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A SURVEY OF LEAF VENATION IN NEW CALEDONIAN SYZYGIUM (MYRTACEAE)

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A SURVEY OF LEAF VENATION IN NEW CALEDONIAN *SYZYGIUM* (MYRTACEAE)

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A SURVEY OF LEAF VENATION IN NEW CALEDONIAN *SYZYGIUM* (MYRTACEAE)

An Abstract of the Thesis by
Jiawei Xu

New Caledonia is a globally recognized biodiversity 'hotspot' characterized by a rich flora and a large number of endemic species. *Syzygium* Gaertn., the largest genus of woody plants in the world, is common in New Caledonia with approximately 70 species. A comparative survey of leaf morphology and architectural traits among 27 species of New Caledonian *Syzygium* was conducted, focusing on leaf venation patterns. Separate and detailed descriptions of leaf morphology and leaf venation characters are provided for the species. In addition to morphological differences, this study found differences at the species level among characters such as the number of intramarginal veins, the number and angle of divergence of secondary veins, whether thinner intersecondary veins can be distinguished from normal secondary veins, patterns of tertiary venation, relative degree of areole development, and the level of ultimate tertiary branching within areoles A cluster analysis separated the sample species into three groups based primarily on differences in leaf morphology, not patterns of venation.

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Chapter I

Introduction

1.1 Introduction to family Myrtaceae

Myrtaceae Juss., the eighth largest angiosperm family (Snow et al., 2011), comprises nearly 6000 species in approximately 132 genera of woody shrubs to tall trees (Wilson, 2011; Christenhusz, Fay and Chase, 2017). Its predominant distribution in the Southern Hemisphere includes numerous biodiversity hotspots, including much of South America and the Neotropics, Madagascar and the Mascarenes, tropical Asia, Australia, New Zealand and various Pacific islands. It is particularly diverse in certain parts of the Australian and Brazilian floras, where collectively it can comprise many of the dominant species in some plant communities (Christenhusz, Fay and Chase, 2017).

Myrtaceae is subdivided into subfamilies Psiloxyloideae R. Schmid and Myrtoideae (Wilson et al., 2005; Wilson, 2011; Christenhusz et al., 2017). The largest genera include *Eucalyptus* L'Her., *Eugenia* L., *Myrcia* DC., *Syzygium* Gaertn., *Leptospermum* J.R. Forst. & G. Forst., *Melaleuca* L., and *Psidium* L. (Christenhusz, Fay and Chase, 2017).

Myrtaceae generally can be distinguished from other families by the following combination of characters: opposite, estipulate, entire aromatic leaves with numerous punctate oil glands containing viscous substances (terpenoids and polyphenols), flowers

with inferior ovaries and often numerous brightly colored and/or highly-exserted stamens, bifacial phloem, and vestured pits on the xylem vessels (Wilson, 2011).

Myrtaceae can be a useful model for studying various aspects of biodiversity, evolution, and conservation due to its wide distribution and high levels of diversity. For example, many species have notable ecological roles in specific ecosystems. In some of eastern Brazil's wet forests, Myrtaceae are the dominant family in terms of the number of species (Mori, Boom & de Carvalino, 1983). It also can have the most individual trees and largest total basal area (Mori et al., 1983). The genus *Eucalyptus* dominates the ecosystem of many vegetation types in Australia apart from rainforests, the central arid zone (where species of *Acacia* Mill. and grasses dominate), and the higher mountainous regions (Wiltshire, 2004). The family often is critical for studying aspects of ecology in its natural range (Williams and Woinarski, 1997).

