineage sorting (polymorphisms due to random ancestral sorting) or paralogy (gene duplication or deletion). The relative positions of divergence among *G. tubifera* and *G.*

ptero calyx and *G. elata* SAB are the same in both cpDNA (Fig. 14) or nrITS (Fig. 15) topologies, assuming a molecular clock premise (i.e., an even rate of base substitution or genetic change during lineage evolution). Also, with incomplete lineage sorting, a degree of polymorphism would be expected at both population and individual levels (Mouly *et al.* 2009b). This was not observed for the sampled *Gardenia* spp., which populations appeared rather consistent morphologically; also background “noise” in the individual molecular profiles was not apparent or minimal and did not cause ambiguity or difficulty during alignments of gene sequences.

According to Pan *et al.* (2007), Hegarty & Hiscock (2005), Soltis *et al.* (1998), Grant (1981), and Stebbins (1950), interspecific hybridisation among plants is common, so the close association between *G. tubifera* and *G. pterocalyx* could indicate past hybridisation between these two taxa. Based on the chloroplast genealogy (Fig. 14), which is taken to represent maternal inheritance (Mogensen, 1996), five of the seven taxa of that clade grouped together with equivocal support (indicated by weak bootstrap support but acceptable Bayesian support), namely, *G. beamanii*, *G. elata* SAB, *G. griffithii*, *G. tubifera*, and *G. sp. A*, have smooth calyx tube and so appear to be a coherent morphologically defined group.

On the other hand, based on the nuclear (ITS) genealogy (Fig. 15), *G. tubifera* was strongly related to *G. pterocalyx* as an individual subclade. This suggests that these two taxa could have been derived from a common paternal ancestor. The discordance between the chloroplast and nuclear topologies, and the individual relationships of *G. tubifera* could feasibly have been derived from introgression of *G. pterocalyx* or its ancestor into the lineage of *G. tubifera*. In terms of Fig. 16, there has been likely introgression of Subclade II into Subclade III.

Subclade III: the *G. beamanii-elata-griffithii*-sp. A alliance

The *G. beamanii-elata-griffithii*-sp. A subclade (Subclade III in Fig. 16) consists of four Sundaland taxa, namely, *G. beamanii*, *G. elata*, *G. griffithii* and *G. sp. A*. Only three of these taxa (i.e., other than *G. sp. A*, which has variable mature fruit size) are similar in having mature fruit diameter exceeding 3 cm (all other Southeast Asian-Sundaland species so far known have smaller fruits), so that this character-state is not a synapomorphy for the subclade. There appears to be no obvious morphological synapomorphy for this subclade III, unless *G. tubifera* from Subclade II is grouped with it, when the whole group would then be unique among Sundaland taxa by its smooth calyx tube character-state. However, as discussed in the foregoing (Subclade II), the position of *G. tubifera* in Subclade II (Fig. 16) could be due to introgression of a Subclade II ancestor into Subclade III. That is, *G. tubifera* is probably derived from past hybridisation events.

The relationships within the *G. beamanii-elata-griffithii*-sp. A subclade are interesting to highlight, as it includes *G. elata*, the taxon with the widest distribution in Sundaland. Two groups were recognised in this subclade, namely, the *G. beamanii-griffithii* group and the *G. elata* group. It is interesting to note that these groups (IIIA and IIIB in Fig. 16) are not mutually exclusive, although they each receive full statistical support in the analysis. This is because a single provenance (PMW) of the widespread *G. elata* (represented in our analysis by four provenances, from East and West Peninsular Malaysia, Sabah and Sarawak, abbreviated PME, PMW, SAB and SAR, respectively), clusters together with *G. beamanii* and *G. griffithii*. Otherwise, the latter two species would make a unique group among SE Asian-Sundaland species, as they are the only ones with an infundibular calyx tube that sheaths at least half of the

corolla tube length. All other *G. elata* provenances (PME, SAB, SAR) cluster with *G. sp. A* (as Group IIIB).

The chloroplast DNA (Fig. 14) and nuclear DNA (ITS) topologies (Fig. 15) for *G. beamanii*, *G. elata* (PME, PMW, SAB & SAR), *G. griffithii*, and *G. sp. A* were incongruent. In the chloroplast genealogy (Fig. 14), *G. beamanii*, *G. elata* SAB, *G. griffithii*, *G. tubifera*, and *G. sp. A* (Subclade III of Fig. 14) shared a common maternal ancestor compared to the PME, PMW and SAR provenances of *G. elata* that were derived from another maternal ancestor (subclade II of Fig. 14). However, based on nuclear (ITS) genealogy (Fig. 15), *G. beamanii*, *G. elata* (PME, PMW, SAB and SAR), *G. griffithii*, and *G. sp. A* (Subclade III of Fig. 15) were derived from a common ancestor that later gave rise to two distinct groups, namely, group IIIA and IIIB (both with high bootstrap and Bayesian values). In short, the SAB and PMW provenances were individually out of a main *G. elata* group including the other three provenances in the chloroplast and nuclear ITS genealogies, respectively.

It is possible to use the same reasoning as for the *G. tubifera-pterocalyx* alliance to interpret that interspecific hybridisation could also have occurred between these four taxa, namely, *G. beamanii*, *G. elata*, *G. griffithii*, and *G. sp. A* (or their ancestors), which could have contributed to the topological incongruence between chloroplast and nuclear genealogies obtained in this study.

In this study, *G. elata* was found to have variable DNA sequences. Based on the chloroplast DNA genealogy (Fig. 14), *G. elata* PMW was strongly related to *G. elata* PME in subclade II. However, based on the nuclear (ITS) genealogy (Fig. 15), *G. elata* PMW instead formed a strong relationship with *G. beamanii* (indicated by high

bootstrap and Bayesian values) in Group IIIA and not with *G. elata* PME which clustered as Group IIIB. The incongruent topologies of *G. elata* PMW based on cpDNA and nrDNA genealogies may be interpreted as *G. elata* PMW sharing a common paternal ancestor with *G. beamanii*, but a maternal ancestor of the main *G. elata* group (including the PME and SAR provenances).

Another interesting taxon, *G. elata* SAB, also has different alliances within the chloroplast DNA and nuclear DNA (ITS) genealogies. Based on the chloroplast DNA topology (Fig. 14), *G. elata* SAB, clustered together with *G. beamanii*, *G. griffithii*, *G. tubifera*, and *G. sp. A* (within subclade III of Fig. 14). In contrast, the nuclear DNA (ITS) topology (Fig. 15) shows that *G. elata* SAB is closely related to *G. elata* PME and *G. sp. A* (in Group IIIB of Subclade III in Fig. 15). Therefore, *G. elata* SAB could have been derived through introgression of a member of the main *G. elata* group (including the SAR and PME provenances; Fig. 15) into a member or ancestor of Subclade III in the chloroplast genealogy (Fig. 14). This translates to hybridisation between a paternal ancestor of *G. elata* and a maternal ancestor of the *G. beamanii-griffithii-tubifera-sp. A* group.

The topological positions of *G. sp. A* were also inconsistent between cpDNA and nrDNA genealogies. Maternally (Fig. 14), *G. sp. A* is related to *G. beamanii* but in the nrITS genealogy (which probably emphasises paternal inheritance as pointed out) (Fig. 15), it was related to *G. elata* SAB and *G. elata* PME. Therefore, *G. sp. A* could have been derived through introgression of *G. elata* SAB or PME (or their ancestor) into *G. beamanii*.

It appears, therefore, that the relationships among Subclade III taxa (as shown in the combined cpDNA-nrITS topology; Fig. 16) are far from simple. Lineage development appears to have been reticulate, very possibly involving hybridisation among the taxa of this subclade (extant or ancestral), or introgressions between taxa from other alliances (e.g., *G. pterocalyx* or its ancestors) and members of this subclade.

Subclade V: the *G. mutabilis-saxatilis* alliance

The *G. mutabilis-saxatilis* group (Subclade V of Fig. 16) consists of two species, namely, *G. mutabilis* (Sulawesi and the Philippines) and *G. saxatilis* (mainland Asia). Both species are distributed in seasonal forest and generally occur on rocky outcrops (*G. saxatilis* on sandstone in Thailand, *G. mutabilis* on limestone in the Philippines and Sulawesi). Apart from this, there appears to be very little similarity in morphological characters. The calyx is cupular-obconical, with a short tube (c. 2 mm long) that flares upwards and a margin with six or more narrow-triangular lobes, in *G. saxatilis*, but cupular-obconical to tubular (c. 17 mm long), with the tube tightly sheathing the corolla tube and a subtruncate margin, in *G. mutabilis*.

Based on the combined chloroplast DNA analysis (Fig. 14), *G. saxatilis* is basal to all other species, whereas *G. mutabilis* is a solitary branch in a polytomy that next resolves, together with three other subclades comprising the remaining species. On the other hand, in the ITS analysis (Fig. 15), *G. saxatilis* and *G. mutabilis* form an equivocal association (strong bootstrap support, weak Bayesian support) as one of five clades in a polytomy. This difference between chloroplast and nuclear phylogenies does not indicate different associations, as *G. saxatilis* and *G. mutabilis* are individually solitary branches (i.e., not clustered with other taxa) in the chloroplast DNA genealogy, and there is not enough evidence to suggest a complex origin. In fact, the present analyses

and taxon sampling do not permit any firm interpretation of their relationships, except that the central Malesian species *G. mutabilis* has an Asiatic affinity (reflected in strong support for clustering of these two species in the combined chloroplast-ITS analysis in Fig. 16).

5.2.7 Phylogenetic, taxonomic and biogeographical implications of the molecular studies

The cpDNA and nrDNA genealogies of Sundaland *Gardenia* had some degree of concordance and various discordant aspects. Discordance between cpDNA and nrDNA genealogies could possibly reflect reticulate evolution of Sundaland *Gardenia* lineages. These may be due to hybridisation and introgression. As discussed above, hybridisation is more likely to have occurred among Sundaland *Gardenia* rather than paralogy or incomplete lineage sorting. The importance of hybridisation as a catalyst for plant speciation has been much highlighted (Stebbins 1959; Grant 1981; Arnold 1992; Rieseberg 1997; Ramsey & Schemske 2002) and some well-studied examples of interspecific hybridisation of plants include *Cuscuta* (Convolvulaceae) (Stefanović & Costea 2008) *Helianthus* (Asteraceae) (Rieseberg *et al.* 1990), *Paeonia* (Paeoniaceae) (Sang *et al.* 1995, 1997) and *Pistacia* (Anacardiaceae) (Yi *et al.* 2008).

Although the molecular-based topologies did not show a simple division into two geographical groups, generally the mainland Asian taxa did not associate with other taxa having an insular Southeast Asian distribution. Of the eight Sundaland taxa included in this study, only *G. thailandica* (occurring in the Malay Peninsula but not in the island masses of Sundaland) was shown to affiliate with the other mainland Asian taxa (Figs. 14, 15). Introgression of a mainland Asian lineage into Sundaland could have occurred in the case of *G. chaniü*, which appears to share the same paternal ancestor of

two mainland Asian taxa, *G. hainanensis* and *G. stenophylla* based on nrDNA genealogy (subclade I, Fig. 15), although in maternal characteristics (combined cpDNA genealogies, subclade III in Fig. 14), it is clearly associated with other Sundaland taxa.

Although these various lineages of Sundaland *Gardenia* appear to be complex due to hybridisation and introgression as indicated above, most taxa have distinct calyx characters. However, several species do have remarkably similar calyx form and other characters are used for species distinction, e.g., the case of *G. elata* and *G. tubifera*. Low & Wong (2009) proposed *G. elata* and *G. tubifera* as distinct taxa based on a suite of morphological characters besides calyx characters, although several previous authorities have considered them the same species. In this study, the combined cpDNA genealogy (Fig. 14), nrDNA genealogy (Fig. 15), and the combined cpDNA-nrDNA genealogy (Fig. 16) fully support the distinction of *G. elata* from *G. tubifera* adopted by Low & Wong (2009).

The results of the molecular phylogenetic analyses have also shed light on the relationship between *G. elata* and *G. sp. A*. These two taxa have similar calyx form, but *G. sp. A* differs from *G. elata* in a suite of morphological characters: generally smaller leaves (3.7–13 cm long and 1.7–4.8 cm wide), and a glabrescent corolla throat inner surface for *G. sp. A*; compared to generally larger leaves ((4.3–)10–22.5(–27) cm long and (2–)4–11(–12) cm wide), and a hairy corolla throat inner surface for *G. elata*. As discussed above, *G. sp. A* could have arisen through hybridisation between *G. beamanii* (the likely maternal taxon) (Fig. 14) and *G. elata* PME or *G. elata* SAB (likely paternal taxa) (Figs. 15, 16). Hybridisation between these two taxa could have been possible as *G. elata* is widely distributed throughout Sundaland (Low & Wong 2009), although *G. beamanii* is restricted to north Borneo (Low & Wong 2007). Morphologically, *G. sp. A*

is closely related to *G. elata* rather than *G. beamanii*. In view of these results, it would be appropriate to consider *G. sp. A* as a variety of *G. elata*.

University of Malaya

Chapter Six: *Systematic Enumeration* *of Sundaland Gardenia*

6.1 Genus references and description

***Gardenia* J.Ellis, nomen conservandum**

Philos. Trans. 51 (2): (1761) 935.

Backer & Bakhuizen, Fl. Java 2 (1965) 313; Tirvengadam, Nord. J. Bot. 3 (1983) 458;

Wong, Tree Fl. Malaya (1989) 348; Puff & Wong, Sandakania 2 (1993) 20; Corner,

Wayside Trees of Malaya 2 (1997) 629.

TYPE SPECIES: *Gardenia jasminoides* J.Ellis

Woody plants of shrub to tree habit, branching extra-axillary, growth architecture conforming to the Leeuwenberg or Scarrone models of Hallé *et al.* (1978).

Stipules interpetiolar, connate into a cupuliform or cylindrical structure, sheathing, the basal part commonly persistent as an annular remain around the node, margin subtruncate and level to weakly 2-several-lobed or oblique and apex resembling a single triangular structure, and generally coated with resin (this sloughing off in older material). **Leaves** opposite to verticillate (three leaves per node), petiolate, margin entire, vein axils on the lower side with domatia. **Flowers** solitary and terminal, fragrant. Corolla hypocrateriform, creamy white at anthesis and darkening to yellow-orange at the post-anthesis stage; tube generally long with 5-several lobes, oblanceolate to obovate. Stamens inserted just below the corolla throat and between corolla lobes,

dorsifixed; filaments very short to inconspicuous; c. a third to half of the total anther length exerted. Pollen issued in tetrads. Style slightly longer than the corolla tube, glabrous to pubescent; stigma club-like, 2-several-lobed, wholly exsert; ovary with several parietal placentas. **Fruit** a capsule or thin-walled drupe, generally medium-sized to large, subglobular to ellipsoid or obovoid, with firm pericarp and bony endocarp; yellowish green, splitting irregularly when ripe. Seeds many, compressed, angular to rounded-elliptic, with areolate testa surface, embedded in a bright orange-red pulp-like placenta.

DISTRIBUTION: Old World Tropics (Africa, South Asia, Myanmar to South China and Indochina, Thailand, Malay Peninsular, insular Southeast Asia, north Australia, Pacific islands).

6.2 Key to Sundaland *Gardenia* species, including two cultivated species

- 1a.** Leaves narrow, 1.4–1.5 cm wide; fruits to 0.6 cm wide **G. sp. ined.**
- 1b.** Leaves broad, more than 1.5 cm wide; fruits more than 0.6 cm wide.
 - 2a.** Calyx tube outer surface smooth or faintly ridged.
 - 3a.** Calyx tube outer surface smooth; leathery and quite rigid.
 - 4a.** Calyx tube of open flowers 4–9 cm long, sheathing about half to more than half of the corolla tube.
 - 5a.** Resin at shoot tips black; veins on both leaf surfaces glabrous; calyx tube of open flowers 4–5 cm long (lowland forest; Borneo: Sabah and Brunei)
..... **G. beamanii** Y.W.Low
 - 5b.** Resin at shoot tips yellowish amber-brown; veins on both leaf surfaces sparsely to densely hairy; calyx tube of open

flowers (5–)7–10 cm long (peat swamp forest; Malay Peninsula, Sumatra and Borneo: Sarawak and Kalimantan)

..... *G. griffithii* Hook.f.

4b. Calyx tube of open flowers 0.6–3.5 cm long, sheathing significantly less than half of the corolla tube.

6a. Veins on the lower leaf surface glabrous (very rarely puberulent); calyx mouth of open flowers 5–8 mm wide (coastal estuarine or swamp forests only)

..... *G. tubifera* Wall. ex Roxb.

6b. Veins on the lower leaf surface puberulent; calyx mouth of open flowers 8–13(–15) mm wide (lowland to lower montane forest).

7a. Corolla throat of open flowers pubescent (widespread throughout west Malesia in the lowlands)

..... *G. elata* var. *elata*

7b. Corolla throat of open flowers glabrescent (Sabah: Mount Kinabalu and Mount Meligan)

..... *G. elata* var. *kinabaluensis* var. nov. ined.

3b. Calyx tube outer surface ridged; membranaceous.

8a. Pedicels of open flowers 0.5–0.9 cm long; fruit pedicel 1–2.3 cm long; mature fruit obovoid, surface with 5 prominent to slightly raised ribs (northern Malay Peninsula)

..... *G. thailandica* Tirveng.

8b. Pedicels of open flowers 0.1–0.3 cm long; fruit pedicel 0.1–0.3 cm long; mature fruit subglobose, surface without ribs (Philippines and Sulawesi; cultivated in Sundaland countries)

..... *G. mutabilis* Reinw. ex Blume

2b. Calyx tube outer surface with keels.

9a. Calyx keels not apically expanded into triangular wings or produced long slender appendages.

10a. Calyx keels very low, hardly 0.5 mm high. Calyx tube length of open flower 0.4–1 cm long.

11a. Calyx keels ending in short but distinct spur-like extensions protruding to 2 mm beyond the calyx tube margin (Malay Peninsula) *G. subcarinata* var. *subcarinata*

11b. Calyx keels without extensions beyond the calyx tube margin (Sumatra)
..... *G. subcarinata* var. *sumatrana* Y.W.Low

10b. Calyx keels fin-like or ribbon-like, at least 2–3 mm high. Calyx tube length of open flower longer than 1 cm

12a. Calyx tube broadly campanulate to broad-cylindric, the mouth widely flared *G. chanii* Y.W.Low

12b. Calyx tube broad-tubular, the mouth never widely flared.

13a. Leaf apex obtuse, rounded to short-cuspidate; mature fruit pedicel 3.5–4.5(–5) cm long (peat swamp forest; Malay Peninsula, Sumatra and Borneo)
..... *G. pterocalyx* Valetton

13b. Leaf apex acuminate to long-cuspidate; mature fruit pedicel 0.5–0.7 cm long (*kerangas* forest; Borneo)
..... *G. costulata* Ridl.

9b. Calyx keels apically expanded into triangular wings or produced into linear-lanceolate processes at least half the calyx tube length.

- 14a.** Calyx tube outer surface with broad triangular keels up to 11 mm wide, apically sometimes forming slight spurs protruding to only 4 mm beyond the calyx margin *G. carinata* Wall. ex Roxb.
- 14b.** Calyx tube outer surface only with narrow ribbon-like keels up to 1.5 mm wide, apically forming conspicuous linear-lanceolate spurs protruding to 25 mm beyond the calyx margin.
- 15a.** Leaf secondary veins 6–9 pairs; calyx tube of open flower 2–6 mm long; calyx tube margin of open flower subtruncate; mature fruit diameter 1–1.9 cm wide (Japan and South China; cultivated in Sundaland countries) *G. jasminoides* J.Ellis
- 15b.** Leaf secondary veins 11–22 pairs; calyx tube of open flower 8–15 mm long; calyx tube margin of open flower oblique; mature fruit diameter 3–4.7 cm wide (native to the Philippines: Palawan) *G. barnesii* Merr.

6.3 Enumeration of native species

Note: A number of findings in the course of this research has been published as Low & Wong (2007) (see Appendix 2), describing two new species (*G. beamanii* and *G. chanii*), and Low & Wong (2009) (see Appendix 3), elucidating the differences between *G. elata*, *G. tubifera* and *G. subcarinata*, and the new variety *G. subcarinata* var. *sumatrana*.

- 1. *Gardenia barnesii*** Merr., Philipp. Gov. Lab. Bur. Bull. 17 (1904) 47; Philipp. J. Sci. 1 Suppl.: 131 (1906); Elmer, Leaflet Philipp. Bot. 1 (1906) 5; Merrill, Enum. Philipp. Fl. Pl.: 531 (1923) in syn. *G. pseudopsidium*.

TYPE: *Barnes* For. Bur. 163, Luzon, Bataan Province, Lamao River (Jan 1904)
(isotypes K! leafy twig; NY! flower bud & open flower; SING! flower bud; US!
open flowers).

Gardenia segmenta Elmer, Leafl. Philipp. Bot. 4 (1912) 1331.

TYPE: *Elmer* 13153, Palawan, Puerto Princesa, Mt Pulgar, 500 ft (May 1911,
open flower) (isotypes A! BO! K! L! NY! US!).

Gardenia megalocarpa Merr., Philipp. J. Sci. 20 (1922) 463.

TYPE: *Ramos* Bur. Sci. 39819, Mindoro, Paluan (April 1921, leafy twig & fruit)
(isotypes A! K! US!). [Type number wrongly listed as 38919 in Merrill (1922)].

(Figs. 17, 18.)

Tree, to c. 9 m high, trunk to c. 15 cm diameter, not buttressed. Bark smooth to slightly scaly to lightly fissured, pale yellowish grey-brown. *Stipules* connate into a sheathing tube, often c. 1–2 cm long, apex acute (the mouth of the stipular tube oblique), outside scantily puberulent and sometimes coated with resin, inside densely covered with fine translucent trichomes except at the base where trichomes are sparsely mixed into a dense covering of slightly shorter, dark-coloured colleters. *Petiole* 0.3–1.2 cm long, 1–1.5 mm thick, densely puberulent, sometimes conspicuously resin-coated. *Leaf* lamina obovate to elliptic; 5.5–22 cm long, 2.5–8.3 cm wide; leaf base cuneate; leaf apex acute to acuminate or obtuse, short-cuspidate; thin-coriaceous; conspicuously coated with resin when young; midrib flat to sunken and subglabrous on upper side, prominent and sparsely to densely puberulent on lower side; secondary veins 11–22 pairs, flat and glabrous on upper side, prominent and sparsely puberulent on lower side, vein axils on the lower side with hair tufts; tertiary venation scalariform. *Flowers* solitary. *Pedicel* 0.3–1.4 cm long and c. 1–1.5 mm thick in open flowers, reaching 0.8–1.8 cm long and 2–3 mm thick at fruit maturity. *Calyx* subfusiform to tubular, tightly

sheathing the corolla tube, the margin oblique, apex acute or torn into two acute portions by corolla emergence; tube 0.8–1.5 cm long, 2.5–4 mm wide at the base, becoming 5–7 mm wide at the apex; outside puberulent to subglabrous, often coated with resin; inside sparsely to densely covered with dark-coloured colleters mixed with translucent trichomes (colleters more conspicuous and longer than trichomes); with 5 ridges or keels to c. 1–1.5 mm wide along the tube, these continuing (and departing from the calyx surface 0.4–1 cm below the apical margin) as linear, bilaterally flattened spurs to 10–16 mm long and 1.5–2 mm wide that are often slightly curved upwards. **Corolla** hypocrateriform, cream turning light, then deep, yellow; tube to 2.6–6 cm long, 1.5–3.5 mm wide at the mid-portion, 3.5–8 mm wide at the throat, outside puberulent to subglabrous, inside largely glabrous except for sparse covering of ribbon-like translucent hairs beneath the stamens; lobes 6–9, oblanceolate to obovate, (12–)37–46 mm long, 7–21 mm wide, glabrous on both sides. **Stamens** 6–9, inserted just below the corolla throat and between corolla lobes, dorsifixed; filaments very short to inconspicuous; anthers 4.5–13 mm long, c. half or more exerted. Style 3–6.5 cm long, glabrous; stigma club-like, 3–5-lobed, 1.5–5 mm long, 1–2.5 mm wide, wholly exert; ovary with several parietal placentas. **Fruits** broad-ellipsoid to obovoid or subglobose, to 3.5–6 cm long, 3–4.7 cm wide, when mature with 5 conspicuous longitudinal ridges or narrow keels especially in the upper half of the fruit; persistent calyx to 0.8–1.5 cm long, 0.5–0.7 cm wide at the mouth; orange-red and splitting irregularly when ripe. **Seeds** many, irregularly angular-rounded to elliptic, flattened, 3–4.5 mm long, 2.5–3.5 mm wide, testa surface fine-areolate, embedded in a bright yellow-orange pulp-like placenta.

DISTRIBUTION. Endemic to the Philippines: Balabac, Busuanga, Catanduanes, Luzon (Abra, Bataan, Batangas, Benguet, Cagayan, Camarines Sur, Laguna, Nueva Vizcaya,

Quezon, Rizal, Sorsogon and Zambales), Masbate, Mindanao (Davao and Zamboanga), Mindoro (Pola (Oriental Mindoro) and Paluan (Occidental Mindoro)), Negros, Palawan (Puerto Princesa municipality), Panay (Antique) and Ticao.

ECOLOGY. In lowland forest.

SPECIMENS EXAMINED.

PHILIPPINES. BALABAC. Palawan Province: Danglis [7°59' N 117 °2' E], 90–150 m, 30 Jun 1994, *Soejarto et al.* 8632, fruit (L!). **BUSUANGA. Palawan Province:** 1901, *Ahern* s.n., open flower (US!). **CATANDUANES. Catanduanes Province:** Mt. Nagpakdit, 14 Sept 1928, *Ramos & Edano* Bur. Sci. 75389, fruit (NY! SING!). **LUZON.** no date, *Lobb* s.n., open flower & flower bud (K!). **Abra Province:** Sallapadan, Poblacion Gangal [17°28' N 120°49.6' E], 250 m, 18 Nov 1996, *Fuentes & de la Rosa* PPI 38651, young fruit (K! PNH!). **Bataan Province:** Lamo River, Mt. Mariveles, May 1905, *Whitford* 1235, leafy twig (K!) fruits (US!); Lamas Forest Reserve, Oct 1906, *Foxworthy* Bur. Sci. 1587, fruits (NY!); Mt. Mariveles, Nov 1904, *Elmer* 6714, fruit (NY!); Mt. Mariveles, Lamao River, Mar 1905, *Borden* For. Bur. 2916, leafy twig (K!) fruit (NY! SING!), Feb 1905, *Meyer* For. Bur. 2788 leafy twig (K!) fruit (SING!) fruits (NY!), 18 Jan 1904, *Williams* 487, fruits (A! NY!). **Batangas Province:** Jul–Aug 1914, *Ramos* Bur. Sci. 22406, fruit (A! K! L!). **Benguet Province:** Sablang, Nov–Dec 1910, *Fenix* Bur. Sci. 12722, fruit (US!); Twin Peaks, May 1904, *Elmer* 6354, flower buds & open flower (NY!) open flowers (K! US!). **Cagayan Province:** Jun–Sept 1914, *Barros* For. Bur. 23253, open flower (A!), Jul–Aug 1915, *Bernardo* For. Bur. 24265, open flower (US!); vicinity of Penablanca, 5 May 1917, *Adduru* 32, fruit (A! US!); Penablanca, Apr 1926, *Ramos & Edano* Bur. Sci. 46592, fruits (SING!). **Camarines Sur Province:** Pasacao, May 1904, *van Wickle* For. Bur.

699, fruit (US!). **Laguna Province:** Mt. Maquiling, Nov 1914, *Foxworthy* s.n. fruit (US!), no date, *Sulit* Phil. Nat. Herb. 7086, open flowers (A!), Nov 1932, *Sulit* Phil. Nat. Herb. 7254, open flower (A!), 10 Dec 1949, *Sulit* Phil. Nat. Herb. 12186, open flower (A!); Mount Maquiling, Los Banos, Jun–Jul 1917, *Elmer* 18320, flower bud (L!) open flower (A! K! NY!); San Antonio, Jun 1912, *Ramos* Bur. Sci. 14990, flower bud (L!). **Nueva Vizcaya Province:** vicinity of Dupax, Mar–Apr 1912, *McGregor* Bur. Sci. 11422, fruit (US!). **Quezon Province:** Quezon National Park, 29 Nov 1991, *Reynoso et al.* PPI 3886, fruit (L!); Quezon National Park, Atimonan [14°4' N 121°55.2' E], 17 Mar 1996, *Castro, Barbon & Garcia* PPI 22254, flower bud (K!); Tayabas, Mar 1908, *Curran* For. Bur. 10278, leafy twig (NY!); Tayabas, Guinayangan, Jan 1884, *Vidal* 833, flower bud (K!) open flower (L!), Mar–Apr 1913, *Escritor* Bur. Sci. 20838, fruit (US!). **Rizal Province:** Aug 1911, *Ramos* 1088, fruit (US!); Antipolo, Oct 1883, *Vidal* 383, open flowers (L!), Dec 1914, *Merrill* Sp. Blancoanae 655, leafy twig (A! K! L! NY!); Bosoboso, Jun 1903, *Merrill* 2631, flower buds (NY!) open flower (US!), Jul 1903, *Merrill* 2817, open flowers (NY! US!); Montalban, 11 Aug 1935, *Bartlett* 14441, fruit (A!), 1906, *Loher* 6386, open flower (K!), Jun 1909, *Loher* 12466, open flowers (A!); Morong, Nov 1884, *Vidal* 1452, fruit (K!). **Sorsogon Province:** Irosin, Mt Bulusan, Sept 1916, *Elmer* 17189, fruits (A! L! NY!). **Zambales Province:** Mt Marayep, Dec 1924, *Ramos & Edano* Bur. Sci. 44809, fruit (NY!). **MASBATE. Masbate Province:** May–Jun 1904, *Clark* For. Bur. 1702, fruit (US!), Jun 1903, *Merrill* 2771, flower bud (K!) open flower (NY! US!), Sept–Oct 1915, *Valencia* For. Bur. 24635, fruit (US!). **MINDANAO. Davao Province,** Mar 1917, *Ceballos* For. Bur. 26598 flower bud (K!) open flower (US!); Zamboanga Province, 1901, *Ahern* s.n., open flower (US!). **Davao City:** Tibunco, Aug 1933, *Kanehira* 2599, leafy twig (NY!); Todaya, Mt Apo, 457 m, Jun 1909, *Elmer* 10964, fruit (A! K! L! NY! US!). **Davao del Sur Province:** Santa Cruz, 10 Jun 1905, *Williams* 2942, fruits (A! K! NY! US!). **Davao Oriental Province:**

Mati, Mar–Apr 1927, *Ramos & Edano* Bur. Sci. 49150, leafy twig (BO! L!) fruit (NY! SING!). **Zamboanga City**: Tetuan, no date, *Quadras* 287, open flower (NY! US!). MINDORO. Jan 1907, *Merritt* For. Bur. 6141, fruits (NY!). **Oriental Mindoro Province**: Pola, May 1903, *Merrill* 2217, flower bud (NY!) open flowers (US!). NEGROS. **Negros Occidental Province**: Murcia, Mambucal Resort Area, 350 m, 23 Mar 1992, *Stone et al.* PPI 6332, fruit (KEP! PNH!). PALAWAN. **Palawan Province**: May 1906, *Curran* For. Bur. 4147, flower buds (US!) flower bud & open flower (BO! L!), May 1906, *Foxworthy* Bur. Sci. 838, flower bud (US!) open flower (NY!), ‘Paragua’, Mar 1886, *Vidal* 2995, leafy twig (K!); Puerto Princesa, Feb 1923, *Cenabre* For. Bur. 29122, open flower (US!); Puerto Princesa, Irawan R. Valley, east side, 24 Mar 1984, *Ridsdale* SMHI 202, flower bud & fruit (L 2 sheets!); Puerto Princesa City, Irawan, Impapay, 23 Sept 1993, *Madulid & Majaducon* 8053, open flower (A!), 17 Sept 1993, *Madulid & Majaducon* 8008, fruit (A!); Sagpangan, Aborlan, 28 May 1955, *Celestino & Ramos* Phil. Nat. Herb. 23092, flower bud, open flower, young fruit (K! L!). PANAY. **Antique Province**: May–Aug 1918, *McGregor* Bur. Sci. 32445, flower bud & open flowers (K! L!) open flower (A! NY!). TICAPO. **Masbate Province**: May–Jun 1904, *Clark* For. Bur. 1023, open flower (K! NY! US!).



Fig. 17. The type specimen of *Gardenia barnesii* Merr.: Barnes 163 (NY).

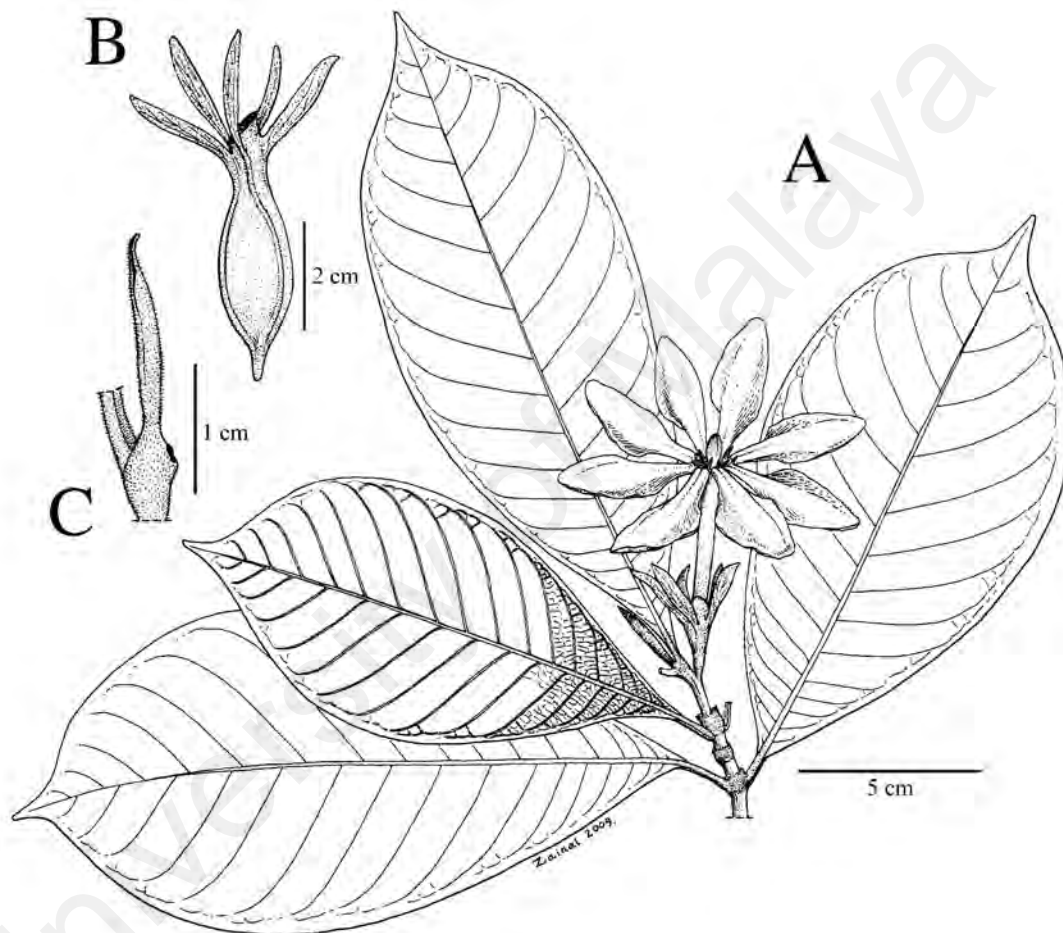


Fig. 18. *Gardenia barnesii* Merr. **A**, Flowering leafy branch. **B**, Immature fruit showing intact calyx tube (with oblique margin) and protruding spurs. **C**, Puberulent sheathing stipule at shoot tip. [A from *Mcgregor* Bur. Sci. No. 32445 (K); B from *Williams* 2942 (K); C from *Celestino & Ramos* Phil. Nat. Herb. 23092 (K).]

2. *Gardenia beamanii* Y.W.Low, Edinburgh. J. Bot. 64 (2007) 26.

TYPE: *P.S. Ashton* BRUN 10, Brunei, Mile 18½, Labi Road, primary forest on yellow sandy clay, hillside, 600 ft [183 m] (20 May 1957, flower) (**holotype** K! **isotypes** BO! KEP! SING!).

(Figs. 19, 20.)

Tree, to c. 23 m high, trunk to c. 45 cm diameter, not buttressed. Bark smooth, light grey-brown to dark brown. *Stipules* connate into a cupuliform structure, 0.5–1 cm long, margin weakly 2-lobed to subtruncate, outside glabrous and generally coated with resin (this sloughing off in older material), inside with a dense covering of dark-coloured colleters mixed with scattered fine translucent trichomes (twice as long as colleters) at the basal half and glabrous at the upper half. *Petiole* 1–2(–3.5) cm long, 2–3 mm thick, glabrous, sometimes conspicuously resin-coated. *Leaf* lamina obovate; 11.5–17(–22.5) cm long, (4–)5–7(–9) cm wide; leaf base cuneate; leaf apex acuminate to short-cuspidate; thin-coriaceous; conspicuously coated with resin when young; midrib prominent and glabrous on both sides; secondary veins 9–13 pairs, prominent and glabrous on both sides, vein axils on the lower side with ciliate pit-domatia; tertiary venation scalariform. *Flowers* solitary. *Pedicel* 0.5–0.8 cm long and 3–4 mm thick in open flowers, reaching 0.5–2 cm long and 4–6 mm thick at fruit maturity. *Calyx* narrowly to broadly infundibular, margin subtruncate; tube 4–5 cm long, 7–9 mm wide at the base, becoming 20–25 mm wide at the apex; outside completely glabrous, often coated with resin; inside glabrous except a dense covering of dark-coloured colleters mixed with translucent trichomes at the lowest 0.5 cm (trichomes longer than colleters and especially conspicuous as a dense fringe at the very base of the calyx tube); surface without keels or ribs. *Corolla* hypocrateriform, cream turning light yellow, then orange-yellow; tube to 9–10 cm long, 4–5 mm wide at the mid-portion, 10–12 mm wide at the

throat, outside completely glabrous, inside glabrous except for a 1–1.5 cm zone of scattered ribbon-like translucent hairs at the throat to about 0.5 cm below the stamens; lobes 8–10, obovate to rounded, 25–30 mm long, 25–29 mm wide, glabrous on both sides. *Stamens* 8–10, inserted just below the corolla throat and between corolla lobes, dorsifixed; filaments very short to inconspicuous; anthers 9–11 mm long, c. half exerted. Style 11.5–12 cm long, glabrous; stigma club-like, 5–7-lobed, 5–7 mm long, 3–4 mm wide, wholly exsert; ovary with several parietal placentas. *Fruits* globose to depressed globose, 3–4.5 cm long, 3.5–5.5 cm wide, surface in mature specimens smooth, slightly ribbed or unevenly longitudinally ridged; calyx persistent at fruit apex, the tube to 2.5–5.5 cm long, flared to 2–4 cm wide at the mouth; yellowish green and splitting irregularly when mature. *Seeds* many, irregularly angular-elliptic, flattened, 6–8 mm long, 4–6 mm wide, testa surface fine-areolate, embedded in a bright yellow-orange pulp-like placenta.

DISTRIBUTION. Endemic to Borneo, restricted to the northern (Sabah and East Kalimantan) and northwest parts (Brunei; possibly adjacent areas of Sarawak).

ECOLOGY. Lowland mixed dipterocarp forest.

SPECIMENS EXAMINED.

BRUNEI: Belait District, Andulau Forest Reserve, compartment 7, mixed dipterocarp forest, 3 May 1988, *Wong* WKM 86, immature fruit (SAN! SING!); Andulau Forest Reserve, disturbed primary forest on hillside, 150 ft [46 m], 15 Jul 1957, *Ashton* BRUN 274, fruit (KEP!) leafy branch (SING!); Andulau Forest Reserve, mixed dipterocarp forest, 66 ft [20 m], 24 Jul 1989, *Puff* 890724-1/5, fruit (K!); Mile 18½, Labi road, primary forest on hillside, 600 ft [183 m], 20 May 1957, *Ashton* BRUN 10, flower

(holotype K! isotypes BO! KEP! SING!). **INDONESIA: Kalimantan**, Nunukan Island, northern part, 30 Oct 1953, *Kostermans* 8638, fruit (BO! SING!). **MALAYSIA: Sabah**, Beluran, Bongaya Forest Reserve, flatland, 50 ft [15m], 22 Jul 1975, *Kodoh & Aban* SAN 82018, fruits (KEP! SAN!); Papar, Mandahan, secondary forest, 10 ft [3 m], 26 Oct 1962, *Talip* SAN 32221, fruit (KEP!); Ranau, TM1, hillside near logging, 21 Feb 1990, sine coll. SAN 128840, fruit (K! KEP! L! SAN!); Sandakan, Bukit Pasir Lungmanis, primary forest, hill ridge, Aug 1962, *Mikil* SAN 31128, fruits (SAN!) fruit (KEP! L! SING!); Sipitang, Merintaman Forest Reserve, growing on swamp forest on riverside, 22 Sept 1972, *Saikeh* SAN 72347, fruit (SAN! SING!).



Fig. 19. The holotype specimen of *Gardenia beamanii* Y.W.Low.: Ashton BRUN 10 (K).

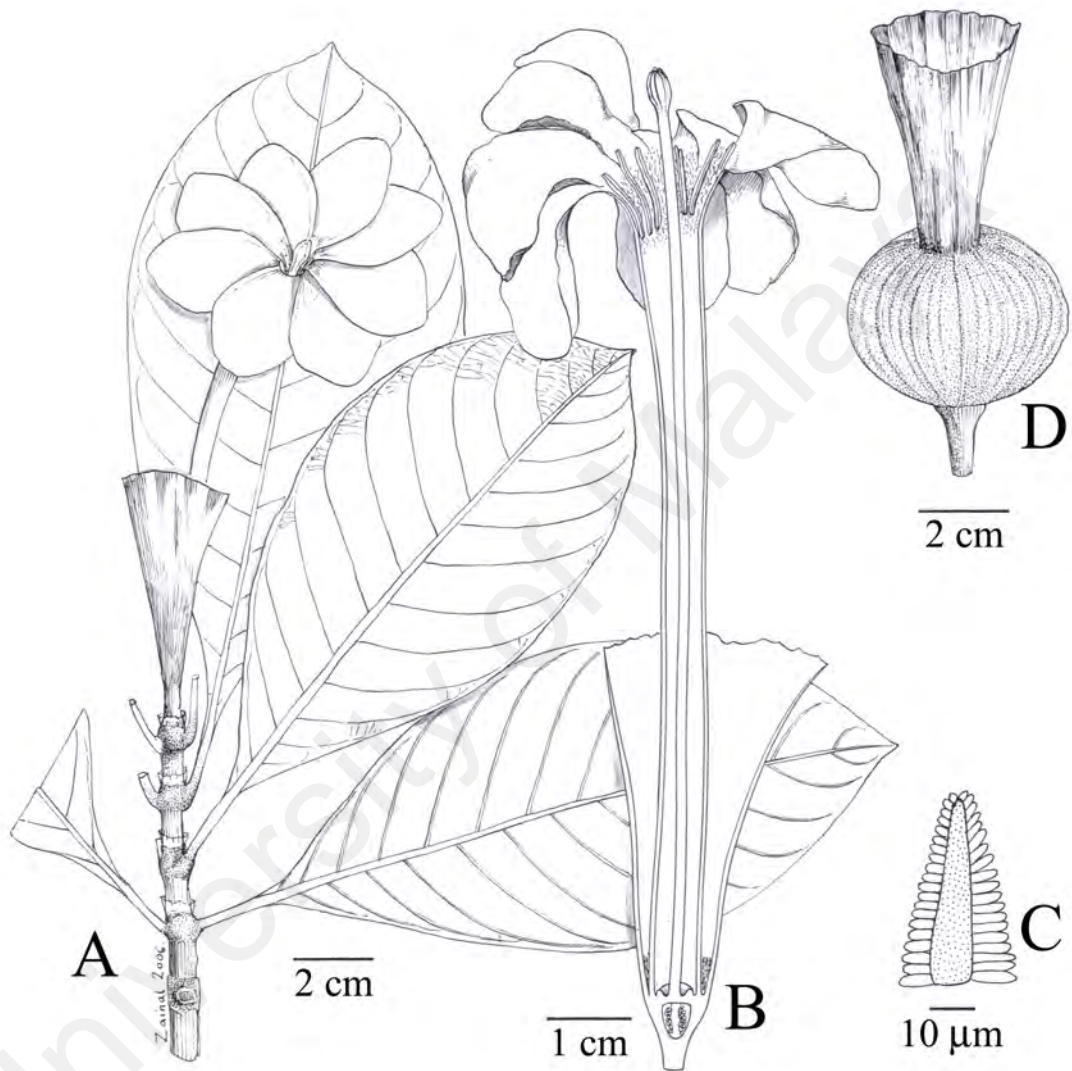


Fig. 20. *Gardenia beamanii* Y.W.Low. **A**, Leafy branch terminated by a solitary flower. **B**, Half-flower (dark small structures at the base on the inside of the calyx are colleters). **C**, Schematic optical longitudinal section of a colleter (shaded part is the axis of longitudinal cells, with outer palisade-like layer of large cells). **D**, Fruit with persistent calyx. [A–C from Ashton BRUN 10: A & B from K; C from KEP; D from *unknown collector* SAN 128840 (L).]

3. *Gardenia carinata* Wall. ex Roxb., Fl. Ind. 2 (1824) 560; Hooker, Fl. Brit. Ind.

3 (1880) 117; King & Gamble, J. Asiat. Soc. Beng. 72 (2) (1903) 218; Ridley, Fl. Malay Penin. 2 (1923) 82; Wong, Gard. Bull. Singapore 35 (1982) 25; Wong, Tree Fl. Malaya 4 (1989) 349; Corner, Wayside Trees of Malaya 2 (1997) 631.

TYPE: *Wallich Catalogue no.* 8271A, Penang, lowland forest on hills (Dec, flowers & fruits) (**holotype** K-W!).

(Fig. 21.)

Tree, to c. 20 m high, trunk to c. 45 cm diameter, not buttressed. Bark smooth, pale grey to brown. *Stipules* connate into a sheathing tube, 1–1.6 cm long, apex acute (mouth oblique), outside covered with short erect hairs and generally coated with resin (this sloughing off in older material), inside with a dense covering of dark-coloured colleters mixed with longer, fine translucent trichomes at the basal half, with scattered fine translucent trichomes covering the upper half. *Petiole* (0.1–)0.5–1 cm long, (1.5–)2–3.5 mm thick, evenly covered with short erect hairs, sometimes conspicuously resin-coated. *Leaf* lamina obovate; (6–)16–24(–28.5) cm long, (2.7–)6–10.5(–13) cm wide; leaf base cuneate; leaf apex acuminate to short-cuspidate; thin-coriaceous; conspicuously coated with resin when young; midrib prominent and densely hairy on both sides, denser on the lower side; secondary veins (9–)13–20 pairs, prominent and densely hairy both sides, denser on the lower side, vein axils on the lower side with hairy pocket-domatia; tertiary venation scalariform. *Flowers* solitary. *Pedice*l 0.5–1.3(–1.8) cm long and 1–2 mm thick in open flowers, reaching 1.5–2.5 cm long and 1.5–4 mm thick at fruit maturity. *Calyx* cupular-obconical, margin subtruncate; tube (0.9–)1.3–2.2 cm long, 2–4 mm wide at the base, becoming 6–10 mm wide at the apex; outside densely covered with short erect hairs, denser at the base, coated with resin; inside covered with scattered dark-coloured colleters mixed with scattered fine

translucent trichomes (colleters longer than trichomes); with 6–8 keels along the tube that often become apically broadened or develop into broad-triangular wings to 11 mm wide just 1–6 mm below the apex margin. *Corolla* hypocrateriform, cream turning light yellow, then orange-yellow; tube to (2–)4.5–6.5 cm long, (3–)4–6 mm wide at the mid-portion, (6–)10–12 mm wide at the throat, outside densely puberulent, inside covered with scattered ribbon-like translucent hairs for the upper half from just below the throat, the lower half glabrous; lobes 6–8, obovate, (24–)35–53 mm long, c. 13–33 mm wide, outside sparsely puberulent (but always glabrous beneath overlaps), inside glabrous. *Stamens* 6–8, inserted just below the corolla throat and between corolla lobes, dorsifixed; filaments very short to inconspicuous; anthers 11–15 mm long, c. a quarter exerted. Style (2.5–)4.3–6.6 cm long, sparsely minute-hairy throughout except on the exerted portion; stigma club-like with 3–4 lobes initially cohered together, 5–12 mm long, 2–7 mm wide, wholly exerted; ovary with several parietal placentas. *Fruits* subglobose to ellipsoid, (1.9–)2.5–3.7(–4.2) cm long, (1.7–)2.2–2.6 cm wide, with 6–8 ribs; calyx persistent at fruit apex, the tube to (1.2–)1.4–2.4 cm long, 0.6–1 cm wide at the mouth, with low rounded to broad-triangular wings; yellowish green and splitting irregularly when ripe. *Seeds* many, irregularly angular-elliptic, flattened, 3–4.5 mm long, 2–3.5 mm wide, testa surface fine-areolate, embedded in a bright yellow-orange pulp-like placenta.