Many species of Myrtaceae have economic significance, including edible fleshy fruits such as jaboticaba (*Plinia cauliflora* (Mart.) Kausel), guava (*Psidium guajava* L. and *P. cattleianum* Afzel. ex Sabine), rose apple (*Syzygium jambos* (L.) Alston) and pitanga (*Eugenia uniflora* L.). They also are cultivated for spices such as cloves (*Syzygium aromaticum* (L.) Merr. & L.M. Perry) and allspice (*Pimenta dioica* (L.) Merr.), and oils from species in *Eucalyptus* and *Melaleuca*. Many members of *Eucalyptus* are planted widely across much of the world and used for timber, pulpwood, paper and energy production (Doughty, 2000). Other species are used in folk medicine as antidiarrheals, antimicrobials, antioxidants, cleansers, and anti-inflammatory agents to decrease blood cholesterol (Stefanello, Salvalino, and Salvador, 2011). The economic

significance of Myrtaceae has been one of the driving forces of continues research in the family (Murray-Smith et al., 2009; Staggemeier et al., 2015; Lucas and Bünger, 2015).

1.2 An overview of the genus *Syzygium* Gaertn.

Syzygium is the largest woody genus in the world, and the largest genus in Myrtaceae (Byng, Phillipson, and Snow, 2015). Most species are evergreen trees and shrubs. Its 1200–1500 species are distributed throughout the Old World (SWG, 2016) from Africa and Madagascar through southern Asia and east through the Pacific.

Its high level of diversity to a large degree explains its relative lack of taxonomic study, including the fact some species have not been described taxonomically (Soh and Parnell, 2011). More broadly, *Syzygium* exemplifies the concept of the "taxonomic impediment" seen in mega-diverse genera; namely, that only a small number of taxonomists have worked on the genus in any sustained manner, given its size and taxonomic complexity. For example, a higher percentage of specimens of this genus probably remain indetermined (=still unidentified at the species level) or misidentified compared to smaller genera. As another example, the Bernice P. Bishop Museum in Hawaii had three full herbarium cases of indetermined material from Malesia and the Pacific as recently as 2010 (N. Snow, pers. comm.), representing approximately 1500 specimens. No serious attempts ever had been made to look at the *Syzygium* globally until the recent creation of the Syzygium Working Group (SWG, 2016), spearheaded by James Byng. In addition, only a few molecular studies have begun to establish the phylogenetic backbone of the genus (Craven and Biffin, 2010, Lucas and Bünger, 2015).

1.3. The separation of *Eugenia* and *Syzygium*

Syzygium and *Eugenia* were considered by many to be one genus for much of the Twentieth Century. However, Schmid (1972) clarified the genetic distinction between them based on aspects of floral anatomy. His research also helped to illuminate the sharp distributional asymmetries pertaining to these genera between the Paleotropics and Neotropics. At that time (Schmid, 1972), many species remained improperly classified in one genus or the other, and the taxonomic transfer of species into the correct genus is an ongoing process. For example, members of *Piliocalyx* Brongn. and Gris from New Caledonia, considered by some to be a distinct genus, recently were transferred to, or given new names in *Syzygium*, which included some names formerly in *Eugenia* (Snow et al., 2017). As another example, Byng et al. (2016) updated and clarified species of both genera from the Comoros Archipelago.

The generic boundaries of *Syzygium* itself have broadened in the view of some recent authors. For example, Harrington and Gadek (2004) studied the taxonomic boundaries of *Syzygium* using sequence data from the nuclear internal transcribed spacer (ITS) and external transcribed spacer (ETS) regions of 66 Australian taxa, including representatives from both subfamilies and five genera. The ingroup taxa included 54 Australian endemics and 13 species with distributions that also range outside continental Australia. Parsimony analysis and Bayesian inference from posterior possibilities from the combined molecular datasets did not corroborate the groups or genera of many taxonomic circumscriptions then common. This included the placement or recognition of species in *Acmena* DC., *Acmenosperma* Kausel, *Anetholea* Peter G.Wilson, *Piliocalyx*, *Syzygium* and *Waterhousea* B. Hyland and further indicated the need for an additional

reappraisal of all currently recognized morphological groups. Biffin et al. (2006) used sequence data from the chloroplast *matK* and *ndhF* genes and *rpl16* intron in their investigations into the relationships of *Syzygium* group and eight outgroup taxa. The results also indicated that many clades were incongruent with contemporary taxonomic groupings (Biffin et al., 2006).