DISTRIBUTION. Peninsular Thailand to Peninsular Malaysia.

ECOLOGY. In lowland forest.

SPECIMENS EXAMINED.

PENINSULAR MALAYSIA: **Kedah**, Alor Star, 10 Jul 1936, *Corner* SFN 31535, leafy branch (SING!) fruits (SING!); Gunung Jerai, Feb 1876, *Murton* s.n., flower & immature fruit (K!). **Kuala Lumpur**, Pantai Valley, 29 Jan 1969, *T. & P.* 215 (KL 2815), flower bud, flowers & fruit (L 2 sheets! SING!); Pantai Valley, University of Malaya campus, cultivated, 8 Mar 1966, *Stone* BCS 6215, flower (KLU! L! SING!); *ibid.*, 16 Feb 1972, *Stone* BCS 1367, flower & fruit (KLU!); *ibid.*, 16 Feb 2006, *Low* s.n., flower (KLU!); University of Malaya campus, Rimba Ilmu Botanic Garden, cultivated at the car park near the main building, 1 Jul 2008, *Low* LYW 195, flowers & immature fruit (KLU!); *ibid.*, 15 Dec 2007, *Low* LYW 234, flower bud & fruits (KLU!).

Melaka, No locality, 1871, *Maingay* KD 837, flowers (K! L!) fruit (K!) leafy branch (K 2 sheets!); Alor Gajah to Tampin, 24 Feb 1936, *Corner* SFN 30758, flower buds & flowers (SING!); Batang Malaka, Jul 1890, *Derry* 906, flower buds & flower (SING!) fruit (K!); Bukit Panchor, 1892, *Derry* 953, flower buds & flower (K!) flower buds, flowers & fruit (SING!). **Negeri Sembilan**, Tampin, Aug 1905, *Md. Nur* s.n., fruit (SING!). **Pahang**, Raub to Gap (Fraser's Hill), disturbed hill forest, 1969 ft [600 m], 14 Jul 1988, *Saw* FRI 36315, fruits (K! SING!); Rompin, Pulau Tioman, Kampung Tekek, road to Kampung Juara, 14 Mar 2007, *Imin et al.* FRI 50940, flowers (SING!); Temerloh, *Burn-Murdoch* SFN 169, 12 Jun 1913, fruits (SING!). **Penang**, No locality, Dec, *Wallich Catalogue no.* 8271A, flowers & fruit (holo K-W! iso K 2 sheets!); Province Wellesley (Seberang Perai), Permatang Bertam, Dec 1895, *Ridley* 6974, flowers (K! SING!); *ibid.*, 15 Mar 1938, *Yahaya* SFN 21418, flowers & immature fruits (SING!); Ravenswood, 500 ft [152 m], Dec 1885, *Curtis* 525, flower (SING!) flowers (SING!). **Perak**, Dinding, Pangkore, Jan 1897, *Ridley* s.n., flowers (SING!); *ibid.*, 30 Mar 1918, *Foxworthy* CF 1090, flower bud, flower & fruit (SING!); Gua Ipoh, 16 Feb 1924, *Bernard* 9652, flower (SING!); Lumut, Telok Batak disturbed forest, 2 May 1972, *Teo* KL 3047, flower bud & flower (K! SING!); Pangkor Forest Reserve, 18 Feb 1967,

Whitmore FRI 3046, flower bud & flower (K!) flower (SING!). **Selangor**, Gombak, Genting Sempah Road, primary forest, 800 ft [244 m], 8 Feb 1966, *Kochummen* KFN 97774, flower bud (K! L!) flower (SING!); Gombak, Sungai Tua Recreation Forest, 11 May 2008, *Wong* s.n., leafy branch (KLU!); Gombak, Ulu Gombak Forest Reserve, 800 ft [244 m], Jul 1970, *Mahmud* s.n., fruit (KLU!); Kepong, Bukit Lagong Forest Reserve, hillside, 800 ft [244 m], 23 Jan 1960, *Kochummen* KFN 79039, flower (L! SING!); Kepong, Forest Research Institute, cultivated at the circus near the Dewan, 24 Jan 1972, *Zainuddin* FRI 17982, flower bud, flowers & fruits (L! SING!); Forest Research Institute, Kampong Jawa, 24 Mar 1980, *Vethevelu* FRI 25249, flower & fruit (L!) fruit (SING!); Shah Alam, cultivated, *Worthington* 12511, 28 Feb 1987, flowers & fruit (L!); Ulu Langat, Gunong Inung, K. Pasom, *Gadoh* KL 1240, 3 Jan 1959, flower (SING!).

Terengganu: Dungun, Bukit Tudung Sagi, 28 May 1986, *T. & P.* 1020 (KL 3520), fruit (SING!) fruits (L!); Kerteh, Recreation forest off Kerteh, 24 Jul 2006, *Low et al.* LYW 147, fruits (KLU!); Ulu Trengganu, Bukit Rambai, Ulu Telemong, 14 Sept 1969, *Loh* FRI 13420, fruit (SING!).

SINGAPORE: Singapore Botanic Garden, lawn D, cultivated, *Kiah* s.n., 9 Dec 1953, flower (SING!); Singapore Botanic Garden, cultivated, *Eugene Tang & Sidek* 1333, 12 Oct 1999, leafy branch (SING!); Woodleigh, Municipal Nursery, seeds originated from Alor Star (Kedah, Peninsular Malaysia), cultivated, *Corner* s.n., Dec 1937, leafy branch (SING!).

THAILAND: Peninsular Thailand, Klaung Tan, Salut, 328 ft [100 m], *Kerr* 14593, 14 Mar 1928, flower & fruits (K!) fruit (L!); Krabi, Nai Chong, Khao Khram, *Hansen & Smitinand* 11995, 18 Jan 1966, flower bud (L!) flower (L! SING!); Narathiwat, Bacho, *Sangkhachand* 114, 2 May 1961, fruits (BKF! L!); Narathiwat, Dak Sin Palace area, *Stone* BCS 13368, 29 Apr 1977, flower buds & flower (KLU!) flower (KEP!); Narathiwat, Kaluwotai, Khao Chana, 164 ft [50 m], *Niyomdham et al.* 982, 12 Sept 1985, fruits (BKF 2 sheets! L!); Songkhla, Khao Noi, *Pnemnanmi* BKF 1678 (BKF 1319), 20 Feb 1941, flower (BKF 2

sheets!); Songkhla, Sadao, *Thonanon s.n.*, flowers (L!); Yala, *Sangkachand et al.* 1559, 11 Feb 1973, flower bud & flower (KLU!); Yala, Be Tong, *Santisuk et al.* 443, 19 Dec 1972, fruit (BKF! L!).



Fig. 21. The holotype specimen of *Gardenia carinata* Wall. ex Roxb.: Wallich Catalogue no. 8271A (K-W).

4. *Gardenia chanii* Y.W.Low, Edinburgh. J. Bot. 64: (2007) 29.

TYPE: Wong WKM 205, Brunei, Belait district, Badas Forest Reserve, peat swamp (13 July 1988, flowers) (**holotype** SING! **isotypes** BRUN! KEP! SAN!).

"*Gardenia pterocalyx*" auct. non Valetton (1912): Anderson, Checkl. Trees Sarawak: 296 (1980); Coode *et al.*, Checkl. Fl. Gymnosperms Brunei Darussalam: 270 (1996), quoad *Bruenig* S 11914, *Corner* BRUN 5346, *Wong* WKM205.

(Fig. 22.)

Tree, to c. 15 m high, trunk to c. 70 cm diameter, not buttressed. Bark smooth to sometimes flaky, light- to grey-brown. *Stipules* connate into a cupuliform structure, 0.6–0.9 cm long, margin weakly 2-lobed to subtruncate, outside glabrous and generally coated with resin (this sloughing off in older material), inside with a dense covering of dark-coloured colleters mixed with scattered shorter, fine translucent trichomes at the basal half, and glabrous at the upper half. *Petiole* 0.5–1(–2.5) cm long, 3–5 mm thick, glabrous, often conspicuously resin-coated. *Leaf* lamina obovate to elliptic; (11–)14–24(–26) cm long, (4.5–)6–7(–10) cm wide; leaf base cuneate; leaf apex obtuse-rounded, acute or short-cuspidate; coriaceous; conspicuously coated with resin when young; midrib prominent and glabrous on both sides; secondary veins 7–14 pairs, prominent and glabrous on both sides, vein axils on the lower side without domatia or occasionally with glabrous or sparsely hairy pocket-domatia; tertiary venation scalariform. *Flowers* solitary. *Pedicel* 0.4–0.6 cm long and 3–4 mm thick in open flowers, reaching 0.7–1 cm long and 4–7 mm thick at fruit maturity. *Calyx* broadly campanulate to broad-cylindric (apex only slightly flared outward), margin subtruncate to (more often) with 8–9 triangular lobes 5–8 mm long and wide, often recurved; tube 4–5 cm long, 5–10 mm wide at the base, becoming 15–35 mm wide at the apex; outside completely glabrous, coated with resin; inside glabrous except for a dense covering of dark-coloured colleters

and translucent trichomes (trichomes shorter than colleters) at the lowermost quarter; with 8–10 keels not extending downward to the hypanthium, to 3.6–4.4 cm long and 4–6 mm wide, narrowing toward apex and base. **Corolla** hypocrateriform, cream turning light yellow, then orange-yellow; tube to 4–8 cm long, 6–8 mm wide at the mid-portion, 10–15 mm wide at the throat, outside completely glabrous, inside glabrous except for narrow patches of ribbon-like translucent hairs in between stamens and just below the corolla throat; lobes 10–13, oblanceolate to obovate, 25–39 mm long, 10–20 mm wide, glabrous on both sides. **Stamens** 10–13, inserted just below the corolla throat and between corolla lobes, dorsifixed; filaments very short to inconspicuous; anthers 12–14 mm long, c. three-quarters exerted. Style 4.7–7 cm long, glabrous; stigma club-like, 5–7-lobed, 10–11 mm long, 5–7 mm wide, wholly exert; ovary with several parietal placentas. **Fruits** globose to depressed globose, 2.5–4 cm long, 3–6 cm wide, mature specimens developing 10–16 prominent ridges on the surface; calyx persistent at fruit apex, the tube to 4.5–6 cm long, flared to 2–5 cm wide at the mouth, with 8–10 keels, to 3.9–5.5 cm long and 4–7 mm wide; yellowish green and splitting irregularly when ripe. **Seeds** many, irregularly angular-elliptic, flattened, 8–10 mm long, 6–8 mm wide, testa surface fine-areolate, embedded in a bright yellow-orange pulp-like placenta.

DISTRIBUTION. Endemic to Borneo (southwest Sabah, Brunei and Sarawak and Central Kalimantan).

ECOLOGY. In peat swamp forest.

SPECIMENS EXAMINED.

BRUNEI: no locality, kerangas site, 1958, *Brunig* S 1191, fruit (SAR!); **Belait district,** Anduki FR, 22 Feb 1959, *Corner* BRUN 5346, fruits (BO! SING!) fruit (KEP!) leafy

branch (A! SING!); Badas Forest Reserve, peat swamp, 13 Jul 1988, *Wong* WKM 205, flowers (holotype SING!) flower (isotypes A! KEP! SAN!); Bukit Sawat, Sungai Mau stateland, behind Mewah Bersatu sawmill, peat swamp forest, 33 ft [10 m], 24 Aug 1996, *Joffre et al.* BRUN 17740, fruit (K! L! SING!). **INDONESIA: Kalimantan,** Central Kalimantan, Kab. Palangkaraya, opposite Kerengbangkirai, S. Sebangau, peat swamp forest, 19 Feb 1994, *Argent & Wilkie* 9475, immature fruit (A! SAN!). **MALAYSIA: Sabah.** North Borneo, Bukau, swamp forest, 12 Aug 1932, *Melegrito* 2512, fruits (A! K! L!); Beaufort, 3 miles East of Seratok Camp, peat swamp forest, 7 May 1963, *Meijer* SAN 33512, fruits (SAN!); Papar, Kimanis Forest Reserve, primary forest, flatland, 80 ft [24 m], 20 Apr 1964, *Ampuria* SAN 41419, fruits (SAN!). **Sarawak.** Batang Baram, freshwater swamp forest, 23 Sept 1955, *Anderson* S 2886, fruit (KEP! SAR 2 sheets! SING!); Binatang, Pulau Bruit, peat swamp forest, Jun 1957, *Rambli* S 4976, immature fruit (SAR! SING!); *ibid.*, 25 Sept 1957, *Sanusi* S 9228, fruit (KEP! SING!) fruits (SAR!); *ibid.*, 8 Sept 1957, *Anderson* S 9026, immature fruit (L! SAR! SING!); Binatang, Pulau Bruit, Sg. Kelepu, peat swamp forest, 10 May 1957, *Anderson* 8034, fruit (SAR!); Tuso, Sg. Tissak, swamp forest, 23 Nov 1955, *Anderson* S 3198, flower (SING!); Sibul, Kayangeran FR, freshwater swamp forest, 29 Jun 1954, *Anderson* S 1562, fruit (SAR 2 sheets! SING!) leafy branch (KEP!); Sibul, Sg. Assan, mixed swamp forest, 24 Nov 1970, *Bujang* S 30574, leafy branch (SAR!); Sibul, Sg. Putus, Loba Kabang, Mar 1971, *Silviculturist Staff* S 30446, fruits (SAR!); Lower Rejang, Batang Belawai, Sg. Mekia, peat swamp forest, 11 Aug 1963, *Anderson* S 18551, flower buds (A! L!) flower bud (SAN! SAR! SING!); near Kuching, *Haviland* 821, flower (SAR!); 3rd Division, Batu Igan, Sg. Tutus logging camp, mixed swamp forest, 21 Nov 1970, *Ahmady* S 30551, leafy branch (SAR!).

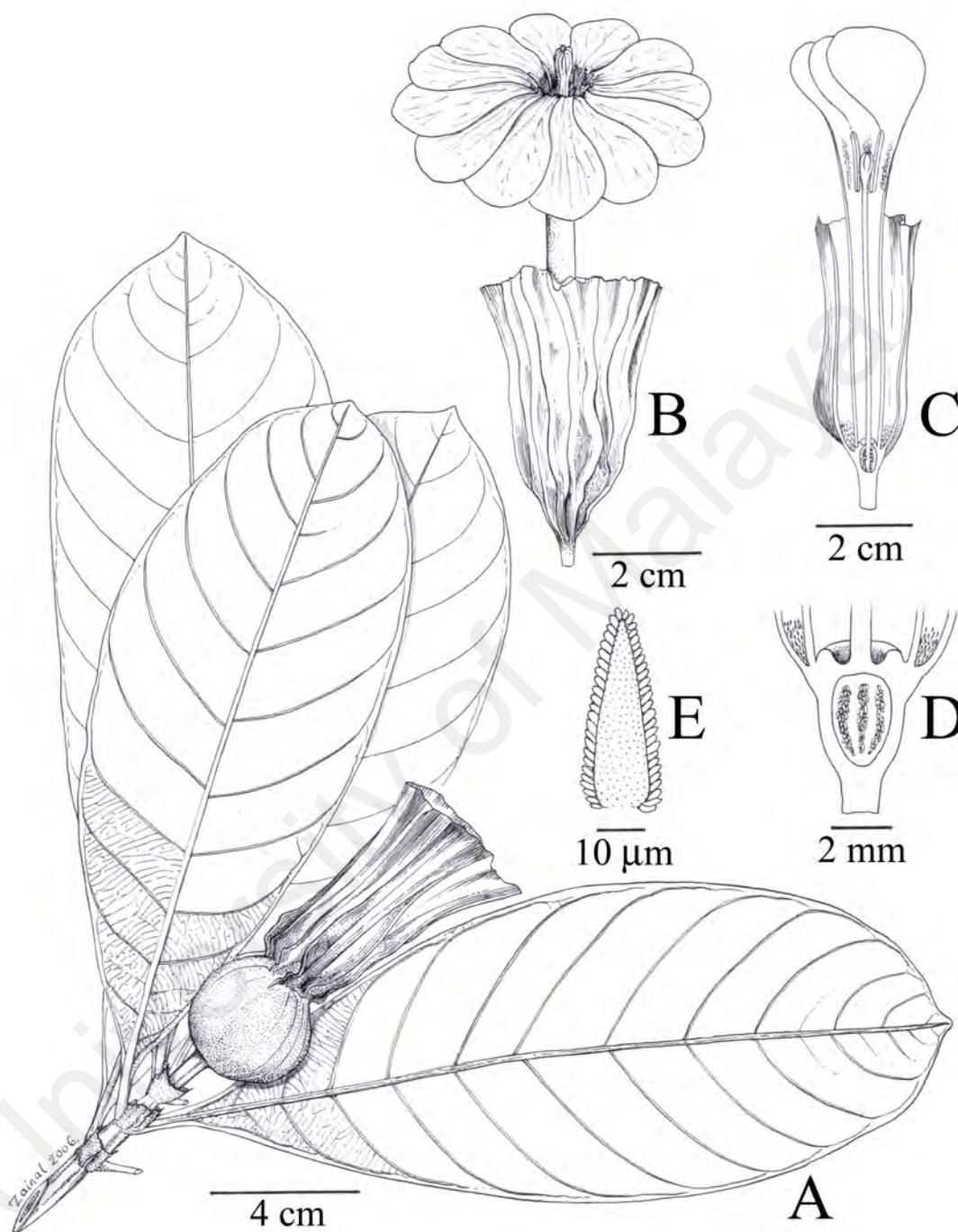


Fig. 22. *Gardenia chanii* Y.W.Low. **A**, Leafy branch with fruit. **B**, Flower with keeled campanulate calyx. **C**, Half-flower. **D**, Detail of longitudinal section of lower part of flower (dark small structures at the base on the inside of the calyx are colleters). **E**, Schematic optical longitudinal section of a colleter (shaded part is the axis of longitudinal cells, with outer palisade-like layer of large cells). [A from Anderson S 2886 (SING); B from Wong WKM 205 (SING); C–E from Anderson S 18551 (SAN).]

5. *Gardenia costulata* Ridl., J. Bot. 72 (1934) 274.

TYPE: *Beccari* 1986, Sarawak, (1865–1868, flower bud & open flower) (**holotype** K!)

Tree, to c. 20 m high, trunk to c. 90 cm diameter, not buttressed. Bark smooth, pale grey to brown. *Stipules* connate into a cupuliform structure, 0.2–0.5 cm long, margin subtruncate, outside subglabrous to minutely puberulent and generally coated with resin (this sloughing off in older material), inside with a dense covering of dark-coloured colleters mixed with scattered longer, fine translucent trichomes at the basal half, and glabrous at the upper half. *Petiole* (0.4–)0.6–2 cm long, 1–2 mm thick, sparsely puberulent, often conspicuously resin-coated. *Leaf* lamina obovate; (8–)10–15(–17) cm long, (3–)4–6(–7) cm wide; leaf base cuneate; leaf apex acuminate to long-cuspidate; thin-coriaceous; conspicuously coated with resin when young; midrib flat to sunken and glabrous on upper side, prominent and puberulent on lower side; secondary veins 10–14 pairs, glabrous and prominent on both sides, vein axils on the lower side with hairy pocket-domatia; tertiary venation scalariform. *Flowers* solitary. *Pedice*l 0.2 cm long and 2 mm thick in open flowers, reaching 0.5–0.7 cm long and 2–2.5 mm thick at fruit maturity. *Calyx* broad-tubular, margin often subtruncate (more often) or with 8–9 triangular-rounded lobes to 0.5 mm long and wide, often slightly recurved; tube 1.5–2.4 cm long, 2–4 mm wide at the base, becoming 5–6 mm wide at the apex; outside densely puberulent at the base and sparsely puberulent to subglabrous at the upper part, coated with resin; inside glabrous except for a dense covering of dark-coloured colleters mixed with translucent trichomes (trichomes longer than colleters) at the lowermost quarter only; with 8–9 keels extending down to the hypanthium, 1.2–2.4 cm long, 1–3 mm wide, narrowing towards the apex and base. *Corolla* hypocrateriform, cream turning light yellow, then orange-yellow; tube to 4–4.5 cm long, 2.5–3 mm wide at the mid-portion, 9–10 mm wide at the throat, outside completely glabrous, inside largely

glabrous except for a 0.8–1 cm zone of scattered ribbon-like translucent hairs just below the throat to about 0.4 cm below the stamens; lobes 7–8, obovate, 23–25 mm long, c. 12–13 mm wide, glabrous on both sides. **Stamens** 7–8, inserted just below the corolla throat and between corolla lobes, dorsifixed; filaments very short to inconspicuous; anthers 9–10 mm long, c. a quarter exerted. Style 4–4.5 cm long, glabrous; stigma club-like, 3–4-lobed, 5–6 mm long, 3–4 mm wide, wholly exerted; ovary with several parietal placentas. **Fruits** globose, 1.9–2.5 cm long, 1.9–2.5 cm wide, surface smooth or (rarely) with 8–9 longitudinal keels to 0.5 mm wide; calyx persistent at fruit apex, the tube to 1.8–2.4 cm long, to 0.5–0.6 cm wide at the mouth, with narrow keels 1.5–2.4 cm long and 1–3 mm wide.

DISTRIBUTION. Restricted to Borneo.

ECOLOGY. In coastal *kerangas* forest.

SPECIMENS EXAMINED.

BRUNEI: Andulau, sine date, *Ashton* A 2865, leafy branch (BRUN!); Bukit Patoi, sine date, *Ashton* 3970, leafy branch (BRUN!). **INDONESIA:** Kalimantan, Soengei Smittau, 1893–1894, *Hallier* B 1285, leafy branch (K! L 4 sheets!). **MALAYSIA:** **Sabah.** Beaufort, Lumat Estate Reserve, primary forest, hillside, 1,000 ft [305 m], 28 Oct 1965, *Madius* SAN 50094, fruits (SAN!). **Sarawak:** no locality, 1865–1868, *Beccari* 1986, flower bud & flower (holotype K!); Bako National Park, 1 Feb 1959, *Brunig* S 5295, fruit (SAR!); Bukit Sungai Tebelian, Sampadi Boundry, mixed dipterocarp forest, 29 Oct 1996, *Jemree et al.* S 74916, fruit (SAR!); Gunung Pueh Forest Reserve, Nov 1955, *Brunig* S 7089, leafy branch (SAR!); Kuching Division, Kubah National Park, Sungai Rayu, riverside forest, 246 ft [75 m], *Rantai et al.* S

68735, 21 Sept 1994, fruits (KEP 2 sheets! SAN! SAR!); Kuching, Matang Massif, trail to Indian Temple, mixed dipterocarp forest, 197–820 ft [60–250 m], *Low* LYW 24, 25 Nov 2004, fruits (KLU!); *ibid.*, Kampung Matang, Batu 10, Mount Mike, trail to Indian Temple, heath forest, 801 ft [244 m], *Low* LYW 212, 20 Jul 2008, immature fruits (KLU!); 1st Division, Lundu District, Gunung Pueh Forest Reserve near Sungai Bakuching, kerangas forest, lowland, 24 Jun 1974, *James et al.* S 34515, flower buds & flower (SAR!) flower bud (SAN!); 1st Division, Matang, proposed Matang National Park, Gunung Selang, kerangas forest, on ridge, 1,542 ft [470 m], 3 May 1987, *Bernard Lee* S 54188, fruit (KEP! SAN!) fruits (L! SAR!); Selama Forest Reserve, Feb 1956, *Brunig* S 7259, leafy branch (SAR!).