1.4 The continued importance of plant morphology in taxonomic studies

As researchers increasingly focused on DNA sequencing studies in recent years, plant morphology often has been underutilized to assess species boundaries and taxonomic relationships. However, morphology itself frequently provides adequate information to differentiate new species from those most morphologically similar, and helps interpret the results of molecular genetic research (e.g., Snow et al., 2003). Historically, plant taxonomy relied mostly on morphology to distinguish plant groups, including to some extent variation in patters of leaf venation.

In the mid-nineteenth century, the Austrian paleontologist Ettingshausen (1861) studied leaf venation patterns of Euphorbiaceae Juss., Fabaceae Lindl., Celastraceae R. Br., Bombacaceae Kunth and others. He devised terminology and descriptive terms concerning leaf venation patterns. Unfortunately, his paper used Greek rather than Latin, which limited its influence. Patterns of leaf venation mostly were ignored until the American researcher Adriance S. Foster found that the differences in secondary venation had great potential for leaf identification and for studying leaf differentiation (Foster, 1952). Later, Hickey (1973; 1975; 1979) published three influential papers about leaf architecture that began to standardize and stabilize terminology, after which the importance of leaf morphology gained increasing attention.

An important component of morphology is “leaf architecture”. According to Hickey (1973), leaf architecture includes such aspects as venation patterns, marginal configuration, leaf shape, and gland position. Architecture is the aspect of morphology that applies to the spatial configuration and coordination of those elements without regard to histology, function, origin, or homology. Given that morphological features typically can be observed with the naked eye or under a dissecting scope, they are considered macroscopic structures of the leaf, unlike the microscopic features, commonly referred to as leaf anatomy. The science and study of leaf architecture as an analytical method has gradually matured and become more operable after decades of research (Ellis et al., 2009).

Plant taxonomists consistently have identified and characterized living plants and leaf fossils based in part on one to several characters of leaf architecture. Whereas reproductive structures such as flowers and fruits often have been the main focus in plant classifications, the application of leaf architecture traits is still necessary and their value increasingly has been appreciated. Since venation characters are generally constant within a species, and they are visible on the plant year-round in tropical evergreen trees (including most Myrtaceae), they potentially are of great significance for plant fossil research and systematic classification.

Some researchers believe that the leaf venation characters can be used as a partial basis for classification between families, genera and species, especially at the species level. Indeed, at a regional level, expert field botanists often can identify most woody genera and species based on solely on their patterns of leaf venation (e.g., Gentry, 1993). Recent further study has found that the marginal ultimate venation (Melvilee, 1976), areole characters (Nicely, 1965) and higher orders of venation also often have significant

taxonomic value. Mohan (1982) conducted a taxonomic study of 29 species in 19 genera of Apocynaceae Juss. based on leaf morphology. Carr et al. (1986) discovered that the apparently brochidodromous venation of leaves of some *Eucalyptus* species arises as a result of differential growth following the inception of intramarginal veins. Leaves with intramarginal veins are ontogenetically acrodromous. Calvillo-Canadell and Cevallos-Ferriz (2002) clarified the systematic positions of *Bauhinia* L. and *Cercis* L. by studying their leaf architectural characteristics. Soh and Parnell (2011) found that a combination of non-unique leaf anatomical characters, including stomatal types, crystal types and frequency, and midrib vascular system (adaxial phloem partition) are diagnostic for subgeneric groups of *Syzygium*.

1.5 Leaf venation in *Syzygium*

Klucking (1988) summarized the venation patterns of Mytaceae in a broad survey of the family, including 123 species of *Syzygium*, including six from New Caledonia. It is the most recent research work about leaf venation in *Syzigium*. Klucking recognized five general patterns of leaf venation for *Syzygium*.

1.6 An overview of New Caledonia

New Caledonia is a special collectivity of France in the southwest Pacific Ocean, approximately 1500 km east of Australia and 2000 km north of New Zealand (Figure 1). The archipelago is part of the Melanesia subregion and includes the main island of Grande Terre, the Loyalty Islands, the Chesterfield Islands, the Belep Archipelago, the Isle of Pines, and a few remote islets. The Chesterfield Islands are in the Coral Sea. Locals refer to Grande Terre as Le Caillou.

Figure 1. New Caledonia. The Southern Province on Grande Terre (green) is administered by the French Government, in contrast to the Northern Province (yellow), which is administered by the native population of Kanaks. (https://geology.com/world/new-caledonia-satellite-image.shtml)

New Caledonia was recognized as one of the original ten "hot spots" of tropical forest diversity (Myers, 1988). Its abundant habitats included dense evergreen forests, maquis shrubland, sclerophyllous (dry) forest, wetlands, savannas, and halophytic vegetation. The high endemism rate of approximately 75% for its over 3300 species of vascular plants is due to edaphic factors and topographic features, which contribute to a high and localized levels of structural complexity of the environment (Morat et al., 2012). It is so diverse that micro-hotspots, or "hotspots within hotspots", are now recognized as well (Gâteblé et al., 2019).

Two main substrates underly the soils in New Caledonia. One is broadly classified as volcano-sedimentary, which cover about 9000 km^2, mostly in the north. The other, known as *terrains miniers,* includes substrates of ultramafic rocks containing serpentinite and peridotite. Ultramafics cover about 5600 km^2, or about 30% of the land surface. Ultramafics differ greatly from non- ultramafic substrates in having low levels of

macronutrients such as phosphorus, calcium and potassium, but having high levels of magnesium, which antagonizes plant calcium uptake (Ibanez et al., 2014). More detrimental to plant growth overall, ultramafic substrates also possess high levels of potentially phytotoxic metals such as nickel, chromium or manganese (Jaffré, 1980; Kazakou et al., 2008; Fernando et al., 2009). The patchy occurrence of ultrabasic substrates likely have contributed to natural selection of physiological tolerances and speciation, producing highly distinctive vegetation with high levels of endemism (Ibanez et al., 2014). High endemism also is maintained by the presence of various microclimates (Bátori et al., 2017; Gâteblé et al., 2019). Fernando et al. (2009) and McLay et al. (2019) studied (respectively) the uptake of foliar manganese and the evolutionary relationships of the genus *Gossia* N. Snow & Guymer of Myrtaceae, which occurs nearly entirely in Australia (Snow et al., 2003) and New Caledonia (Snow, 2020), the latter study of which focused in part on distributions at the species level on ultramafics.

Given New Caledonia's high plant biodiversity, the conservation and intelligent management of the island's biota is now a high priority among scientists in that country (e.g., Ibanez et al., 2019; Gâteblé et al., 2019). Continued economic development promotes human disturbances, such as that from open-cast mining, which is common across New Caledonia, especially nickel mines. Intentionally set fires as a form of political protest, along with urbanization and exotic species introduction, also are reducing the exceptional floristic diversity of New Caledonia. These activities have led to a 75% reduction of the original vegetation cover since the arrival of humans approximately 3500 years ago (Ibanez et al., 2019).

The rarer species of *Syzygium* also are increasingly threatened by the non-native myrtle rust, *Austropuccinia psidii* G. Winter (Giblin, 2013), and local mining. Any new ecological or distributional information discovered is important for protecting those species, and the ability to properly identify species is the first critical step to a more thorough understanding where they are in greatest need of conservation. Thus, knowledge of leaf venation characters can help document and discern between different species of *Syzygium*, which may furthermore help discover new populations in the field and thus indirectly contribute of their conservation.

Chapter II

Methods

2.1 Experimental Design

Representative herbarium samples of species of New Caledonian *Syzygium* from the Missouri Botanical Garden or from Pittsburg State University were measured for a suite of leaf anatomical characters. One or more mature leaves of each species were used from the most recent growth. The clearing methods were mainly based on Vasco et al. (2014).