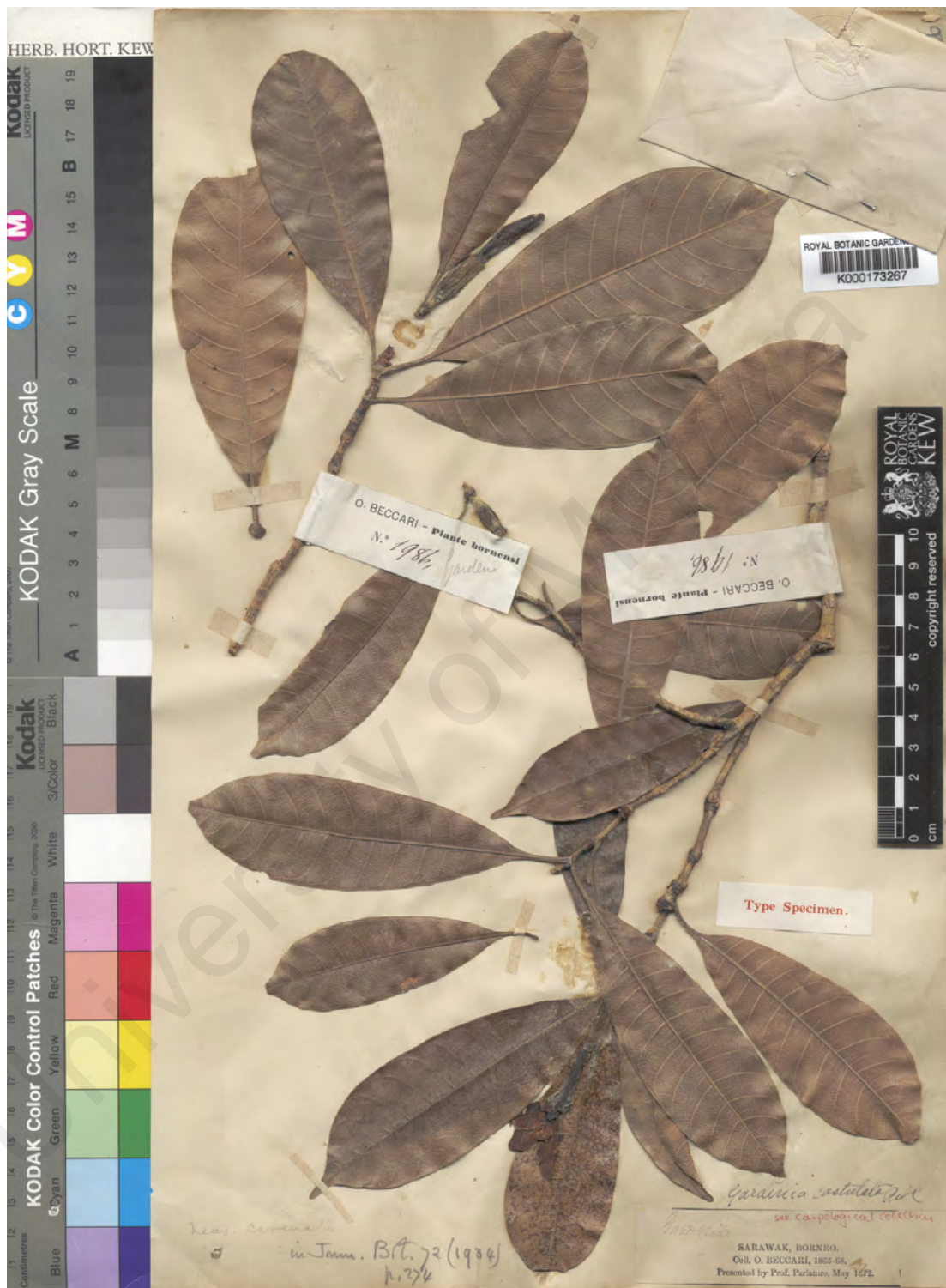


Fig. 23. The holotype specimen of *Gardenia costulata* Ridl.: Becarri 1986 (K).

6. *Gardenia elata* Ridl., J. Straits Branch Roy. Asiat. Soc. 79 (1918) 81; Ridley, Fl. Malay Penin. 2 (1923) 83; Low & Wong, Gard. Bull. Singapore 61 (2009) 107.

Gardenia tubifera var. *tubifera* forma *elata* (Ridl.) K.M.Wong, Gard. Bull. Singapore 35 (1982) 22, Tree Fl. Malaya 4 (1989) 349; Coode *et al.*, Checkl. Fl. Pl. Gymnosperms Brunei Darussalam 270 (1996), quoad *Ashton BRUN 1008*, *Ashton S 7834*, *Niga 52*, *Niga 63*, *Sands 5869*, *Simpson 2007*, *Wong WKM 571*.

TYPE: Ridley 11332, Singapore, Bukit Timah, (1898) (**lectotype** K! **isolectotype** SING).

Randia speciosa Hook., Icon. Pl. 5 (1852) t. 824, nom. illeg., haud *Randia speciosa* DC., Prodr. 4 (1830) 388; *Gardenia speciosa* Hook.f., Fl. Brit. Ind. 3 (1880) 117, King & Gamble, J. Asiat. Soc. Beng. 72 (2) (1903) 220, Ridley, Fl. Malay Penin. 2 (1923) 83, nom. illeg., haud *Gardenia speciosa* Salisb., Prodr. Stirp. Chap. Allerton (1796) 63, nec *Gardenia speciosa* Roxb. ex Wight & Arn., Prodr. Fl. Ind. Orient. (1834) 422.

TYPE: Hook., Icon. Pl. 5 (1852) t. 824 (*Randia speciosa* Hook.).

Gardenia lobbii Craib, Fl. Siam. 2 (1932) 120. (Craib proposed this as nom. nov. for *G. speciosa* Hook.f.). See above.

Gardenia longiflora S.Vidal, Revis. Pl. Vasc. Filip. (1886) 153, nom. illeg.; Merrill, Enum. Philipp. Fl. Pl. (1923) 530; haud *Gardenia longiflora* Ruiz & Pav., Fl. Peruv. 2 (1799) 67, t. 219, nec *Gardenia longiflora* (Salisb.) Dryander in Aiton, Hortus Kew., ed. 2, 1 (1810) 368.

TYPE: Vidal 832, Luzon, Camarines Province, Paracale (Jan 1884, open flower & fruit) (isotype K!).

Gardenia longituba Ridl., J. Bot. 72 (1934) 274.

TYPE: Fraser 164, British North Borneo, Kudat (Jul 1885, flower bud) (holotype K!).

"*Gardenia glutinosa*" auct. non Teijsm. & Binn. (1866): Elmer, Leafl. Philipp. Bot. 4 (1912) 1331: quoad *Elmer 13064*.

"*Gardenia tubifera*" auct. non Wall. ex Roxb. (1824): Corner, Gard. Bull. Straits Settle. 10 (1939) 46, pro parte: quoad *G. speciosa* Hook.f. & *G. elata* Ridl. in syn.; Corner, Wayside Trees of Malaya 1 (1952) 541, pro parte; Anderson, Checkl. Trees Sarawak 297 (1980); Kessler *et al.*, Secondary Forest Trees of Kalimantan, Indonesia (2000) 135, quoad Fig. 134.

(Figs. 24, 25.)

Tree, to c. 30 m high, trunk to c. 120 cm diameter, not buttressed. Bark smooth, light grey-brown to dark brown. *Stipules* connate into a cupuliform to cylindrical structure, (0.4–)0.6–1.5 cm long, margin weakly 2-lobed to subtruncate, outside puberulent and generally coated with resin (this sloughing off in older material), inside with a dense covering of dark-coloured colleters mixed with scattered, slightly longer, fine translucent trichomes over the basal half and glabrous at the upper half. *Petiole* (0.3–)1.1–3.5(–3.8) cm long, 1–2(–2.5) mm thick, evenly puberulent, sometimes conspicuously resin-coated. *Leaf* lamina obovate to rarely elliptic; (3.7–)10–22.5(–27) cm long, (1.7–)4–11(–12) cm wide; leaf base cuneate to rarely oblique; leaf apex acuminate, tip pointed to short-cuspidate; thin-coriaceous; conspicuously coated with resin when young; midrib flat to sunken and puberulent to subglabrous on upper side, prominent and sparsely hairy on lower side; secondary veins (7–)14–22 pairs, flat and subglabrous on upper side, prominent and sparsely hairy on lower side, vein axils on the lower side with hair tufts or hairy pocket-domatia; tertiary venation scalariform. *Flowers* solitary. *Pedice*l 0.1–0.4(–1) cm long and 2–3 mm thick in open flowers, reaching 0.2–1(–1.5) cm long and (2–)4–10 mm thick at fruit maturity. *Calyx* cupular-obconical, the margin often subtruncate; tube (0.6–)1.4–2.5(–3.5) cm long, 3–6 mm

wide at the base, becoming 8–13(–15) mm wide at the apex; outside densely puberulent at the base and sparsely puberulent to subglabrous at the upper part, often coated with resin; inside glabrous except for a dense covering of dark-coloured colleters mixed with translucent trichomes at the basal half (trichomes especially conspicuous as a dense fringe at the very base of the calyx tube and longer than colleters); without keels or ribs. **Corolla** hypocrateriform, cream turning light yellow, then orange-yellow; tube to (3.1–)7–15 cm long, 2–5 mm wide at the mid-portion, 5–13 mm wide at the throat, outside glabrous to sparsely puberulent, inside largely glabrous except for dense ribbon-like translucent hairs covering the mouth, base of corolla lobes and extending down to midtube; lobes 7–10, oblanceolate to obovate, (12–)32–45(–50) mm long, 10–20(–24) mm wide, glabrous on both sides. **Stamens** 7–10, inserted just below the corolla throat and between corolla lobes, dorsifixed; filaments very short to inconspicuous; anthers 7–10 mm long, c. a third to half exerted. Style (3.4–)9–15.5 cm long, glabrous; stigma club-like, 4–8-lobed, (4–)6–11 mm long, 3–5 mm wide, wholly exert; ovary with several parietal placentas. **Fruits** globose, rarely depressed globose or obovoid, (2.3–)4–6.5 cm long, (2.2–)4–7 cm wide, surface in mature specimens smooth; calyx persistent at fruit apex, the tube to 1–2.5 cm long, 0.8–1.5 cm wide at the mouth; yellowish green and splitting irregularly when ripe. **Seeds** many, irregularly angular-elliptic, flattened, 3.5–7 mm long, 3–8 mm wide, testa surface fine-areolate, embedded in a bright yellow-orange pulp-like placenta.

DISTRIBUTION. Widespread in Sundaland, including Palawan (Philippines), and also adjacent smaller islands such as Bali and Sumbawa.



Fig. 24. The lectotype specimen of *Gardenia elata* Ridl.: Ridley 11332 (K).

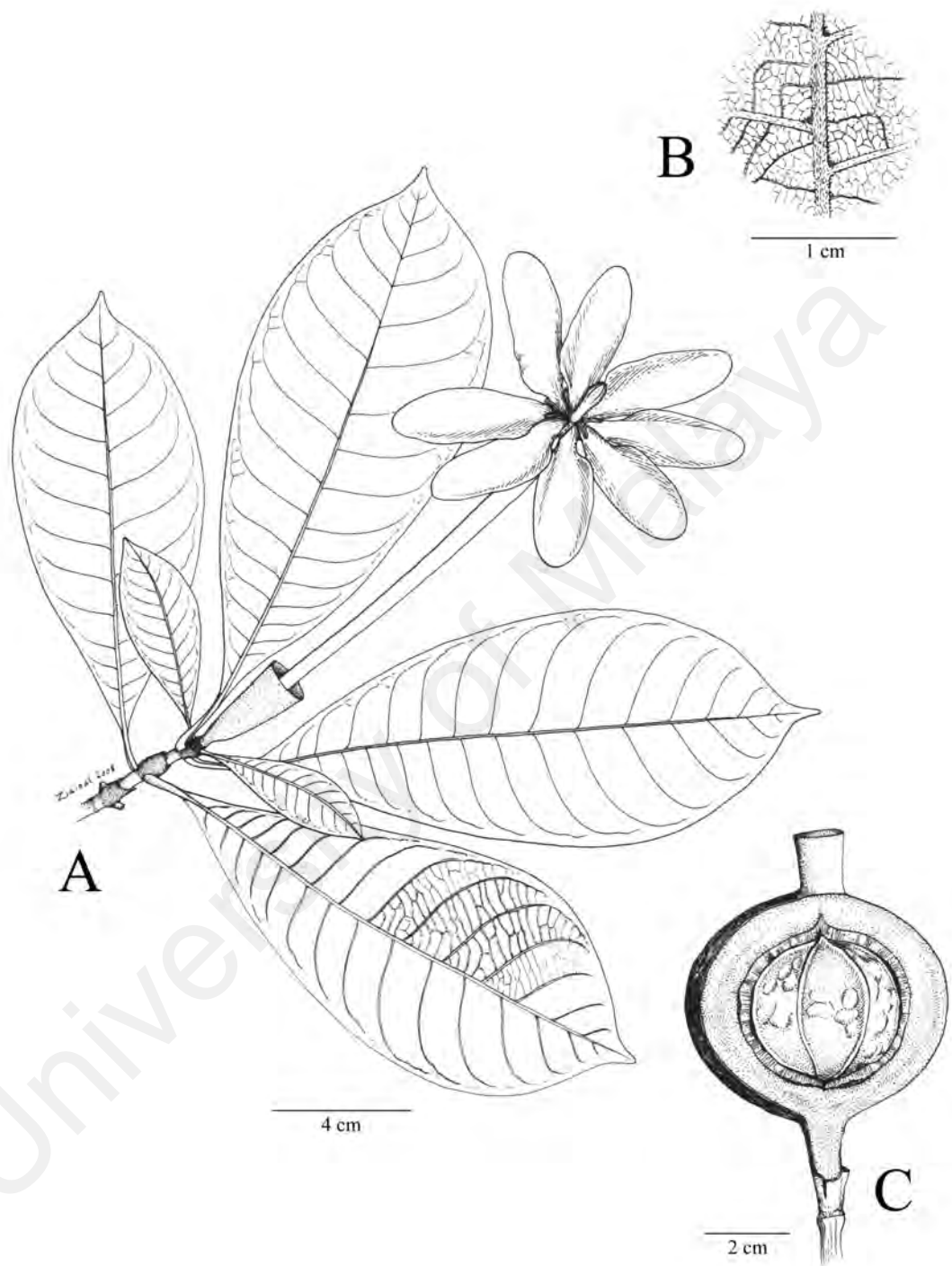


Fig. 25. *Gardenia elata* var. *elata*. **A**, Flowering leafy branch. **B**, Detail of puberulent veins on lower leaf surface. **C**, Longitudinal section of fruit, calyx shown intact. [A & B from *Symington* 24190 (SING); C from *Sigin & Ismail* SAN 100264 (L).]

ECOLOGY. In lowland forests (including on ultramafic and volcanic soils in north Borneo and the Philippines), very rarely in freshwater swamp forest (and then more typically on drier mounds or banks).

SPECIMENS EXAMINED.

BRUNEI: Belait District. Andulau Forest Reserve, compartment 5, 10 Jun 2008, *Low et al.* LYW 180, fruits (BRUN! KLU!); Belait river, upstream from the Malayan river, 23 Oct 1988, *Wong* WKM 571, flower (A! BRUN! KEP!), flowers (L! SAN!); Bukit Sawat, Sungai Mau, along Sungai Belait, 15 Oct 1991, *Simpson* 2007, fruit (A! BRUN! KEP! L! SAN! SING!); Sukang, Kampong Sukang, 21 Jul 1993, *Sands et al.* 5869, fruit (A! BRUN! SAN! SING!); Sungai Mau, 18 Aug 1988, *Nangkat* NN 52, fruit (A! BRUN! SAN! SING!); *ibid.*, 28 Jan 1989, *Nangkat* NN 63, flower (KEP! L! SAN! SING!), flowers (A! BRUN!), fruit (SING!); **Muara District.** Berakas Forest Reserve, 31 Sept 1959, *Ashton* BRUN 1008, fruit (BRUN! SING!); *ibid.*, 12 May 1957, *Ashton* S 7834, flower (A! BO! BRUN! KEP! SAR!). **INDIA: Nicobar Island.** North Nicobars, Katchall Island, 17 May 1975, *Chakrakanly* 2557, flower (L!). **INDONESIA: Java.** Cult. Hort. Bogor V.10.49, 1903, Anon. s.n., flower (A!); Tjibodas, sine date, Anon. s.n., flowers (IBSC!). **Kalimantan. East Borneo.** Berau, Inhutani area, Km 37 near transect I, plot 6, 7 Oct 1997, *Ambriansyah et al.* Berau 841, fruit (A!), fruits (L!); Commisi Kap. Genderen Stort., Gunung Samenggaris, Dec 1912, *Amdjah* 1094, flower (K! SING!), flowers (A! BO 2 sheets!), fruit (BO!); Lojanan to Tenggarong road, Kampung Rempaya, 26 Oct 1995, *Ambri et al.* AA 1416, flower (A! K! KEP! L! SAN!); Sei. Seluang, 20 km from Wanariset, Waduk road, 11 Jul 1995, *Ambri et al.* AA 1291, fruit (A! BO! SAN!), fruits (L!); **South Borneo.** Sungai Wain region, North of Balikpapan, Oct 1950, *Kostermans* 4323, immature fruit (A!); **West Borneo.** Pontianak, Bentiang, Gunung Sekaju, West of Kampung Madamang, 6 Nov 1980, *Shea* 27578,

fruit (A!); West Koetai, 21 Aug 1929, *Endert* 2765, fruit (A! BO!). **Sumatra**, Bangka, Lombok Besar, 1 Sep 1949, *Kostermans & Anta* 282, fruit (A! KEP!), fruits (L! NY! SING!); East Coast, Asahan, Kuala Masihi, Apr 1927, *Yates* 2397, flower (L! US!), flowers (A! NY! SING!); North Siberut Island, Gunung Simapipit, 26 May 1994, *Afriastini* 2737, fruit (K!), fruits (L!); Palembang, 16 Dec 1916, *Lambach* 1354, flowers (BO!); Riau, Tigapuluh Mountains, 15 km Southwest of Talanglakat, Rengat-Jambi road, vicinity of Sungai Serisih, 24 Nov 1988, *Burley et al.* 1680, fruit (KEP! L! NY! SING!), fruits (A!); South Sumatra, Barisan Range, Seleman Enim, Bukit Seburong near Muara Dua, 15 Mar 1972, *de Vogel* 1299, fruits (L!); Southeast Sumatra, Lampung, Way Kambas, 3 Feb 1972, *Mochtan* 24A, fruits (L!); West of North Sumatra, Simaloer Island, 1 Nov 1918, *Achmad* 709, fruit (L!). **Sumbawa**, Central Sumbawa, Dompu, Raba Baka Trail to Matuatoi, 6 Jun 1961, *Soejarto* 60, fruits (BO!); West Sumbawa, Semongkat Atas, 17 km South of Sumbawa Besar, 2 May 1961, *Kuswata* 112, fruit (BO! SING!), fruits (A! BO!). **MALAYSIA: Peninsular Malaysia. Johor**, Kota Tinggi, Sungei Bang, 13 Mar 1966, *Sinclair* 10863, flowers (US 2 sheets!); Mawai to Jemilang Road, Sungai Berassau, 6 Feb 1935, *Corner* 28736, fruits (SING!), Sungai Kayu near Sungai Sedili, 10 Mar 1937, *Kiah* SFN 32368, fruits (A! SING!), Sungai Sedili, 28 Mar 1937, *Corner* 32440, flower (BO!), flowers (A! SING 3 sheets!). **Kedah**, Koh Mai Forest Reserve, 3 Apr 1938, *Kiah* SFN 35148, flowers (A! SING 2 sheets!); Ulu Muda Forest Reserve, 21 Jan 1969, *Chan* FRI 6777, fruit (A!). **Kelantan**, Kuala Krai, Taman Negara, Kuala Koh Headquarters, 30 Mar 1995, *Latiff et al.* 4168, flower (K! L!); Ulu Lebir Forest Reserve, 12 Aug 1970, *Suppiah* FRI 11681, fruit (L 2 sheets!). **Melaka**, Chaban, 28 Sep 1885, *Alvin* 2364, fruits (SING!); Kemandore, 14 Jul 1917, *Burkill* 2509, fruits (SING!). **Negeri Sembilan**, Pasoh Forest Reserve, 6 Jul 1988, *LaFrankie* 3032, fruits (A!); *ibid.*, 16 Jul 2008, *Wong & Zulkapli* s.n., leafy branch (KLU!). **Pahang**, Rompin, Pulau Tioman, Sungai Asah to waterfall, 29 Apr 1995,

Zainudin & Bedul 5477, flowers (L!), Ulu Sungai Sat, 11 Jul 1970, *Mohd Shah & Mohd Noor* MS 1833, fruit (A! L! US!), fruits (SING!). **Perak**, Gopeng, Apr 1884, *King's collector* 5830, flower (L!); Gunong Bubu via Trong, 27 Apr 1970, *Suppiah* FRI 11673, fruit (K! L!), near Selangore, Apr 1886, *King's collector* 8736, flowers (K!); Selama, 1894, *Wray* 4265, flowers (SING!). **Selangor**, Gombak, 27 Jun 1960, *Poore* 185, fruit (KLU!); Kajang, Bukit Enggang, 9 Apr 1930, *Symington* 24190, flower (SING!); Sungai Buloh, 1891, *Ridley* s.n., fruits (SING!); Sungai Buloh Reserve, 25 Mar 1919, *Abu* 3313, flowers (SING!). **Terengganu**, Kuala Trengganu, Jerteh, Gunung Tebu Forest Reserve, compartment 65, 12 Oct 1971, *Zainuddin* FRI 17945, fruit (A! L! SING!), Kuala Trengganu, logging school area, 14 Nov 1978, *Suppiah* FRI 28251, fruit (A!). **Sabah**. **Beaufort**, Membakut, Kampung Binsulok Forest Reserve, 23 Apr 1984, *Ag. Amin & Haya* SAN 102465, flower (A! KEP! L! SAN! SING!), flowers (SAN!); **Beluran**, Tongod, Ulu Sungai Pinangah, 16 Oct 1984, *Amin et al.* SAN 107143, fruit (SAN 2 sheets!); **Kalabakan**, Benaword logged over area, 11 Apr 1980, *Fedilis & Sumbing* SAN 91785, fruit (SAN!); Maliau Basin, Rafflesia Camp to Resak Island, 26 Apr 2000, *Ming et al.* MB 283, fruit (KEP! SAN!); **Keningau**, Shang Lian logging area, LANAS, 16 Oct 1986, *Mantor* SAN 118392, fruit (SAN!) fruits (SAN!); **Kinabatangan**, Gunung Rara Forest Reserve, Maliau river, 11 April 1996, *Puff* 960411-1/2, flowers (SAN!); Lamag, Gunong Lotung, 5 miles Southeast of Inarat, 7 May 1976, *Cockburn* SAN 83039, flower (A! KEP! SAN! SING!); Lamag, Sogo-sogo, Kampung Tongod, 22 Nov 1979, *Madani* SAN 91125, flower (K! KEP! SING!), flowers (SAN!); Lamag, Tanegang Kechil, 26 May 1965, *J. Singh & Eging* SAN 51864, flowers (K! SAN! SING!); Sukau, Sungai Menanggul, 13 May 1996, *Azmi et al.* RA 512, flower (L!), flowers (KEP!), flower & flower bud (K! SAN!); **Kuala Penyu**, Kepayan, 20 Aug 1993, *Ag. Amin* SAN 127290, fruit (K!), fruits (SAN!); Mempatul, Malikai, 25 Feb 1937, *Mail* 7060, flower (A! SING!); **Kudat**, without locality, 7 Aug

1885, *Fraser* 164, flowers (K!); Berambangan, 9 Jul 1962, *Brand* SAN 30870, fruit (SAN!); Dumpirit, 7 Feb 1933, *Balajadia* Nbfd 2843, flower (BO!), flowers (A!); **Lahad Datu**, Mile 17.7 of Kalumpang-Tawau road, 16 Sep 1962, *Chai* SAN 29828, fruit (BO! KEP! SAN! SING!); Pulau Sakar, 16 Mar 1961, *H.S.M. & D. Brand* SAN 24552, flower (SING!), flowers (SAN!), flowers & fruit (BO! KEP!); **Nabawan**, Sepulut, Sepulut Forest Reserve, Labang, 17 Oct 1988, *Fedilis & Sumbing* SAN 125652, fruit (SAN!); Sungai Tibow, 18 Jul 1984, *Fedilis & Sumbing* SAN 105342, fruit (SAN!); **Papar**, Mandahan Forest Reserve, 8 Jul 1987, *Ag. Amin* SAN 103348, immature fruit (SAN!), fruits (K!); **Ranau**, without locality, 23 Feb 1990, *Majawat* SAN 125800, fruit (KEP! L!); Bongkud, 26 Mar 1986, *Amin et al.* SAN 105640, flower (A! K! KEP! SAN! SING!); **Sandakan**, Kretam, Sungai Kulamba, 9 Apr 1984, *Sundaling* SAN 55998, flower (A! L! SAN 2 sheets!); Labuk Road Forest Reserve, 11 Feb 1993, *Wong* WKM 2600, flowers (SAN!); Sepilok Forest Reserve, Jalan Hg. Tanjong Cpt. 13, 24 Sep 1968, *Patrick* SAN 63508, fruit (L!), fruits (SAN!); Sungai Dagat, 14 Jul 1987, *George et al.* SAN 120736, fruit (K! KEP!), fruits (SAN!); Sungai Malikop, 25 Aug 1984, *Sigin & Ismail* SAN 100264, fruit (L! SAN!); Telupid, Kampung Wonod, 19 Mar 1974, *Aban & Saikeh* SAN 79413, flower (A! K! SING!) flowers (A! KEP! SAN!); **Semporna**, Bodgaya, 6 May 1939, *Valera* SHN 10263, flower (SING!), flowers (KEP!); Semporna, Mile 25 of Pagagau Road, 11 Mar 1965, *J. Singh et al.* SAN 48883, flower (NY!), flowers (SAN!); **Sipitang**, Melaliah, 19 Oct 1961, *Md. Thaufeck* SAN 27148 No. 19, fruit (BO! SING!), fruits (SAN!); **Tawau**, Bombay Burmah Timber Company Concession, Sub-compartment no. 2 of Compartment no. 1, 28 Nov 1954, *Wood* SAN A3973, fruit (KEP!), flowers & fruits (L!); Elphinstone Province, Oct 1922–Mar 1923, *Elmer* 20544, fruit (A 2 sheets! IBSC! L! NY! SING!); Mostyn, Tengkeyu Waterfall, Sabah Timbers Company, 28 May 1965, *Madani* SAN 47171, flower (K!), flowers (SAN!); Kalabakan Road, Mile 12, 26 Jul

1962, *Aban* SAN 30557, fruit (L! SAN!), fruits (KEP!); **Tenom**, Mandalom Forest Reserve, 17 Sep 1986, *Mantor* SAN 116647, fruit (SAN 2 sheets!). **Sarawak**. without locality, 1865–1868, *Beccari* 3250, flower (K!), sine date, *Native Coll.* 214, flowers (US!); **1st Division**, Kuching, Matang, Aug 1912, *Anderson* 6, flowers (SING!); Kuching, Matang Road, 10 Jul 1964, *Salleh* 12092, flower (A! K! NY!); Mount Matang, 27 Oct 1929, *J. & M.S. Clemens* 22334, flower (K! SAR!), flowers (A! K! NY!); Kuching, Santubong, 19 Nov 1904, *Egon* 252, fruit & flower (SAR!); Simunjan, Serian to Simanggang Road, Ulu Simpang Sabal Aping, Gunong Gaharu, 9 Oct 1974, *Ilias & Azahari* S 35687, fruit (KEP! L! SAN! SAR!); 26th Mile Bau/ Lundu Road, Sampadi Forest Reserve, 17 Jun 1968, *Jugah* S 24948, flower (SAN!) flowers (A! K! SAR!); **2nd Division**, Sri Aman, 95th Mile, Kampong Pungor Tapang, 9 Mar 1981, *Ilias* S 42712, fruit (KEP! L! SAN!); **3rd Division**, Kapit, Balleh, Ulu Sungai Mengiong, Apan Entelit, 14 Mar 1996, *Rantai et al.* S 74211, fruit (K! KEP! SAN! SAR! SING!); **4th Division**, Bintulu, Nyabau Catchment Area, 22 Jun 1966, *Sibat* S 24617, flower (A! BO! KEP! SAN! SING!), flowers (K! SAR!); **5th Division**, Baram district, Miri river, Feb 1895, *Hose* 506, flowers (K! L!). **PHILIPPINES: Busuanga**. without locality, Sep 1922, *Ramos* Bur. Sci. 41218, immature fruit (K! L!); NE of Coron, 2 km north of San Nicolas, along Wayan Creek, 29 Jun 1984, *Bourell* 2439, fruit (A!). **Culion**, without locality, 29 Apr 1931, *Herre* 1085, flowers (A!), flower & flower buds (NY!); Apr 1931, *Herre* 1088, fruit (NY!). **Luzon**, Camarines Province, Paracale, Jan 1884, *Vidal* 832, flower & fruit (K!); Laguna Province, Dahican River, Sep 1912, *Ramos* 1325, fruit (A! L! NY! SING!); Tayabas Province, May–Jun 1916, *Cailipan* For. Bur. 25640, fruit (K! US!); Lucban, May 1907, *Elmer* 7732, fruit (A!). **Mindanao**, Zamboanga, Feb 1908, *Whitford & Hutchinson* For. Bur. 9492, flower (NY! US!). **Palawan**, without locality, May 1913, *Merrill* 1360, flower bud & fruit (A! NY! SING!); Bataraza, Bgy. Sumbiling, Sitio Gamayon, Bulanjao Range, 8°33'N 117°24'E, 21 Mar 1995, *Soejarto*

& *Madulid* 9030, fruit (A! PNH!); Puerto Princesa, Irawan, Impapai hills above BFD Field Station, 9°51'N 118°37'E, 26 Jun 1992, *Soejarto & Fernando* 7750, flower & flower buds (K! NY!); Irawan, Irawan River Valley, Tatanarom, road to Benguet mine, Mt Beaufort, 9°50'N 118°40'E, 16 Jul 1988, *Soejarto & Madulid* 6066, fruit (NY! SING! US!); Irawan R. valley head, 19 Mar 1984, *Ridsdale* SMHI 145, flower bud (A! BO! K! KEP! L!); lower slopes of Mt Beaufort, 30 Mar 1984, *Ridsdale* SMHI 291, flowers & flower bud (A! BO! K! L! SAN!); Puerto Princesa, Mt Pulgar, Apr 1911, *Elmer* 13064, flower (NY, US), flower & immature fruit (A!); Pulot, Massin River, 12 km N. Brooks Point, 23 Oct 1985, *Ridsdale* 998, fruit (A! L 2 sheets!); Taytay, May 1913, *Merrill* 1279, flower (A! NY! SING!); Taytay, island on Lake Manguao, ca 10 km SE of Taytay town, 10°50'N 119°33'E, 30 Jan 1991, *Soejarto & Fernando* 7419, fruit (A! PNH!); valley stream leading into NNW bay of lake, 7 Apr 1984, *Ridsdale* SMHI 357, fruit (A! BO! KEP! L! SAN!). **Panay**, Capiz Province, Oct–Nov 1925, *Edano* Bur. Sci. 46123, fruits (A! BO! NY! SING!). **Sibuyan**, Capiz Province, Magallanes, Mt Giting-Giting, Mar 1910, *Elmer* 12103, flower & flower buds (A! flower (NY! US!). **Tawitawi**, Sulu Province, Jul–Aug 1924, *Ramos & Edano* Bur. Sci. 44127, fruit (A! NY! SING! US!). **SINGAPORE**: Bukit Timah, 1898, *Ridley* 11332, flower (K! SING!), Bukit Timah Reserve, tree no. 166, 21 Jul 1938, *Ngadiman* SFN 35595, fruit (A!); Gutta Valley, 1907, *Ridley* s.n., fruit (SING!). **THAILAND**: **Peninsular Thailand**, Narathiwat, Waeng, Klong A-re-ma, 3 May 1999, *Puudja* 561, flower (BKF!); Pattani, Banang, 22 Jul 1923, *Anon.* 7275, fruit (K!); Sukinin District, Tomo Mine, 25 Dec 1999, *Wongprasert* 9912-38, fruit (BKF!); Trang, Talay Songkong, 19 Mar 1915, *Vanpruk* 661, flower (BKF!), flowers (K!).

Gardenia elata* var. *kinabaluensis var. nov. ined.

TYPE: *Lajangah* SAN 44406, Sabah, Ranau, Kinabalu, mile 36, Tamparuli to Ranau, 4000 ft. [1219 m], (**holotype** K! **isotype** SAN!)

"*Gardenia* cf. *tubifera*" auct. non Wall. ex Roxb. (1824): Beaman & Anderson, Pl. Mt. Kinabalu 5 (2004) 301, quoad: *Brand & Anak* s.n., *Clemens* s.n., *Clemens* 29721, *Clemens* 30344, *Clemens* 30715, *Clemens* 32176, *Clemens* 32144, *Lajangah* SAN 44406.

(Fig. 26.)

DISTRIBUTION. Endemic to Borneo (Sabah: Mount Kinabalu and Mount Meligan; Kalimantan: Mount Beratus).

ECOLOGY. A lower montane forest species.

NOTES. This variety differs from the typical variety by its glabrescent, not pubescent, corolla throat.

SPECIMENS EXAMINED.

INDONESIA: Kalimantan. peak of Balikpapan's Gunung Beratus, Berikan bulu, sandstone, mossy forest, 2,952 ft [900 m], 11 Jul 1952, *Kostermans* 7440, flowers (A!) flowers & fruit (K!). **MALAYSIA: Sabah.** Kota Belud district, Kampung Kiau Nuluh, Nuluhon, 2 Aug 1993, *Duaneh* 426, flowers (K! KEP!); Mount Kinabalu, Penibukan, on ridge above Dahobang, 4,000 ft [1,219 m], 4 Jan 1933, *J. & M.S. Clemens* 30715, fruit (A! BO! NY!) leafy branch (BO!); *ibid.*, 14 Mar 1933, *J. & M.S. Clemens* 32144, flower (BO!) flowers & fruit (A!) fruit (NY!) leafy branch (BO 2 sheets!); *ibid.*, Feb 1933, *J. & M.S. Clemens* s.n., flower (A!) fruit (NY!) leafy branch (BO!); *ibid.*, 17 Mar 1933, *J. &*

M.S. Clemens 32176, flowers (A!) flowers & fruit (NY!) fruit (BO!), Mount Kinabalu, Tenompok, edge of jungle, 5,000 ft [1,524 m], 24 May 1932, *J. & M.S. Clemens* 29721, flower (NY!) flowers (A! BO! K!); *ibid.*, Feb–May 1932, *J. & M.S. Clemens* 30344, fruit (BO 3 sheets! NY!); Mount Kinabalu, Mahansui river, 3,500 ft [1,066 m], 13 Mar 1933, *Carr* SFN 26547, flowers & fruits (SING!); Ranau, below jalan Kinabalu mile 35 Ranau road, primary forest, 4,000 ft [1,219 m], 25 Jun 1963, *Mikil* SAN 37713, fruits (SAN!); Ranau, Kinabalu, Mile 36, Tamparuli to Ranau, primary forest, 4,000 ft [1,219 m], 26 Jun 1963, *Lajangah* SAN 33883, flowers (SAN!); Ranau, Mile 42¹/₄ Ranau road, primary forest, 4,000 ft [1,219 m], 20 Apr 1965, *Lajangah* SAN 44406, flowers (holotype K!) flower (isotype KEP!) flowers (isotypes A! SAN!); Ranau, Sungai Mentaki, primary forest, 2,500 ft [762 m], *Brand & Anak* SAN 25318, 16 May 1961, flower (SAN!) flowers (SING!); Sipitang, Meligan Forest Reserve, montane forest, 4,000–5,000 ft [1,219–1,524 m], 16 Jul 1991, *Madani* SAN 132858, fruit (SAN!) fruits (KEP 2 sheets!).

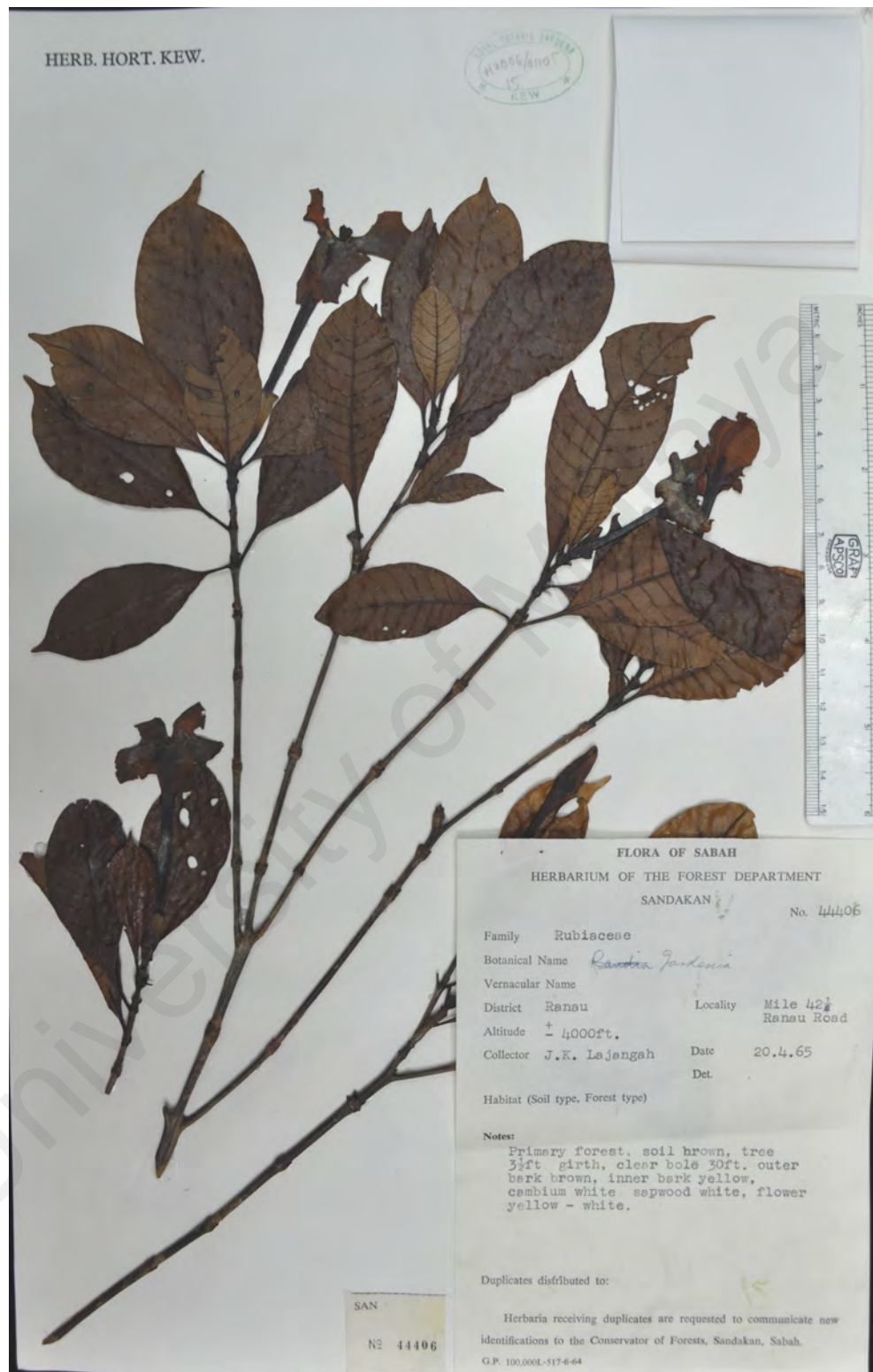


Fig. 26. The proposed type specimen for *Gardenia elata* var. *kinabaluensis* var. nov. ined.: Lajangah SAN 44406 (K).

7. *Gardenia griffithii* Hook.f., Fl. Brit. India 3 (1880) 118; King & Gamble, J.

Asiat. Soc. Beng. 72 (2) (1903) 221; Ridley, Fl. Malay Penin. 2 (1923) 83; Wong, Gard. Bull. Singapore 35 (1982) 25; Wong, Tree Fl. Malaya 4 (1989) 349; Corner, Wayside Trees of Malaya 2 (1997) 631; Low & Wong, Edinburgh J. Bot. 64 (2007) 29.

TYPE: *Griffith* K. D. 2821, Malacca, (no date, open flowers) (**holotype** K [sheet no. K000173266]! **isotype** K [sheet no. K000173265]!).

Gardenia griffithii var. *maingayi* Hook.f., Fl. Brit. India 3 (1880) 118; King & Gamble, J. Asiat. Soc. Beng. 72 (2) (1903) 221; Ridley, Fl. Malay Penin. 2 (1923) 84.

TYPE: *Maingay* K. D. 841, Malacca (no date, fruit) (holotype K [sheet no. K000173264]! isotype K [sheet no. K000173263]!).

Gardenia dolichantha Merr., Pap. Michigan Acad. Sci. 23 (1937 publ. 1938) 196.

TYPE: *Rahmat* 3925, Sumatra, East Coast, Laboehan Batoe, Kota Pinang, Goenoeng Si Papan, Kaloebi Concession (topographic sheet 41, southeast quarter) (7–14 April 1933, flowers) (holotype NY! isotypes A! K! L! MICH 2 sheets! US!).

(Fig. 27.)

Tree, to c. 115 m high, trunk to c. 50 cm diameter, not buttressed. Bark smooth, whitish light-brown to dark brown. *Stipules* connate into a cupuliform structure, (0.6–)1.5–1.7 cm long, margin 2–4-lobed, outside covered with short erect hairs and generally coated with resin (this sloughing off in older material), inside with a dense covering of dark-coloured colleters mixed with scattered, slightly longer, fine translucent trichomes at the basal half, sparsely covered with short erect trichomes at the upper half. *Petiole* (0.4–)1–1.5(–3.5) cm long, 2–3 mm thick, evenly covered with short erect hairs, sometimes conspicuously resin-coated. *Leaf* lamina obovate to broadly

elliptical; (8.5–)11–20.5 cm long, (3–)6–9.5 cm wide; leaf base cuneate; leaf apex acute to obtuse, rounded to short-cuspidate; thin-coriaceous; conspicuously coated with resin when young; midrib prominent and sparsely to densely hairy on both sides, denser on the lower side; secondary veins (6–)10–14 pairs, prominent and sparsely to densely hairy on both sides, denser on the lower side, vein axils on the lower side with hair tufts; tertiary venation scalariform. **Flowers** solitary. **Pedicel** 0.2–0.4 cm long and 3–4 mm thick in open flowers, reaching 0.3–0.8 cm long and 4–10 mm thick at fruit maturity. **Calyx** broadly infundibular, the margin subtruncate but often wavy with 8–10 triangular lobes to 2–5(–15) mm long, 4–6(–10) mm wide; tube (5–)7–10 cm long, 7–10 mm wide at the base, becoming 20–30 mm wide at the apex; outside subglabrous, often coated with resin; inside with a dense covering of dark-coloured colleters mixed with translucent trichomes at the basal part (colleters denser and longer than trichomes); surface without keels or ribs. **Corolla** hypocrateriform, cream turning light yellow, then orange-yellow; tube to 7–15 cm long, (3.5–)6–7 mm wide at the mid-portion, 10–17 mm wide at the throat, outside sparsely puberulent, inside glabrous except for a zone of scattered ribbon-like translucent hairs from the throat to just below the stamens; lobes 10–12, obovate to rounded, 20–45 mm long, 16–25 mm wide, glabrous on both sides. **Stamens** 10–12, inserted just below the corolla throat and between corolla lobes, dorsifixed; filaments very short to inconspicuous; anthers 8–10 mm long, c. half exserted. Style 10–11 cm long, glabrous; stigma club-like, 3–7-lobed, 5–6 mm long, 3–5 mm wide, wholly exsert; ovary with several parietal placentas. **Fruits** globose to depressed globose, 3.5–5 cm long, 3.5–5.5 cm wide, surface unevenly longitudinally ridged; calyx persistent at fruit apex, the tube to 6.5–7.5 cm long, flared to 2.5–3 cm wide at the mouth; yellowish green and splitting irregularly when ripe. **Seeds** many, irregularly angular-elliptic, flattened, 5–7 mm long, 4–6 mm wide, testa surface fine-areolate, embedded in a bright yellow-orange pulp-like placenta.



Fig. 27. The holotype specimen of *Gardenia griffithii* Hook.f.: Griffith 2821 (K).

DISTRIBUTION. Malay Peninsula, Sumatra and Borneo (southwest Sarawak and south Kalimantan).

ECOLOGY. A peat swamp forest species.

NOTES. The Sumatran specimen (*Rahmat 3925*) with long corolla and calyx tubes described by Merrill (1937) as *G. dolichantha* conforms to the characteristics of *G. griffithii*. Infact the length of the corolla and calyx tube varies greatly even in Sumatran material. The extent of lower leaf surface hairiness is also variable among Sumatran collections.

SPECIMENS EXAMINED.

INDONESIA: Kalimantan. Central Kalimantan, Arboretum Nyaru Menteng, 28 km of Palangkaraya, freshwater swamp, 18 Sept 1993, *Sidiyasa & Arifin 1082A*, fruit (BO!); *ibid.*, swamp forest along arboretum trail, 30 Oct 1996, *Kessler et al. PK 1559*, fruit (BO! L!); *ibid.*, peat swamp forest, 131 ft [40 m], 7 Oct 2001, *Sidiyasa 2516*, fruit (A!); **Sumatra.** East Coast, Laboehan Batoe, Kota Pinang, Goenoeng Si Papan, Kaloebi Concession, 7–14 Apr 1933, *Rahmat 3925*, flowers (holotype NY!) flower (isotypes A! K!) flowers (isotypes L! MICH! US!) flower & immature fruit (isotype MICH!); Jambi, Sungai Enam Belas, Taman Nasional Berbak, riverbank, 39 ft [12 m], 18 Dec 2005, *Arief & Widjaja AH 1042*, fruits (KLU 2 sheets!); Riouw, Karimoen, Kampoeng dei Goentoeng, Nov 1922, *Oenoos BB 4940*, flower (BO!) leafy branch (BO!); *ibid.*, Jaganadja, 3 ft [1 m], 6 Mei 1923, *Oenoos BB 5387*, immature fruit (BO!) leafy branch (BO!). **MALAYSIA: Peninsular Malaysia. Johor**, Lenggur Forest Reserve, swamp, *Teo & Tetu KL 4735*, 28 Aug 1997, fruits (KEP! KLU!); **Melaka**, no locality, 1861–1862, *Griffith KD 2821*, flowers (holo K 2 sheets!); *ibid.*, 24 Jul 1867, *Maingay KD*

841, fruits (holo K 2 sheets!) (type for *G. griffithii* var. *maingayi*); Merlimau, 1892, *Derry* 1045, fruit (SING!); *ibid.*, Jun 1889, *Derry* 223, flowers (SING!); **Pahang**, MENCHALI Forest Reserve, 1 May 2008, *Low et al.* LYW 168, leafy branch (KLU!); Rompin, Sungai Sekin, margin of swamps, 328 ft [100 m], 19 Feb 1980, *Maxwell* 80-47, fruit (L 2 sheets!); *ibid.*, 1 May 2008, *Low et al.* LYW 166, flower (KLU!); Tasik Bera, edge of swamp channel, 24 Apr 1980, *Gianno* 36gb, fruits (KLU!); **Sarawak**: Binatang, primary peat swamp forest, 23 Nov 1959, *Sanusi* 12265, fruits (SAR! SING!) leafy branch (L!); Kuching, Astana Road, mixed swamp forest, 11 Oct 1964, *Bujang S* 20882, fruit (SAR! SING!); Kuching, 4½ Miles, Matang Road, Ulu Sungai Midin, peat swamp forest, 13 May 1970, *Bujang S* 29362, immature fruit (SAR!); Simanggang, one mile from Triso, peat swamp forest, 13 Apr 1960, *Anderson* 9797, fruits (SING!) leafy branch (SAR!); Division III, swamp forest, 8 Jul 1954, *Brooke* 8784, immature fruit (SING!) fruit (US!). **SINGAPORE**: Bukit Madai, 1891, *Ridley* 2857, fruit (SING!); *ibid.*, 1891, *Ridley* 6673, fruit (SING!); *ibid.*, 22 May 1889, *Ridley* s.n., flower (SING!); Chan Chu Kang, 21 Apr 1888, *Hullett* 611, flowers (SING!); **THAILAND: Peninsular Thailand**. Narathiwat, Todaeng, Puyo, Sungai ko-lok, swamp forest, *Niyomdham* 759, 17 Jul 1983, fruit (BKF!).