Leaves were placed in a shallow beaker and re-hydrated in a distilled water bath at 25°C for 24 hours to soften tissues. Blades were immersed in a 5-10 % NaOH, with stainless steel weights placed over the leaf to keep them flat. Beakers were covered with parafilm and placed in a water bath at 55ºC for one to several days, given that the time needed varied from leaf to leaf depending on the size, thickness and specimen quality. The NaOH solution was changed when it became dark. Beakers were removed from the water bath after the leaf parenchyma tissue fell off from the leaf. After it cooled down to room temperature, the leaf was rinsed carefully with tap water. Any remaining leaf tissue was removed by using a soft-bristled, fine paint brush. Blades then were bleached in 4-5% sodium hypochlorite for 20 s to 5 min depending on the thickness of the leaf. After rinsing gently with tap water a few times once the leaf turned white, leaves were immersed in 50%, 70%, and 95% ethanol (respectively) for 30 min to dehydrate the leaf,

which strengthens the cell walls. The leaf was stained with Safranin, which was added to 95% ethanol for 3 h to overnight. Pure (100%) ethanol was acidified with 3-6 drops of HCl 37% and used to de-stain the leaf for 10-30 min until the venation became clearer. A piece of white paper was placed under the container to monitor the progress of the staining process. The leaf was placed in 100% ethanol at least 24 h to make it firmer and a piece of parafilm was used to keep the alcohol from evaporating. The leaf was then placed on glass plates and digital images were captured after the staining process. Characters associated with gross leaf morphology and venation patterns were recorded. Vouchers of specimens are cited in the Results.

2.2 Cluster analyses

Cluster analyses were carried out using the morphological characters of the sampled species. Cluster analysis is a multivariate technique that clusters the research objects in two dimensional phenograms according to their levels of overall similarity. The closer the objects cluster, the higher degree of overall similarity. Individuals clustering in different groups have a higher degree of dissimilarity (Han and Kamber, 2002).

The program Statistical Product and Service Solutions (SPSS) (Pallant and Manual, 2007) used the unweighted pair-group method with arithmetic means (UPGMA) to perform a cluster analysis of 18 variable characters associated with leaves to assess phenetic relationships as revealed from those traits (Table 1).

Table 1. Leaf architectural characters and related morphological characters.

Code	Characters	Character States
1	Blade symmetry	(0) symmetrical; (1) asymmetrical
2	Leaf shape	(0) elliptic; (1) ovate; (2) obovate; (3) lanceolate-oblong
3	Leaf size	(0) small (length≦ 5 cm); (1) medium (length 5-10 cm); (2) large (length≧ 10 cm)
4	Leaf base	(0) attenuate; (1) cuneate; (2) rounded; (3) cordate
5	Leaf apex	(0) acute; (1) acuminate; (2) obtuse
6	Petiole length	(0) sessile; (1) short; (2) long (>1 cm)
7	Leaf margin	(0) revolute; (1) involute; (2) flat
8	Oil glands	(0) visible; (1) invisible
9	Texture	(0) chartaceous; (1) leathery
10	Secondary vein size	(0) moderate; (1) thick
11	Secondary vein divergence angle	(0) wide (>65°); (1) moderate (45 °-65 °); (2) narrow (<45 °)
12	Intersecondary vein	(0) present; (1) absent
13	Tertiary veins	(0) reticulate; (1) ramified; (2) mixed
14	Ultimate veinlet in ultimate areolas	(0) 1-3 branched; (1) dendritic (4 or more branched)
15	Areole development	(0) well-developed; (1)moderately-developed; (2) poorly-developed
16	Areole arrangement	(0) atypical (areoles of different size and shape); (1) typical
17	Marginal ultimate venation	(0) present and looped; (1) irregularly connecting to margin
18	Outer intramarginal vein	(0) present; (1) absent

The morphological characters (Table 1) were converted numerically (Table 2). The hierarchical (k-mean) algorithm in SPSS software (Verma, 2012) was used for clustering based on characters in Table 2.

Table 2. Data matrix of characters of leaf architecture in *Syzygium*.