8. *Gardenia pterocalyx* Valetton, *Icon. Bogor.* t. 339 (1912); Wong, *Gard. Bull. Singapore* 35 (1982) 25, *Tree Fl. Malaya* 4 (1989) 349; Low & Wong, *Edinburgh J. Bot.* 64 (2007) 34.

TYPE: *Hallier* 1416B, Borneo, Sunger Kenepai (23 Jan 1894, fruit) (lectotype L [sheet no. L0518199]! isolectotypes BO! K! L [sheet no. L0518196]!).

(Fig. 28.)

Tree, to c. 20 m high, trunk to c. 15 cm diameter, not buttressed. Bark smooth, pale grey to brown. *Stipules* connate into a cupuliform structure, 0.3–0.6 cm long, margin subtruncate, outside glabrous and generally coated with resin (this sloughing off in older material), inside with a dense covering of dark-coloured colleters mixed with scattered shorter, fine translucent trichomes at the basal half and glabrous to scattered hairy at the upper half. *Petiole* 0.5–1 cm long, 2–3 mm thick, glabrous, often conspicuously resin-coated. *Leaf* lamina obovate; 4.5–12.5(–15) cm long, 3.5–4.5(–5) cm wide; leaf base cuneate; leaf apex obtuse, rounded to short cuspidate; coriaceous; conspicuously coated with resin when young; midrib prominent and glabrous on both sides; secondary veins 7–10 pairs, prominent and glabrous on both sides, vein axils on the lower side with ciliate pit-domatia; tertiary venation scalariform. *Flowers* solitary. *Pedicel* (1–)2–2.5 cm long and c. 2 mm thick in open flowers and mature fruit. *Calyx* broad-tubular, margin subtruncate; tube (1.5–)2.5–4 cm long, 4–5 mm wide at the base, becoming 4–7 mm wide at the apex; outside completely glabrous, coated with resin; inside glabrous except for a dense covering of dark-coloured colleters mixed with translucent trichomes (trichomes shorter than colleters) at the lowermost quarter only; with 8–9 keels to 2–5 cm long and 2–5 mm wide, narrowing toward the apex and base. *Corolla* hypocrateriform, cream turning light yellow, then orange-yellow; tube to 3.5–4.5 cm long, 2–3 mm wide at the mid-portion, 5–10 mm wide at the throat, outside completely glabrous, inside glabrous except for a 1–1.5 cm zone of scattered ribbon-like translucent hairs at the throat to about 0.5 cm below the stamens; lobes 6–8, obovate, 18–20 mm long, c. 15 mm wide, glabrous on both sides. *Stamens* 6–8, inserted just below the corolla throat and between corolla lobes, dorsifixed; filaments very short to inconspicuous; anthers 12–13 mm long, c. a quarter exerted. Style 4–5 cm long, glabrous; stigma club-like, 4–5-lobed, 5–6 mm long, 3–5 mm wide, wholly exert; ovary with several parietal placentas. *Fruits* subglobose to broad-ellipsoid, (1.5–)2.5–3

cm long, 1.5–2 cm wide, mature specimens with 8–9 keels to 1–2 mm wide; calyx persistent at fruit apex, the tube to (2–)3.5–4 cm long, to 0.5–0.9 cm wide at mouth, with keels (2–)3.5–4 cm long, 4–7 mm wide at the basal third, narrowing toward the apex and base; yellowish green and splitting irregularly when ripe. *Seeds* many, irregularly angular-elliptic, flattened, 4–7 mm long, 3–5 mm wide, testa surface fine-areolate, embedded in a bright yellow-orange pulp-like placenta.

DISTRIBUTION. Malay Peninsula, Sumatra and Borneo (Sarawak and south Kalimantan).

ECOLOGY. A peat swamp forest species.

SPECIMENS EXAMINED.

INDONESIA: Kalimantan. West Kalimantan, Danau Sentarum Wildlife Reserve, Lake Sekawi, 115 ft [35 m], 2 Dec 1993, *Zulkarnain & Giesen* 429, immature fruit and fruits (L!); Kajoe Landak, sine date, *Teysmann* 8333, immature fruit (BO!) leafy branch (L!); Kapoeas, Landak, sine date, *Teysmann* 8267, immature fruit (BO!); Poeloe Madjang, sine date, *Jaheri* 1893, flower & fruit (L!); *ibid.*, 6 Oct 1949, *Polak* 1889, flower & fruit (BO!) fruit (L!); *ibid.*, sine date, sine coll., fruit (L!); *ibid.*, 12 Nov 1924, *Boschproefstation* BB 7690, flower (BO! L!); Semitau, 115 ft [35 m], 12 Aug 1932, *de Wol* b.b. 17087, flower buds (SING!) immature fruits (A! BO 2 sheets!), Sungei Kenepai, 23 Jan 1894, *Hallier* 1416 B, fruits (lectotype L sheet no L0518199! isolectotypes BO! K! L sheet no 0518196!); **Sumatra.** Jambi, Sungai Enam Belas, Taman Nasional Berbak, riverbank, 39 ft [12 m], 18 Dec 2005, *Arief & Widjaja* AH 1040, fruits (KLU 2 sheets!); Siak, Nov 1897, *Ridley* 8997, fruits (SING!).

MALAYSIA: Peninsular Malaysia. Pahang, Rompin, Menchali Forest Reserve, along

the road to Kuala Rompin, 17 Apr 2004, *Ong EL 41*, fruit (KLU!); *ibid.*, kerangas forest, 18 Jun 2004, *Chan & Wong CML 18*, flower & flower bud (KLU!); *ibid.*, 17 Apr 2004, *Chan s.n.*, fruit (KLU!); Rompin from Pasir Panjang, swampy area, 16 Nov 2003, *James s.n.*, fruits (KLU 2 sheets!); Sungai Bebar, peat swamp forest beside blackwater stream, *Low et al. LYW 27*, 9 Apr 2005, flowers (KLU!); *ibid.*, *Low et al. LYW 30*, 9 Apr 2005, fruit (KLU 2 sheets!); Tasek Bera, in the lake, 29 Jan 1967, *Stone BCS 6614*, flower (KLU!); 50 ft [15 m], 30 Jul 1970, *Stone BCS 9484*, flowers (KLU!); forest edge in swamp, 110 ft [33 m], 28 Oct 1961, *Poore 951*, fruits (KLU!); Tasek Bera, Pos Iskandar, freshwater swamp forest, beside a stream, 1 Jul 2006, *Wong s.n.*, flower (KLU!); 15 Oct 1930, *Henderson SFN 24138*, fruits (SING!); freshwater swamp, edge of the lake, 7 Sept 2005, *Low et al. LYW 68*, fruits (KLU!); **Selangor/Pahang**, Road to Gunung Ulu Kali, 1200 ft [366 m] [locality statement on specimen likely in error], May 1970, *Mahmud s.n.*, flower (KLU!); **Terengganu**, Kuala Terengganu, Paya Bukit Pakbeh near Sebarang Takir, sandy gelam forest at seashore, 6 Sept 1955, *Sinclair & Kiah SFN 40733*, flowers (A! US!) flowers & fruits (L! SING!).



Fig. 28. The isotype specimen of *Gardenia pterocalyx* Valet.: Hallier B 1416 (K).

9. *Gardenia subcarinata* (Corner) Y.W.Low, Gard. Bull. Singapore 61 (2009)

116.

Basionym: *Gardenia tubifera* var. *subcarinata* Corner, Gard. Bull. Straits Settlements 10 (1939) 48; Wong, Gard. Bull. Singapore 35 (1982) 22; Wong, Tree Fl. Malaya 4 (1989) 349.

TYPE: Curtis 686, Penang, Government Hill (Feb 1889, flowers & fruit) (**holotype** SING 0048397! **isotype** SING 0048383!).

"*Gardenia resinifera*" auct. non Roth, Nov. Pl. Sp. (1821): Ridley, Fl. Malay Penin. 2 (1923) 83.

"*Gardenia tubifera*" auct. non Wall. ex Roxb. (1824): King & Gamble, J. Asiat. Soc. Beng. 72 (2) (1903) 219 (as "Form 2"); Corner, Wayside Trees of Malaya 2 (1997) 631, pro parte.

(Fig. 29.)

Tree, to c. 20 m high, trunk to c. 80 cm diameter, not buttressed. Bark smooth, light grey-brown to dark brown. *Stipules* connate into a cupuliform structure, 0.2–0.5 cm long, margin 2-lobed to subtruncate, outside puberulent and generally coated with resin (this sloughing off in older material), inside with a dense covering of dark-coloured colleters mixed with scattered, slightly longer, fine translucent trichomes over three-quarters of the surface from the base, and glabrous at the upper part. *Petiole* (0.5–)0.6–1.5 cm long, 1–2 mm thick, evenly puberulent, sometimes conspicuously resin-coated. *Leaf* lamina obovate; (4.5–)7–14 cm long, (1.9–)2.2–4.6 cm wide; leaf base cuneate; leaf apex acuminate to short-cuspidate; thin-coriaceous; conspicuously coated with resin when young; midrib slightly raised to flat and puberulent on upper side, prominent and puberulent on lower side; secondary veins 7–12 pairs, flat to sunken and glabrous on upper side, prominent and puberulent on lower side, vein axils on the lower

side with hairy pocket-domatia; tertiary venation scalariform. **Flowers** solitary. **Pedicel** 0.1–0.5 cm long and 1.2–2 mm thick in open flowers, reaching 0.1–0.4 cm long and 2–3 mm thick at fruit maturity. **Calyx** cupular-obconical, margin subtruncate or (rarely) with 7–9 subtriangular to rounded lobes about 0.5–1 mm high; tube 0.4–1 cm long, 2–3 mm wide at the base, becoming 4–8 mm wide at the apex; outside densely puberulent, often coated with resin; inside glabrous except for a dense covering of dark-coloured colleters mixed with translucent trichomes at the basal half (trichomes longer than colleters and especially conspicuous as a dense fringe at the very base of the calyx tube); with 7–8 keels broadening upwards from base to apex and then not or (rarely) forming narrow apical spurs (protruding 2 mm beyond the calyx margin) alternating with the calyx lobes. **Corolla** hypocrateriform, cream turning light yellow, then orange-yellow; tube to 4–6(–9) cm long, 1.5–3 mm wide at the mid-portion, 7–8 mm wide at the throat, outside glabrous to puberulent, inside glabrous except for sparse ribbon-like translucent hairs in narrow zones between stamens from the throat to just below the anthers; lobes 6–9, oblanceolate to obovate, 12–22 mm long, 6–13 mm wide, glabrous on both sides. **Stamens** 6–9, inserted just below the corolla throat and between corolla lobes, dorsifixed; filaments very short to inconspicuous; anthers 5–7 mm long, c. a third to half exerted. Style 7.5–9 cm long, glabrous; stigma club-like, 3–4-lobed, 2–5 mm long, 1.5–3 mm wide, wholly exerted; ovary with several parietal placentas. **Fruits** subglobose, 1.5–2.5(–3) cm long, 1.8–3 cm wide, surface in mature specimens smooth; calyx persistent at fruit apex, the tube to 0.5–1 cm long, 0.5–0.8 cm wide at the mouth, with low keels that apically form broad-triangular wings; yellowish green and splitting irregularly when ripe. **Seeds** many, irregularly angular-elliptic, flattened, 5–6 mm long, 4–7 mm wide, testa surface fine-areolate, embedded in a bright yellow-orange pulp-like placenta.

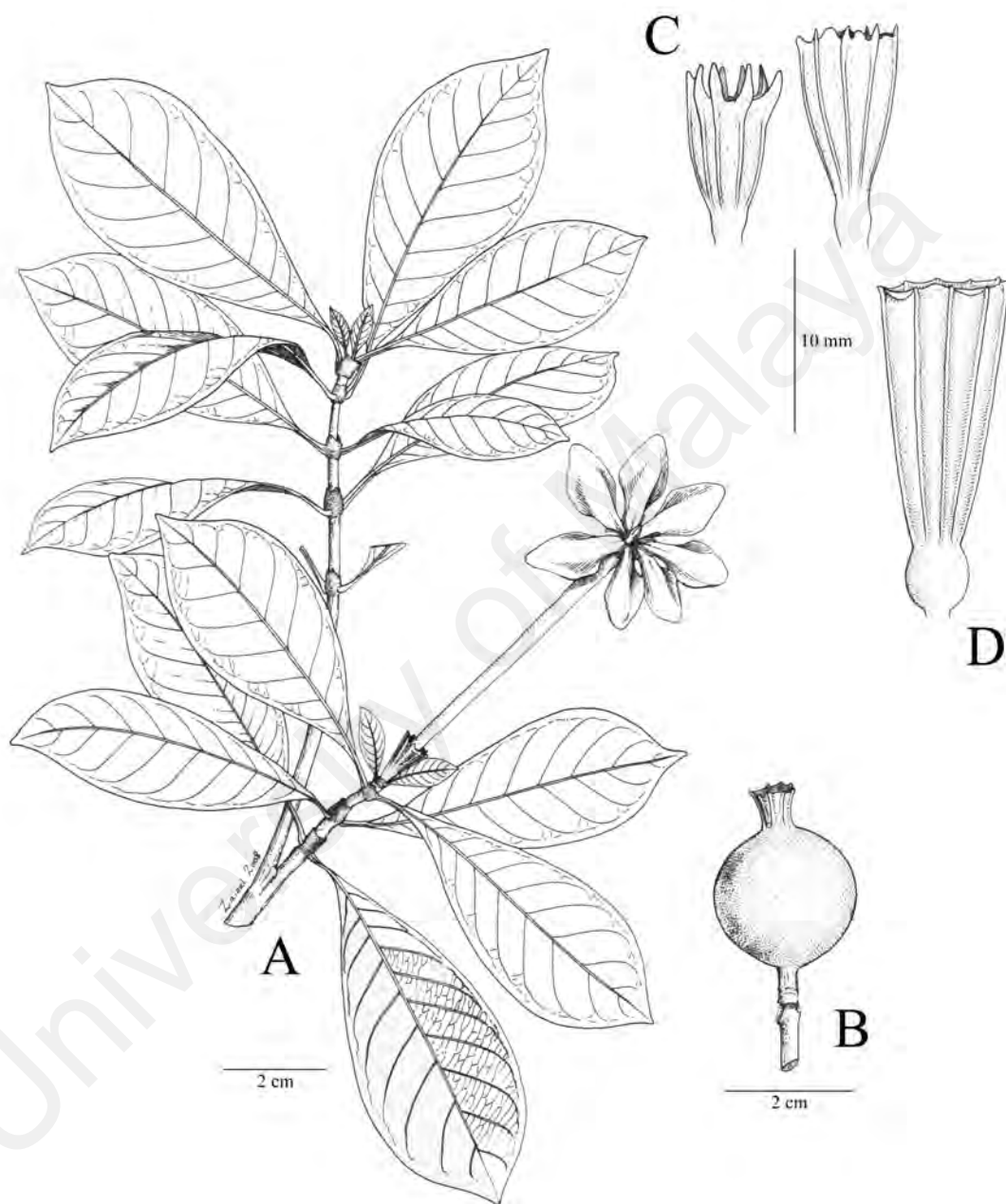


Fig. 29. *Gardenia subcarinata*. **A–C**, *Gardenia subcarinata* var. *subcarinata*: **A**. Leafy branches, one terminated by a solitary flower; **B**. Fruit with persistent calyx; **C**. Calyx with protruding apical keels of the less common (left) and the more common condition (right). **D**, *Gardenia subcarinata* var. *sumatrana*, calyx without protruding apical keels. [A from *T. & P.* 389 (KL 2989) (L); B from *Curtis* 686 (SING barcode no. 0048386); C from *Ngadiman* SFN 34926 (A) (left) and *Zahir* KEP 99132 (A) (right); D from *Rahmat* 1727 (A)].

DISTRIBUTION. Restricted to Malay Peninsula and Sumatra.

ECOLOGY. Lowland forest (near sea level to about 1750 ft [533 m]).

NOTES. A variety from Sumatra, namely, *G. subcarinata* var. *sumatrana*, shares much similarity with the typical form but differs in having keels which do not expand into apical spurs or teeth.

SPECIMENS EXAMINED.

MALAYSIA: Peninsular Malaysia. Johor, Bandar Tenggara, Linggiu Forest Reserve, 23 Jul 1991, *Lesmy* FRI 35917, flower (A! L! SING!). **Kedah**, Bukit Enggang, Bukit Enggang Forest Reserve, 4 Dec 1969, *Everett* FRI 13766, fruit (L!), fruits (A!); Pedu, road from Pedu to Belatik, 15 May 1995, *Zainudin & Bedul Moh* 5541, flowers (L!). **Pahang**, Raub, Sungai Sempam, 15 Apr 1970, *Soepadmo* 666, fruit (BO! KUL!); Taman Negara, path to Terangan hide, 1 Apr 1975, *Chan* FRI 23851, flower (A! L! SING!); Taman Negara, trail from Terenggan to Kumbang Salt Lick, 1 May 1975, *Balgooy* 2603, flower (NY), flowers (L!); Ulu Krau, Gunung Benom Game Reserve, 22 Apr 1967, *Zahir* KEP 99132, flower (A!). **Penang**, without locality, Mar 1881, *King's collector* 1474, flower (L!); Government Hill, Feb 1889, *Curtis* 686, flowers & fruit (SING [sheet nos. 0048397 and 0048383]!); *ibid.*, Mar 1890, *Curtis* 686, flowers & fruits (SING [sheet nos. 0048386 and 0048520]!); *ibid.*, Jul 1893, *Curtis* 686, flowers (SING [sheet nos. 0048524 and 0048394]); Telok Bahang, Pantai Aceh Forest Reserve, 15 Sep 1966, *Chelliah* KEP 98143, fruits (A!); Tiger Hill, 18 Nov 1950, *Sinclair* SFN 39095, flowers & fruit (L! SING!); *ibid.*, 18 Nov 1950, *Sinclair* 6705, fruit (US!). **Perak**, Sungai Kerian Estate, 29 May 1938, *Spare* SFN 34574, fruits (A!); Taiping, 30 Oct 1969, *Everett* FRI 13596, fruits (A!), Taiping, Maxwell Hill, 27 Feb

1983, *Khairuddin* FRI 31835, flower & fruit (A!); Maxwell Hill road, 30 Oct 1969, *Kochummen* FRI 2919, fruit (A!). **Selangor**, Kanching Forest Reserve, 25 Oct 1979, *Kochummen* FRI 11496, flower & fruit (A!); Kuala Selangor, Sungai Tinggi, 18 Oct 1937, *Md Nur* 34129, flower & fruits (A!), fruit (L!); Kuala Lumpur to Kuala Selangor, 27 May 1971, *T. & P.* 389 (KL2989), flowers (L! SING!). **Terengganu**, Dungun, Bukit Bauk Forest Reserve, 19 Nov 1978, *Chan* FRI 25155, fruit (A!), Bukit Bauk, 27 May 1986, *T. & P.* 1017 (KL 3517), fruit (L!); *ibid.*, 25 Jul 2006, *Low et al.* LYW 131, leafy branch (KLU!). **SINGAPORE**: Garden jungle, 9 Dec 1889, *Ridley* 2588, flowers (SING); Bukit Timah, 4 Apr 1938, *Ngadiman* SFN 34926, flowers (A! L!).

Gardenia subcarinata* var. *sumatrana Y.W.Low, Gard. Bull. Singapore 61 (2009) 120.

TYPE: *Lörzing* 14218, North Sumatra, Bila, Estate Aek-Buro (15 Oct 1928, flowers & fruit) (**holotype** SING! **isotypes** A! L!).

(Fig. 29D.)

DISTRIBUTION. Endemic to Sumatra.

ECOLOGY. Lowland forest (near sea level to about 3281 ft [1000 m]).

SPECIMENS EXAMINED.

Specimens examined: INDONESIA: **Sumatra**, East Coast Sumatra, vicinity of Rantau Parapat, Bila, 28 Mar–10 May 1932, *Rahmat Si Toroës* 1727, flower (A! NY! US!); North Sumatra, Bila, Estate Aek-Buro, 15 Oct 1928, *Lörzing* 14218, flowers (A! SING!), flowers & fruit (L!); North Sumatra, Sibolangit, 1–4 Apr 1918, *Bruinier* 4,

flowers (L!); Baven Bandarbarat, 11 Aug 1918, *Lorzing* 5914, flowers (L!); Palembang, Banjoeasin, 16 Nov 1915, *Grashoff* 826, flowers (L!).

10. *Gardenia thailandica* Tirveng., *Nordic J. Bot.* 3 (1983) 462.

TYPE: *Niyomdham et al.* 225, Peninsular Thailand, Phuket (7 Jul 1979, flower & fruit) (holotype BKF! isotypes A! AAU! C!).

"*Gardenia coronaria*" auct. non Buch.-Ham. (1809): Craib, *Fl. Siam.* 2 (1932) 117; Wong, *Gard. Bull. Singapore* 35 (1982) 25; Wong, *Tree Fl. Malaya* (1989) 349, pro parte: quoad *Alphonso & Samsuri* A 128, *Chelliah* FRI 6916, *Corner* s.n., *Curtis* s.n., *Hanif & Nur* SFN 7560, *Holttum* SFN 15082, *Keith* 221, & *Kerr* 16478, *Rahim* KEP 12363.

(Fig. 30.)

Tree, to c. 15 m high, trunk to c. 35 cm diameter, not buttressed. Bark smooth, pale grey to brown. *Stipules* connate into a sheathing tube, 0.5–1.5 cm long, apex acute (the mouth of the stipular tube oblique), outside scantily to densely puberulent and generally coated with resin (this sloughing off in older material), inside largely glabrous except for a dense covering of dark-coloured colleters mixed with longer fine translucent trichomes at the lowest quarter. *Petiole* 0.4–0.7(–1.5) cm long, 1–2 mm thick, minutely puberulent, sometimes conspicuously resin-coated. *Leaf* lamina obovate; (5.8–)7.5–14(–24) cm long, (2.2–)4.2–6(–9) cm wide; leaf base cuneate and often asymmetric; leaf apex acute to acuminate, short-cuspidate; thin-coriaceous; conspicuously coated with resin when young; midrib prominent and glabrous to sparsely hairy on the upper side, prominent and subglabrous to sparsely hairy on the lower side; secondary veins 9–17 pairs, prominent and glabrous on the upper side, prominent and subglabrous to sparsely hairy on the lower side, vein axils on the lower side with hairy

pocket-domatia; tertiary venation scalariform. **Flowers** solitary. **Pedicel** 0.5–0.9 cm long and 1–1.5 mm thick in open flowers, reaching 1–2.3 cm long and 1.5–3 mm thick at fruit maturity. **Calyx** subfusiform to tubular, tightly sheathing the corolla tube, the margin (gently to steeply) oblique, apex acute; tube (0.5–)1–2 cm long, 3–4 mm wide at the base, becoming 3–6 mm wide at the apex; outside scantily to sparsely covered with short erect hairs, coated with resin; inside densely covered with dark-coloured colleters mixed with scattered longer, fine translucent trichomes; with 5 faint to conspicuous ridges along the tube. **Corolla** hypocrateriform, cream turning light yellow, then orange-yellow; tube to 3–5.8 cm long, 3–5 mm wide at the mid-portion, 7–10 mm wide at the throat, outside densely puberulent, inside largely glabrous but often with scanty ribbon-like translucent hairs just beneath the stamens; lobes 5, obovate, 15–21 mm long, c. 10–16 mm wide, outside sparsely puberulent (but always glabrous beneath overlaps), inside glabrous. **Stamens** 5, inserted just below the corolla throat and between corolla lobes, dorsifixed; filaments very short to inconspicuous; anthers 10–14 mm long, c. a quarter exerted. Style 3.4–5.2 cm long, sparsely covered by minute appressed hairs except on the exerted portion; stigma club-like, 2–3-lobed, 3–5 mm long, 2–2.3 mm wide, wholly exerted; ovary with several parietal placentas. **Fruits** obovoid, 2.5–4 cm long, 1.6–3 cm wide, often (not always) with 5 longitudinal ribs sometimes extending downward to the upper half of the pedicel; calyx not persistent at fruit apex; yellowish green and splitting irregularly when ripe. **Seeds** many, irregularly angular-elliptic, flattened, 1–3 mm long, 1–2 mm wide, testa surface fine-areolate, embedded in a bright yellow-orange pulp-like placenta.

DISTRIBUTION. Peninsular Thailand and north Peninsular Malaysia (Kedah).

ECOLOGY. Lowland forest.



Fig. 30. The isotype specimen of *Gardinia thailandica* Tirveng.: Niyomdham et al. 225 (A).

SPECIMENS EXAMINED.

MALAYSIA: Peninsular Malaysia. Kedah, Langkawi, 21 Aug 1925, *Holttum* SFN 15082, fruits (SING!); Bukit Penarak, 26 Nov 1921, *Haniff & Nur* SFN 7560, fruits (SING!); Penarak Forest Reserve, 2 May 1929, *Rahim* 12363, flower & fruit (SING!); Kuah, *Corner* s.n., 12 Nov 1941, fruits (SING!); Kuah camp, *Alphonso & Samsuri* A 128, Nov–Dec 1960, fruits (SING!); southeast of Kuah Rest House, *Students* 26, 12 May 1967, flowers (KLU!); primary forest near sanatorium, *Chelliah* FRI 6916, 14 Mar 1969, fruits (SING!); Pulau Dayang Bunting, *Teo* KL 3315, 24 Feb 1982, fruit (SING!); *ibid.*, *Low & Wong* LYW 210, 7 Jul 2008, flower bud (KLU!), *Low & Wong* LYW 208, 209 & 211, 7 Jul 2008, leafy branch (KLU!); *ibid.*, *Zainudin et al.* AZ 4388, 19 Nov 1992, fruit (L 2 sheets!); *ibid.*, *Zahid et al.* ZMS 54, 29 Apr 2004, flower bud & immature fruits (KLU!); Sawak Forest Reserve, *Zainudin et al.* AZ 5234, 10 Aug 1994, fruit (L!); Terutao, *Curtis* s.n., Mar 1892, flower (SING!) flower & immature fruit (SING!).

THAILAND: Peninsular Thailand. Kanchanaburi, Songkla, Rattapoom, Dton Nga Chang falls, 492 ft [150 m], *Maxwell* 84-153, 30 Aug 1984, fruits (BKF!); Puket, Ranawng, La-un, *Kerr* 16478, 12 Jan 1929, fruit (K!); Puket, Ranong, Kamphoun, Klong Naka Wildlife Sanctuary, 15–30 ft [50–100 m], *Niyomdham & Ueachirakan* 3509, 22 Feb 1994, flower buds & fruits (BKF!); Puket, Ranong, Ngaw Waterfall Forest Reserve, *Nobuyuki & Weerachai* T 35871, 6 Sept 1984, fruit (BKF!); Puket, Tapli, *Kloss* 6749, sine date, fruits (K!); Rachaburi, Bangtaphan, 2 Apr 1890, *Keith* 221, flower buds & flower (SING!); *ibid.*, 16 May 1890, *Keith* 391, flowers (SING!); Satun, Muang, Adang Island, Tarutao National Park, 656 ft [200 m], *Maxwell* 87-346, 15 Apr 1987, flowers & fruit (L!) flowers & fruits (BKF!).

11. *Gardenia tubifera* Wall. ex Roxb., Fl. Ind. 2 (1824) 562.

TYPE: Singapore, Oct 1822, *Wallich Catalogue no.* 8266, (**holotype** K-W! **isotypes** K 2 sheets [sheets no. K000173277 & K000173278]!).

Gardenia tubifera "form 1" & "form 3" sensu King & Gamble, J. Asiat. Soc. Beng. 72 (2) (1903) 219, non "form 2" (= *G. subcarinata*).

Gardenia tubifera sensu Corner, pro parte, Gard. Bull. Straits Settlem. 10 (1939) 46, excl. *G. speciosa* Hook.f. & *G. elata* Ridl.; Wayside Trees of Malaya 1 (1952) 541, pro parte.

Gardenia resinifera Korth., Ned. Kruidk. Arch. 2 (1851) 191, nom. illeg., non *Gardenia resinifera* Roth, Nov. Pl. Sp. (1821) 150, nec *Gardenia resinifera* sensu Ridley, Fl. Malay Penin. 2 (1923) 83.

TYPE: *Korthals* s.n. Borneo (syntype L 4 sheets!).

Gardenia glutinosa Teijsm. & Binn., Cat. Hort. Bot. Bogor. (1866) 119, nom. invalid. (Figs. 31, 32.)

Tree, to c. 13 m high, trunk to c. 46 cm diameter, not buttressed. Bark smooth, light grey-brown to dark brown. *Stipules* connate into a cupuliform structure, 0.4–0.7 cm long, margin 2-lobed to subtruncate, outside puberulent and generally coated with resin (this sloughing off in older material), inside with a dense covering of dark-coloured colleters mixed with scattered longer, fine translucent trichomes over the basal half and glabrous at the upper half. *Petiole* 0.2–1.5 cm long, 1–1.3 mm thick, subglabrous to evenly puberulent, sometimes conspicuously resin-coated. *Leaf* lamina obovate; 4.5–12.5(–21) cm long, 2.3–5.6(–6.3) cm wide; leaf base cuneate; leaf apex acuminate to acute, tip short-cuspidate; thin-coriaceous; conspicuously coated with resin when young; midrib flat to sunken and glabrous on upper side, prominent and glabrous to very rarely sparse minute puberulent on lower side; secondary veins 9–15(–17) pairs,

flat and glabrous on upper side, prominent and glabrous or glabrescent on lower side, vein axils on the lower side with glabrous or hairy pocket-domatia; tertiary venation scalariform. **Flowers** solitary. **Pedicel** 0.2–0.5 cm long and 1–2 mm thick in open flowers, reaching 0.2–1.5 cm long and 1.5–4 mm thick at fruit maturity. **Calyx** cupular-obconical, the margin subtruncate; tube 0.6–1.5(–1.9) cm long, 2–4 mm wide at the base, becoming 5–8 mm wide at the apex; outside densely puberulent at the base and sparsely puberulent to subglabrous at the upper part, often coated with resin; inside glabrous except for a dense covering of dark-coloured colleters mixed with translucent trichomes at the basal half (trichomes especially conspicuous as a dense fringe at the very base of the calyx, longer than colleters); without keels but rarely (upon drying) with a few faintly visible longitudinal ribs (the main vascular traces). **Corolla** hypocrateriform, cream turning light yellow, then orange-yellow; tube to (2.4–)3.9–9.4 cm long, 1.5–3 mm wide at the mid-portion, 5–9 mm wide at the throat, outside glabrous, inside largely glabrous except for dense ribbon-like translucent hairs covering the mouth, the base of corolla lobes and extending down to just below the anthers; lobes 6–9, oblanceolate to obovate, 14–29 mm long, 7–18 mm wide, glabrous on both sides. **Stamens** 6–9, inserted just below the corolla throat and between corolla lobes, dorsifixed; filaments very short to inconspicuous; anthers 6–8 mm long, c. a third to half exserted. Style (2.5–)4.3–9.7 cm long, glabrous; stigma club-like, 4–5-lobed, (3–)5–7 mm long, 2–4 mm wide, wholly exsert; ovary with several parietal placentas. **Fruits** subglobose, 2.3–3.3 cm long, 2.4–3 cm wide, surface in mature specimens smooth; calyx persistent at fruit apex, the tube to 0.5–1.4 cm long, 0.6–0.8 cm wide at the mouth; yellowish green and splitting irregularly when ripe. **Seeds** many, irregularly angular-elliptic, flattened, 4–5 mm long, 4–6 mm wide, testa surface fine-areolate, embedded in the bright yellow-orange pulp-like placenta.

DISTRIBUTION. Widespread from Thailand (Chonburi, Kao Sabab and Peninsular Thailand), Malay Peninsula, Sumatra to Borneo (Kalimantan only).

ECOLOGY. Confined to coastal estuarine and swamp forest.

SPECIMENS EXAMINED.

INDONESIA: Kalimantan. Central Borneo, Kec. Mentaya Hilir Utara Sei Sampit, Bagendang, 25 Feb 1982, *Afriastini* 341, flower (L!); Kumai, Sungai Bekunyir, 14 Mar 1975, *Anderson* (1975)2, flowers & fruit (BO 2 sheets!); **East Borneo**, Pesiangan Bengka and Muara Kaman, Mahakam river, 24 Aug 2000, *Adriansyah* AA 3002, fruit (A! K!); Samarinda, Sungai Pedang Kota Bangun Ulu, 23 Feb 1992, *Ambri & Arifin* AA 443, fruit (A! K!); **South Borneo**, Bangarmassing, 1857–1858, *Motley* 341, flowers (K!); Maharanda, 1918, *Anon.* 15b, flowers (BO!); Pleihari, 22 Aug 1965, *Sauveur* 965, flowers (L!); Poeloe Lampei, sine date, *Korthals* s.n., fruits (L!); *ibid.*, sine date, *Korthals* 2415, leafy branch (L!); *ibid.*, sine date, *Korthals* 2416, leafy branch (L!); *ibid.*, sine date, *Korthals* 2417, leafy branch (L!); Rantau to Maugasari, 14 Dec 1988, *Giesen* 70, fruit (L!), fruits (L!); Tanah Laut District, Hutan Kintap base camp, 20 Apr 1985, *Leeuwenberg & Rudjiman* 13460, flowers & fruit (L!); Z. O. Borneo (Southeast Borneo), Veenbosch bij Tamban, 10 Oct 1939, *Polak* 480, fruit (A! BO! L! SING!); **West Borneo**, Kenepai, sine date, *Teysmann* 8332, fruits (L!); Lake Tajan, 22 Oct 1949, *Main* 1746, immature fruit (A! K!) fruit (BO!); Salimbauw, sine date, *Hallier* B 1257, flowers (L 2 sheets!) flower & fruit (L!); Soeka Lanting, sine date, *Hallier* B 183, fruit (L!); Soengai Kenepai, sine date, *Hallier* B 1906, fruit (L!); Sungei Batang Putus, South of Danau Sentarum Wildlife Reserve, 31 Mar 1986, *Giesen* 1, flowers (L!) flower & fruit (L!); West Koetai, No. 3 near Kampong Sabentoeloeng, 20 Jun 1925, *Endert* 1518, fruits (L 2 sheets!), flower & fruit (A! BO! SING!). **Sumatra**, Palembang, Sematang,

19 Jan 1920, *Endert E* 808, flowers (L!); Palembang, Kajoeagoeng, 29 Mar 1928, *de Voogd* 139, flowers (L 2 sheets!); *ibid.*, 23 Jan 1929, *de Voogd* 283, flower (BO!); Upper Riau, Pekanbaru, Tenajan Reserve, 11 Aug 1960, *Soepadmo* 20, fruit (K! SING!). **MALAYSIA: Peninsular Malaysia.** without locality, 1862–1863, *Griffith* KD 2816, flower (L!), flowers (K!). **Johor**, Bekok River, 1880, *Ridley* 11139, flower & fruit (SING!); Kluang, 5 Mar 1973, *Hardial Singh & Samsuri* HS 1092, fruit (US!), flower & fruit (A!); Kota Tinggi, Dec 1892, *Ridley* 4209, flower & fruit (SING!), Kota Tinggi, Sungai Bang, 13 Mar 1966, *Sinclair* 10863, flower (A! SING!); Kuala Sembrong, 1892, *Lake & Kelsall* 4088, flowers & fruit (SING!); Sungai Sedili, Bagan Limau, 18 Feb 1931, *Corner* SFN 24625, flower & fruit (SING!), Sungai Sedili, Danau, 27 Mar 1932, *Corner* SFN 25971, flower & fruits (BO! SING!). **Kuala Lumpur**, University of Malaya, Rimba Ilmu Botanic Garden, cultivated opposite the medicinal plants section near the front entrance, 24 Dec 2008, *Low* LYW 228, flower (KLU!). **Melaka**, without locality, sine date, Anon. s.n., flower (SING!), 1845, *Griffith* s.n., flowers & fruit (K! NY!), Aug 1886, *Hervey* s.n., flower & fruit (K), sine date, *Lobb* 347, flowers (K!), 1871, *Maingay* KD 838, flowers & fruit (K 2 sheets! L!), 1871, *Wright* s.n., flowers (K!); Bt. Sadanau, Feb 1890, *Derry* 360, flowers & fruit (SING!); Merlimau, Jun 1889, *Derry* 199, fruits (SING!); Sungai Tebong, South of Bukit Putus, 30 Jan 1916, *Burkill* SFN 1434, flower (SING!); 5 miles South of Malacca, Batu Berendam Road, 29 Apr 1961, *Burkill* HMB 2640, fruits (A! SING!). **Negeri Sembilan**, 12 miles Simpang Pertang-Kuala Pilah roadside, 2 Sept 1977, *Asri* FRI 25738, fruit (A!). **Pahang**, Lubuk Paku, 28 Nov 1924, *Ngadiman* SFN 16114, flower & fruits (SING!); Muazam Shah to MENCHALI Road, road to Kampung Sedaik Asal, 1 May 2008, *Low et al.* LYW 167, fruit (KLU!); Pekan, 28 Nov 1929, *Burkill & Haniff* SFN 17129, flowers (A!), flowers & fruit (SING!); *ibid.*, 20 Aug 1909, *Ridley* s.n., flower (SING!); *ibid.*, May 1890, *Ridley* 1375, flower (BO!), flowers (BO! SING!); Pekan, Nenasi Forest Reserve, 17 Apr 2004,

Ong EL 36, flower & fruits (KLU 2 sheets!); Pekan, Sungai Bebar, 10 Apr 2005, *Low et al.* LYW 35, flower & fruit (KLU!); *ibid.*, 30 Oct 2007, *Low & Zulkapli* LYW 163, fruit (KLU!); Rompin, Menchali Forest Reserve, 1 May 2008, *Low et al.* LYW 169, fruit (KLU!); Tasek Bera, 24 Apr 1980, *Gianno* 370, flower & fruit (KLU!); *ibid.*, 7 Sept 2005, *Low et al.* LYW 70, fruits (KLU!); *ibid.*, 10 Nov 1975, *Stone et al.* 12264, flower (KLU!), flowers (KLU!), fruit (NY!); Tasek Bera, Kota Iskandar, 1 Feb 1962, *Anon.* 1061, flowers & fruit (KLU!); Tasek Bera, near Sungai Bera, 15 Oct 1930, *Henderson* SFN 24126, fruit (NY!). **Perak**, Sungai Kerian Estate, 29 May 1938, *Spare* SFN 34574, fruits (SING!). **Perlis**, Kangar, Jalan Batu Pahat (cultivated?), 22 Aug 1991, *Zainudin et al.* AZ 3825, fruit (L!), leafy branch (K!). **Selangor**, Petaling Jaya, Section 16, cultivated inside a bungalow compound (private property), 3 Mar 2006, *Low et al.* LYW 164, flowers (KLU!); Sungei Buloh Reserve, Kuala Lumpur, 3 Mar 1923, *Foxworthy* 7960, flowers (SING!). **SINGAPORE**: without locality, sine date, *Burkill* 324, fruits (US!), Oct 1822, *Wallich Catalogue no.* 8266, fruit (holo K-W! iso K 2 sheets!). **THAILAND**: Chonburi, Sriracha, 4 Feb 1927, *Collins* 1407, fruits (US); *ibid.*, 7 Dec 1927, *Collins* 1833, flower (US 2 sheets!); Kao Sabab, 18 Jan 1958, *Sorensen et al.* 506, fruit (BKF! L!); Peninsular Thailand, Chumpon, Langsuan, 10 Jan 1977, *Santisuk* 908, fruit (A!); Satul, Kuan La Long, 30 Jan 1961, *Ploenchitr* 1602, flower (BKF!).



Fig. 31. The holotype specimen of *Gardenia tubifera* Wall. ex Roxb.: Wallich Catalogue no. 8266 (K-W).

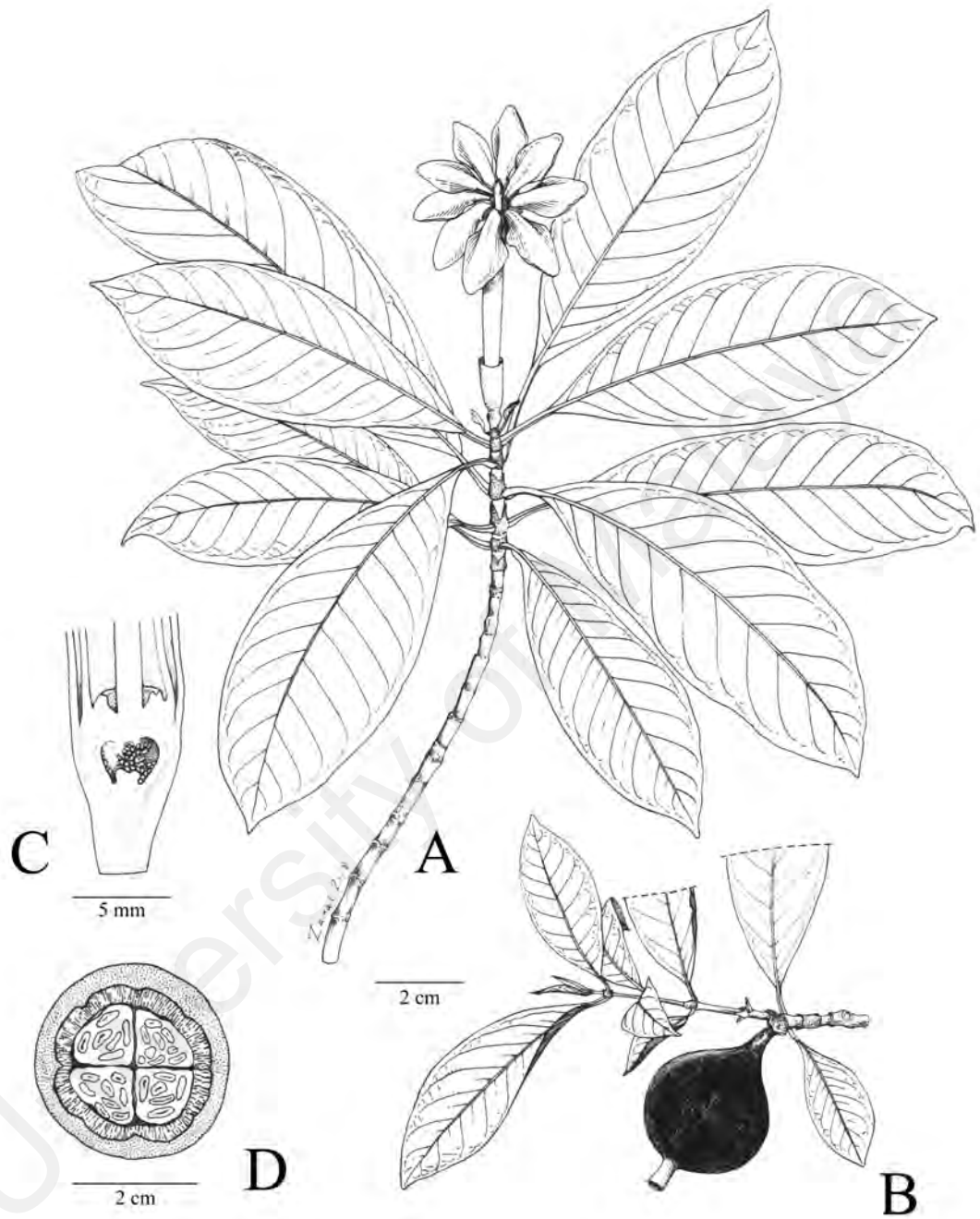


Fig. 32. *Gardenia tubifera*. **A**, Flowering leafy branch. **B**, Leafy branch with fruit. **C**, Longitudinal section through lower part of flower including hypanthium. **D**, Transverse section of fruit. [A from *Low* LYW 228; B from *Low & Zulkapli* LYW 163; C & D from *Low et al.* LYW 35 (all KLU)].

12. *Gardenia* sp. ined.

Tree, to c. 4 m high. *Stipules* connate into a cupuliform structure, 0.2–0.5 cm long, margin 2-lobed to subtruncate, outside puberulent and generally coated with resin, inside with a dense covering of dark-coloured colleters mixed with scattered, slightly longer, fine translucent trichomes. *Petiole* 0.4–0.6 cm long, 1 mm thick, evenly puberulent, sometimes conspicuously resin-coated. *Leaf* lamina obovate; 3.9–4.4 cm long, 1.4–1.5 cm wide; leaf base cuneate; leaf apex acuminate to short-cuspidate; thin-coriaceous; conspicuously coated with resin when young; midrib flat to slightly raised and puberulent on upper side, prominent and densely puberulent on lower side; secondary veins 6–7 pairs, inconspicuous on upper side, prominent and sparsely puberulent on lower side, vein axils on the lower side with hairy pocket-domatia; tertiary venation scalariform. *Flowers* unknown. *Pedice*l 0.3 cm long and 2 mm thick at fruit stage. *Fruits* subglobose, 0.6 cm long, 0.6 cm wide, surface with 6–8 ribs; calyx cupular-obconical, margin subtruncate, persistent at fruit apex, the tube to 0.5 cm long, 0.3 cm wide at the base, becoming 0.5 cm wide at the mouth, with 6–8 ribs along the tube that extend down to the fruit wall.

SPECIMENS EXAMINED.

INDONESIA: Kalimantan. East Borneo (East Kalimantan), East Kutei, Gunung Sekrad, south of Sangkulirang, coral limestone rocks, 400–500 m asl, 12 Jul 1951, *Kostermans* 5963, fruit (L!) leafy branch (BO!).

6.4. Cultivated species

1. *Gardenia jasminoides* J.Ellis, Philos. Trans. 51 (2) (1761) 935, t. 23.

TYPE: Philos. Trans. 51 (2) (1761) 935, t. 23.

Gardenia florida L. Sp. Pl. ed. 2 (1762) 305.

Gardenia augusta Merr., Interpret. Rumph. Herb. Amboi. (1917) 485; Smith, American J. Bot. 61 (1974) 113; Tirvengadam, Bull. Mus. natn. Hist. nat., Paris, 3^e sér. 521, Bot. 35 (1983) 17; Wong, Tree Fl. Malaya (1989) 349.

Shrub with several slender stems commonly to 2 m high (cultivated forms in southeast Asia), to small tree to c. 5 m high with trunk to c. 9 cm diameter, not buttressed (in south China and Japan). Bark smooth, pale grey to brown. **Stipules** connate into a sheathing tube, 0.6–0.9(–1.5) cm long, apex acute (the mouth of the stipular tube oblique), outside glabrous to sparsely puberulent and coated with resin, inside with a mixture of dark-coloured colleters and slightly longer, fine translucent trichomes sparsely covering the basal half and glabrous at the upper half. **Petiole** 0.2–0.7 cm long, 1–2 mm thick, glabrous to sparsely puberulent, sometimes resin-coated. **Leaf** lamina obovate to elliptic; (3.2–)6.4–10.7 cm long, (2.2–)2.8–5.2 cm wide; leaf base cuneate; leaf apex acute to obtuse, short-cuspidate; thin-coriaceous; coated with resin when young; midrib flat to sunken and glabrous to sparsely puberulent on upper side, prominent and glabrous to sparsely puberulent on the lower side; secondary veins 6–9 pairs, flat and glabrous on upper side, prominent and glabrous on the lower side, vein axils on the lower side with hair tufts or ciliate pit- or pocket-domatia; tertiary venation scalariform. **Flowers** solitary. **Pedicele** 0.2–0.7 cm long and 1–1.5 mm thick in open flowers, reaching 0.5–1.3 cm long and 1–2 mm thick at fruit maturity. **Calyx** cupular-obconical, the margin subtruncate; tube 2–6 mm long, 3–4 mm wide at the base, becoming 5–7 mm wide at the apex; outside subglabrous, coated with resin; inside with dark colleters evenly covering the basal half and sparsely covering the upper half (never reaching the calyx tube margin); with 5–7 low keels to c. 1–1.5 mm wide along the tube, these continuing beyond the tube margin as linear, bilaterally flattened spurs to 25 mm long and 1–3 mm wide that are often slightly curved inwards or outwards. **Corolla**

hypocrateriform, cream turning light yellow; tube to 2.6–5.2 cm long, 2.2–6 mm wide at the mid-portion, 5–13 mm wide at the throat, outside glabrous, inside generally covered with ribbon-like translucent hairs (denser at the upper part); lobes 6–7 (up to 20 or more for the double-flowered form), obovate, 17–29 mm long, 11–17 mm wide, glabrous on both sides. **Stamens** 6–7, inserted just below the corolla throat and between corolla lobes, dorsifixed; filaments very short to inconspicuous; anthers 15–18 mm long, c. a quarter to half exerted. Style 3–5 cm long, glabrous; stigma club-like, 2–4 lobed, 7–10 mm long, 3–8 mm wide, wholly exert; ovary with several parietal placentas. **Fruits** ellipsoid to obovoid, 1.5–4.2 cm long, 1–1.9 cm wide, when mature with 5–7 longitudinal keels or ribs; calyx tube persistent at fruit apex to 2–6 mm long, 5–7 mm wide at the mouth; yellowish-green and splitting irregularly when ripe. **Seeds** many, irregularly angular-elliptic, flattened, 3–4 mm long, 1.5–2.8 mm wide, testa surface fine-areolate, embedded in a bright yellow-orange pulp-like placenta.

DISTRIBUTION. Native to South China and Japan, but widely cultivated in Sundaland countries.

SPECIMENS EXAMINED.

INDONESIA: Java, Buitenzorg, sine date, *Boerlage* s.n., fruits (L!); Sulawesi, Sulawesi Tengah, Oo, Langkapa, Kulawi Donggala, 10 Jun 2001, *Ramadhanil et al.* 471, flower buds (K!). **MALAYSIA: Peninsular Malaysia. Kuala Lumpur:** Lady Templer Hospital Ground, 2 Jul 1965, *Tan* s.n., flower bud (KLU!); Pantai Valley, University of Malaya, Rimba Ilmu Botanic Garden, planted next to the Conservatory of Rare Plants & Orchids, 17 Sept 2004, *Low LYW 236*, flower (KLU!); *ibid.*, planted in the medicinal garden, 17 Sept 2004, *Low LYW 237*, flowers (KLU!); **Pahang:** Beserah, 6 Dec 1924, *Burkill & Md. Haniff* SFN 17576, leafy branch (SING!); Pekan, 29 Nov

1924, *Burkill & Md. Haniff* SFN 17213, flower (SING!); *ibid.*, 30 Nov 1924, *Burkill & Md. Haniff* SFN 17274, leafy branch (SING!); **Perak**, Kuala Kangsar, Lubuk Merbok, *Md. Haniff* SFN 15585, 21 Oct 1924, leafy branch (SING!); Tanjong Malim, 4 Jul 1924, *Burkill & Md. Haniff* SFN 13498, leafy branch (SING!); Tapah, 10 Jul 1924, sine coll. SFN 13972, leafy branch (SING!); Teluk Anson (Teluk Intan), Bagan Datoh, 30 Sept 1924, *Md. Haniff* SFN 16156, leafy branch (SING!); Teluk Anson (Teluk Intan), Durian Sabatang, 30 Sept 1924, *Md. Haniff* SFN 15633, leafy branch (SING!); Teluk Anson (Teluk Intan), Hutan Melintang, 30 Sept 1924, *Md. Haniff* SFN 15914, leafy branch (SING!); Teluk Anson (Teluk Intan), 30 Sept 1924, *Md. Haniff* SFN 10311, leafy branch (SING!); *ibid.*, 30 Sept 1924, *Md. Haniff* SFN 15950, flower bud (SING!); **Sabah**: Tenom, Kampung Pulong, 9 May 1998, *Ambuli* 83, flower (KEP!). **Sarawak**: Kapit, Upper Rejang river, 1929, *Clemens* 21407, flower buds (SAR!). **PHILIPPINES**: Mindanao, Agusan Norte, Tungao, Nalco, secondary forest, Barbon, 14 May 1991, *Romero & Fernando* PPI 1818, flower (K!).

2. *Gardenia mutabilis* Reinw. ex Blume, *Bijdr. Fl. Ned. Ind.* 16 (1827) 1016;

Koorders, *Flora N.O. Celebes* (1898) 494; Koorders & Schuman, *System Verzeichnis, III Abteilung* (1914) 120; Koorders, *Suppl. Fl. Celeb.* 3 (1922) 59, Plate 124.

TYPE: *Reinwardt* 1567, Celebes (**holotype** L!).

Shrub to tree, to c. 10 m high, trunk to c. 15 cm diameter, not buttressed. Bark smooth to scaly, very pale yellowish brown. *Stipules* connate into a sheathing tube, often c. 0.7–1.8 cm long, apex acute (the mouth of the stipular tube oblique), outside puberulent and often coated with resin, inside largely glabrous except for a dense covering of dark-coloured colleters mixed with scattered, slightly longer, translucent

trichomes at the very base. **Petiole** 0.6–1.5 cm long, 1–1.5 mm thick, glabrous to minutely puberulent, sometimes resin-coated. **Leaf** lamina obovate to elliptic; (5–)12–17.4 cm long, (2–)5–7.5 cm wide; leaf base cuneate and often asymmetric; leaf apex acute to acuminate or obtuse, short-cuspidate; thin-coriaceous; coated with resin when young; midrib flat and glabrous to rarely minute puberulent on upper side, prominent and glabrous to rarely puberulent on lower side; secondary veins 7–8(–12) pairs, flat and sparsely puberulent on upper side, prominent and sparsely puberulent on lower side, vein axils on the lower side with ciliate pocket-domatia; tertiary venation scalariform. **Flowers** solitary. **Pedice**l 0.1–0.3 cm long and c. 1–1.5 mm thick in open flowers, reaching 0.1–0.3 cm long and 2.5–4 mm thick at fruit maturity. **Calyx** cupular-obconical to tubular, tightly sheathing the corolla tube, the margin subtruncate; tube (0.6–)0.9–1.1(–1.7) cm long, 1.5–4 mm wide at the base, becoming 2.5–5 mm wide at the apex; outside subglabrous to puberulent, coated with resin; inside glabrous for most of the upper half from the tube margin, sparsely covered with dark-coloured colleters at the basal half; with 5 ridges along the base of the tube. **Corolla** hypocrateriform, cream turning light yellow, then orange yellow; tube to (4.2–)7.5–14.3 cm long, 1.5–2.5 mm wide at the mid-portion, 3.5–6 mm wide at the throat, outside glabrous to minutely puberulent, inside with dense ribbon-like hairs from around the base of the anthers to the mouth and base of corolla lobes, glabrous lower down; lobes 7–8, oblanceolate to obovate, (20–)24–32 mm long, 6.5–10 mm wide, outside glabrous to sparsely puberulent (but always glabrous beneath overlaps), inside glabrous. **Stamens** 7–8, inserted just below the corolla throat and between corolla lobes, dorsifixed; filaments very short to inconspicuous; anthers 7–12 mm long, c. a third to half exerted. Style (5–)9–15.5 cm long, glabrous; stigma club-like, 5–8-lobed, 3.5–6 mm long, 2–3 mm wide, wholly exert; ovary with several parietal placentas. **Fruits** subglobose, 1.9–2.9 cm long, 2–3 cm wide; epidermis in mature fruit lenticellate to rugose, flaking off as a thin,

pale grey-brown layer; calyx not persistent at fruit apex; yellowish green and splitting irregularly when ripe. *Seeds* many, irregularly angular-rounded, flattened, 3–3.5 mm long, 2–2.5 mm wide, testa surface fine-areolate, embedded in a bright yellow-orange pulp-like placenta.

DISTRIBUTION. Philippines (Bohol and Samar), Sulawesi and Maluku, but widely cultivated in Sundaland countries.

SPECIMENS EXAMINED.

INDONESIA: Java, Bogor Botanical Garden, V.D. 60, sine date, *Koorders* 35, flowers & immature fruit (L!); *ibid.*, sine date, sine coll. 532, flowers & immature fruit (L!); *ibid.*, sine date, sine coll. 15, flower (K!); *ibid.*, sine date, sine coll. s.n., flowers (SING!); *ibid.*, sine date, sine coll. s.n., fruit (L!); *ibid.*, Feb 1973, *Vogel* 2167, fruit (L!); *ibid.*, 27 Aug 1957, *Koerniasih* 7, flower buds & flower (SING!) flower buds & flowers (L!); Bogor Botanical Garden, 1975, *Meijer* 8017, flowers & fruit (L!); **Maluku**, Sula Islands, P. Seho, 30 Mar 1914, *Atje* 302, flower & immature fruit (SING!); **Sulawesi**, no locality, sine date, *Reinwardt* 1567, flower (holotype L!); *ibid.*, sine date, *Reinwardt* s.n., flower (L!); North Sulawesi, Minahasa, Menado, 12 Mar 1895, *Koorders* KDS 18593 B, immature fruit (K! L!) immature fruits & fruits (BO!); *ibid.*, 1 Feb 1895, *Koorders* KDS 18595 B, flower bud, flowers, immature fruits & fruit (L!) flowers & immature fruits (L!) immature fruit (K!); *ibid.*, 5 Mar 1895, *Koorders* KDS 18597 B, fruits (BO!) leafy branch (L!); Central Sulawesi, west of Batudaka Island, Kayome, 10 ft [3 m], 25 Dec 1999, *Sidiyasa & Didi* 1892, immature fruits (K!); South Sulawesi, Soroako, Northeast Malili, Matano Lake, 15 Jul 1976, *Meijer* 11124, flowers (BO!) flower & fruits (BO!) flowers & immature fruit (SING!) flower, immature fruits & fruits (L!); Soroako, Lake Matano, 1312 ft [400 m], 13 Jun 1979,

Vogel 5757, immature fruit & fruits (BO!); South Sulawesi, Pangkadjene, sine date, *Teysmann* 11953, immature fruits (BO 2 sheets!). **MALAYSIA: Peninsular Malaysia.** **Kuala Lumpur**, University of Malaya, Rimba Ilmu Botanic Garden, 13 Jun 2005, *Low* s.n., flowers (KLU!); **Perak**, Batu Gajah, May 1918, sine coll. s.n., flower (SING!). **PHILIPPINES: Bohol**, Logarita, Bilar, 22 Mar 1993, *Madulid et al.* PPI 7705, flower (KEP!) flower bud, flower & immature fruits (K!) flower & immature fruits (BO!); **Samar**, Wispal, Basey, 5 Feb 1992, *Barbon et al.* PPI 5922, fruits (K!). **SINGAPORE:** Singapore Botanic Garden, Economic Garden, cultivated, 30 Sept 2008, *Leong & Koh* SING 2008-402, flowers (SING!).

Chapter Seven: Conclusions

A total of 12 species including four varieties of *Gardenia* were recognised in this study for Sundaland: *G. barnesii*, *G. beamanii*, *G. carinata*, *G. chanii*, *G. costulata*, *G. elata* (*G. elata* var. *elata* and *G. elata* var. *kinabaluensis* var. *ined.*), *G. griffithii*, *G. pterocalyx*, *G. subcarinata* (*G. subcarinata* var. *subcarinata* and *G. subcarinata* var. *sumatrana*), *G. thailandica*, *G. tubifera*, and an unnamed but distinct species *G. sp.* Besides these, the mainland Asian *G. jasminoides* and Wallacean *G. mutabilis* are widely cultivated in the region. Taxa diagnosed through, and published during, the present revision include *G. beamanii* and *G. chanii* (Low & Wong 2007; see Appendix 2), and *G. subcarinata* var. *sumatrana* (Low & Wong 2009; see Appendix 3).

From this study, various aspects of the taxonomy, phylogenetic relationships and biogeography of *Gardenia* have become clearer. Although *Gardenia* ranges from Africa to the Pacific and is by no means completely revised or even always considered well circumscribed throughout this distribution, most modern revisions from the 1970s onward (section 2.2) have managed to clarify limits in Southeast Asia. Problems remain in some areas, for example, African taxa still named *G. leopoldiana* and *G. vogelii* have slightly curved, narrowly cylindrical fruits quite alien to the large part of the genus even by today's much narrower circumscription (section 2.2.), so there is interesting research to be carried out in ascertaining the status of these taxa, which should be included in a wider study to establish generic limits over the entire range.

7.1 Genus characters of *Gardenia*

Various studies in the Asia-Pacific region (Smith 1974; Darwin 1979; Tirvengadam 1978, 1983; Wong 1982; Puttock & Quinn 1999), some having removed morphologically aberrant taxa to other genera, have led to a much smaller group of taxa retained in *Gardenia* today. As remarked by Tirvengadam (1978) and Robbrecht & Puff (1986), the tetrad characteristic of pollen grains is probably a fundamental state that distinguishes *Gardenia* from most or all other Asian genera of the tribe.

While it was not the main objective of this thesis to clarify generic limits, for Southeast Asia, it has been possible to directly compare characters of native taxa with those of the type (*G. jasminoides*) and others morphologically close to it (the type alliance, including *G. hainanensis* and *G. stenophylla*) (Chapter 4). From the present survey, it can be affirmed that a taxonomically useful suite of character-states for delimiting *Gardenia*, some of which have also been summarized by various modern studies since the work of Keay (1958) and later authors, includes the following—

woody plants of shrub to tree habit; branching extra-axillary; growth architecture conforming to the Leeuwenberg or Scarrone models of Hallé *et al.* (1978); interpetiolar stipules connate into a tube, with the basal part commonly persistent as an annular remain around the nodes; vegetative and floral buds resinous; flowers solitary and terminal, fragrant when open; corolla tubes creamy white at anthesis and darkening to yellow-orange after floral opening and just before flower deterioration; stamens exerted slightly; pollen issued in tetrads; stigma exerted; secondary pollen presentation present; fruits generally medium-sized to large, subglobular to ellipsoid or obovoid, with thick pericarp and bony endocarp, irregularly dehiscent; seeds many, compressed, angular to rounded-elliptic, embedded in an orange-red pulp at fruit maturity, with areolate testa.

7.2 Taxonomic characters for species distinction

Most species recognised in this study can be distinguished based on unique morphological character-states, or combinations of character-states, of the calyx (see Key, Chapter 6). A synopsis of the usefulness of such features is as follows:

G. barnesii — calyx tube sheathing with oblique mouth, tube with long, linear, bilaterally flattened spurs

G. beamanii — calyx tube sheathing about half the corolla tube

G. carinata — calyx tube with narrow keels distally broadening into triangular wings

G. chanii — calyx tube distally broadened, trumpet-like, with keels along the tube not extending to the hypanthium

G. griffithii — calyx tube sheathing more than half the corolla tube

G. jasminoides — calyx tube distally broadened, obconical, with long, linear, bilaterally flattened spurs

G. pterocalyx — calyx tube cylindrical, with keels along the tube extending to the hypanthium

G. subcarinata — calyx tube with narrow keels protruding slightly at the mouth, forming short spurs or teeth

G. thailandica — calyx tube sheathing with oblique mouth, surface smooth and without keels or spurs.

Members of two species-pairs (*G. elata* and *G. tubifera*; *G. costulata* and *G. pterocalyx*) share similar calyx form but are different in other morphological characters and ecology. *Gardenia elata* and *G. tubifera* are taxa with short-obconic, unornamented calyx (i.e., smooth, without keels or spurs) but distinguishable as follows (see also discussions in the species enumeration, Chapter 6):

G. elata — sparsely hairy lower leaf surfaces; generally larger fruits (restricted to the lowland forest on drier sites)

G. tubifera — glabrous (very rarely puberulent) lower leaf surfaces; generally smaller fruits (coastal estuarine and swamp forest)

On the other hand, *G. costulata* and *G. pterocalyx* both have broad tubular calyx tubes with keels, but can be distinguished as follows (see also species enumeration, Chapter 6):

G. costulata — long-cuspidate leaf apices; mature fruit surface generally smooth (rarely with low keels) (*kerangas* forest)

G. pterocalyx — rounded leaf apices; fruit surface with keels (coastal estuarine and swamp forest)

Other individual species unique characters were also discerned for three Sundaland species (Chapter 4): (i) *G. beamanii* is the only taxon with black resin, while the remaining taxa have yellowish amber-brown resin; (ii) the unnamed *Gardenia* sp. from Sangkulirang, Indonesian Borneo, has the smallest leaves; and (iii) *G. thailandica* is the only taxon with obovoid fruits while the remaining species have subglobose or broad-elliptic fruits).

At the outset of this work, a plausible hypothesis was that suites of closely related species would share similar calyx character-states. This has not been possible to demonstrate in a straightforward way, as there is reticulate inheritance demonstrated through the various genealogies presented (sections 5.2.6, 5.2.7), but two mainland Asian lineages (*G. hainanensis*-*G. stenophyla* and *G. sootepensis*-*G. thailandica*) do

conform to this expectation: members of a gene lineage have much basic similarity in calyx structure. This lends some support to the few species clusters that were resolved which share fundamental calyx similarities in the morphological analysis carried out (section 5.1.2).

7.3 Phylogenetic relationships, biogeographical aspects and conservation implications

Mainland Asian *Gardenia* lineages appear to be generally distinct from those in Sundaland, with only limited introgression into the latter (section 5.2.7). With the disjunction of Malesia from the more northerly Asian region (van Steenis 1950, Good 1964, Whitmore 1986) largely corresponding to the change from a wetter, less markedly seasonal climate to a distinctly seasonal one, the divergence of the floras of the two regions is not unexpected. The disjunction is usually referred to in botanical terms as the Kangar-Pattani line near the Thailand-Malaysia border at the neck of the Malay Peninsula. Good (1964) terms the regions the Continental SE Asiatic and Malayan Floristic Provinces, respectively.

In fact, such regional differentiation was already noticed by Wallace (1876), who had recognised a major faunal transition between the Malay Archipelago and Thailand. More recently, however, Woodruff (2003) has re-examined distributions of birds and plants across this transition and found that a significant number of bird species and subspecies range limits occur just north of the Isthmus of Kra (between 11° and 13°N, and not at 7°N near the Thai-Malay border), as in a number of animal groups also. He points out how the botanical transition emphasised by van Steenis (1950) and others have in fact been intuitively arrived at, and not based on actual plant generic limits. Two changes in forest type occur on this part of the peninsula: a northern transition between

seasonal evergreen rain forest and mixed moist deciduous forest (north of the Isthmus of Kra), and a better-known southerly transition between wet seasonal evergreen rain forest and perhumid evergreen rain forest (equivalent to the Kangar-Pattani line). Woodruff (2003) suggests that such biological transition, which appears to occur along a stretch of the peninsula's neck region, rather than at some specific limit, could not be entirely explained by climatological differences today. He suggests (Woodruff 2003, Woodruff & Turner 2009) that a major reason for this biological disjunction could have been an area effect caused by repeated sea-level changes in the last 5 million years (Morley 2000, Voris 2000) that have caused range compression and extinctions in the narrow central and northern parts of the peninsula. It is possible that the narrowing of land connections have restricted geneflow between the two regions, with vicariance and consequent lineage specialisation in the different parts. Thus, the distinction of the mainland Asian and Sundaland *Gardenia* lineages is a possible consequence of past biogeographical influences.

Introgression of a mainland Asian lineage into Sundaland was inferred from the genealogical characteristics of *G. chanii*, which has paternal ancestry from a mainland Asian lineage including *G. hainanensis* and *G. stenophylla*, and maternal ancestry from a Sundaland group of species (section 5.2.7). Somewhat similar introgression has been demonstrated to have occurred among primates. Tosi *et al.* (2002) have, based on discordance between maternally-inherited mitochondrial DNA and paternally inherited Y-chromosome genealogical topologies, demonstrated how the north Indian-Chinese *Macaca mulatta* has hybridised with the more southerly but related Myanmar-Indochinese *Macaca fascicularis*. This hybridisation represents the introgression of the *M. mulatta* Y-chromosome into *M. fascicularis* populations southwards, which, however, has not been detected south of the Isthmus of Kra, where Y-chromosomes of

male *M. fascicularis* are distinguished by a base deletion and a base insertion. This suggests that the Kra Isthmus represents reduced opportunities or unsuitable environment for transgression of *M. mulatta* males farther south. Given the biogeographic disjunction that exists between mainland Asia and Sundaland, gene-barrier transgressions may justifiably be expected to be uncommon, hence possibly reflected only in relatively few cases of introgression (although genealogical studies in plants across this disjunction must be rare).

Within Sundaland lineages, reticulate evolution has been demonstrated with the gene regions used, including both chloroplast and nuclear regions (Chapter 5). In the case of *G. elata*, it was possible to detect how a provenance of this widespread species (represented by the East Peninsular Malaysia–Sabah provenances) could have introgressed into a more localised lineage that includes *G. beamanii* and given rise to *G. elata* var. *kinabaluensis*, today restricted to a few mountains in Borneo. During Pleistocene sea-level minima (Morley 2000, Voris 2000), there was much land contiguity between today's islands in Sundaland, allowing widespread lowland species like *G. elata* to be more common and a greater chance of contact with other species. Also, the cooler climates during Pleistocene ice-ages lowered the elevational limits of montane environmental regimes (Flenley 1979; Morley 2000), so that possibly new taxa such as *G. elata* var. *kinabaluensis* arising from hybridisation of lowland taxa could have adapted to a montane climate that later became more restricted to mountains, as cooler conditions retreated upslope. Therefore sea-level and climatic changes during and after the Pleistocene are likely to have had an impactful consequence for the restriction of, and exchange between, lineages (gene pools) in Southeast Asian *Gardenia*.

There is also limited evidence of a relationship between mainland Asian and central Malesian taxa, where there was support for clustering of *G. saxatilis* (Thailand) and *G. mutabilis* (Philippines-Sulawesi) by ITS and combined ITS-chloroplast gene characteristics (section 5.2.6.2). It is also notable that morphologically, the long calyx spurs that are only characteristic of a mainland Asian lineage (*G. jasminoides*, *G. hainanensis*, *G. stenophylla*) in the present study also appear in a Philippine species (*G. barnesii*) and in various Pacific taxa such as those in Fiji (Smith 1974) and Hawaii (St. John & Kuykendall 1949). However, there can be little additional comment without including the central Malesian and Pacific taxa in more comprehensive studies.

These biogeographical interpretations are important in a conservation context. First, there are few truly widespread species in Sundaland, so most species may be regarded as rare or having a restricted distribution. Second, it would be true that, given today's drastic reduction in lowland forest area in Southeast Asia generally (Sodhi *et al.* 2004), even a formerly widespread and common species such as *G. elata*, which shows genealogical variation in different parts of its range, would have a severely fragmented distribution. This is expected to have disadvantageous consequences including restriction of gene flow connecting populations. Third, the continued destruction and transformation of coastal, especially peat swamp, forest land in Southeast Asia would likewise be detrimental because there is an interesting complex of rare species distributed in peat swamps (*G. chanii*, *G. griffithii*, *G. pterocalyx*, *G. tubifera*) and the often adjoining coastal *kerangas* forests (*G. costulata*).

Although *in situ* conservation measures are clearly desirable for conserving populations and samples of genetic ranges, it is important also to consider *ex situ* conservation. This, fortunately, would be supported by collecting programmes because

Gardenia species, by virtue of their large and attractive flowers produced in abundance, would be horticulturally valued. In relation to this, the present revision also provides a guide to species recognition and where they may be collected. Certainly, the lowland forest, peat swamp forest and *kerangas* forest *Gardenia* species should receive priority for such conservation collecting.

7.4 Future work

Field collecting is important for improving our knowledge of incompletely known species, such as *G. costulata* (Sarawak Borneo), the unnamed *Gardenia* sp. from Sangkulirang (Kalimantan Borneo), and *G. barnesii* from the Philippines (for proper assessment of its relationship with mainland Asian and Sundaland taxa). It is also important that conservation assessments be carried out after obtaining more field perspectives, which at the same time could support some *ex situ* conservation collecting programmes.

Morphological studies into *Gardenia* may be extended also. In particular, micromorphological characteristics, such as leaf surface micro-morphology and palynology, may yield further useful characters for species and group recognition. Chromosome numbers adduced through the Index to Plant Chromosome Numbers (IPCN) at <<http://mobot.mobot.org/W3T/search/ipcn.html>> accessed on 14 April 2010 showed that the species documented from Africa, India, mainland Asia and the Pacific have $x=11$ or $2n=22$, so that apparently there is no or little variation in chromosomal number to be expected. Nevertheless, the chromosome numbers and ploidy levels of Sundaland species (which display reticulate evolution and some exciting morphological variation in calyx morphology) have not been documented, so these would be of interest to add to our knowledge.

In terms of phylogenetic understanding, the relationships of Sundaland *Gardenia* lineages could be better understood with inclusion of more mainland Asian, central and east Malesian, and Pacific taxa in future analyses. The use of more informative gene regions should also be attempted. In a larger context, African representatives of *Gardenia*, including morphologically aberrant taxa such as *G. leopoldiana* and *G. vogelii*, should also be studied together with Asian and Pacific taxa, so that a wider phylogenetic perspective can be obtained.

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