Taxon	Characters																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
S. wagapense	1	1	1	1	0	1	1	1	1	1	0	0	2	1	0	0	0	0
S. tripetalum	1	2	1	1	2	1	0	1	1	0	0	0	2	1	0	1	0	1
S. tenuiflorum	1	1	0	3	0	1	2	0	0	1	1	0	0	1	1	0	0	1
S. schlechterianum	1	2	0	1	0	1	1	1	1	1	1	0	2	1	1	0	0	1
S. schistaceum	0	3	1	1	1	1	2	1	1	1	1	0	0	1	1	1	0	1
S. rivulare	1	2	1	1	1	1	2	1	1	0	1	0	2	1	1	0	0	1
S.propinquum	0	1	1	2	0	0	0	1	1	0	1	0	2	1	0	1	0	0
S. poyanum	1	1	1	1	0	1	2	1	1	1	0	0	0	1	0	0	0	0
S. pancheri	0	0	1	1	0	1	0	1	1	1	0	0	2	1	1	0	0	1
S. ngoyense	0	1	0	1	2	1	0	1	1	0	0	0	2	0	1	0	0	1
S. neocaledonicum	0	1	2	1	1	2	0	1	1	0	1	1	2	0	1	1	0	1
S. mouanum	0	2	1	1	2	1	0	0	1	1	1	0	2	0	0	0	0	1
S. meorianum	1	0	2	1	0	2	0	1	1	1	0	0	2	0	0	0	0	0
S. macranthum	1	2	2	1	2	2	0	0	1	1	1	0	1	1	1	0	0	1
S. lecardii	0	1	1	3	0	1	0	1	1	1	0	0	0	1	0	1	0	1
S. lateriflorum	0	0	2	1	0	1	1	0	1	1	0	0	2	1	1	1	0	1
S. kuebiniense	1	0	1	1	2	1	0	1	1	0	2	0	1	1	0	0	0	1
S. kriegeri	0	2	1	0	2	2	0	1	1	0	0	1	1	0	1	0	0	1
S. jaffrei	0	1	1	3	1	1	0	1	1	1	0	0	1	1	1	0	0	1
S. densiflorum	1	0	2	1	1	1	0	1	1	1	0	1	2	0	1	0	0	1
S. capillaceum	0	1	0	2	0	1	0	1	1	1	0	1	2	1	1	0	0	1
S. brongniartii	1	2	1	1	2	1	1	1	1	0	1	0	1	1	0	0	1	1
S. boulindaense	0	0	0	1	0	1	0	1	1	1	1	0	0	1	0	0	0	1
S. balansae	0	1	2	1	0	1	0	1	1	1	1	0	0	0	0	1	0	0
S. austrocaledonicum	1	1	2	0	1	2	1	0	1	0	2	0	1	0	2	0	1	1
S. arboreum	0	1	1	1	2	1	0	1	1	1	1	0	2	0	1	0	0	1
S. micans	0	2	0	0	1	1	0	0	1	0	1	0	2	0	1	0	0	1

Chapter III

Results

3.1 Characters of leaf architecture and patterns of leaf venation in selected species of New Caledonian *Syzygium*

Generalized description of leaf blades: Leaf venation simple brochidodromous. Secondaries joining in a series of prominent arches or loops of secondary gauge. Blades elliptic, ovate, obovate, lanceolate to oblong; base attenuate, cuneate, rounded to cordate; margins flat, revolute or involute; apex usually acute or acuminate, sometimes rounded, rarely cuspidate or mucronate; adaxial (upper) surface usually leathery, shiny, rarely punctate, the midvein mostly sulcate ca. ¾ of the length from base of leaf and becoming flush distally; abaxial (lower) surface punctate (appearing as black punctate dots in dried material), the midvein always prominently raised.

Description of venation patterns: Secondary veins 7–32 per side, 0.8–5 mm apart; divergence angle either consistent or variable. Intersecondary veins mostly present and variable numerically per intercostal area. Tertiary veins reticulate, ramified or mostly mixed (Figure 30). Higher order veins present up to the fifth order, but fourth order veins generally anastomosing with fifth order veins to form areolas. Areolas are poorly, moderately, or strongly developed, sometimes as imperfectly closed meshes of triangular, quadrangular or irregular shape. Veinlets of ultimate areolas branched 1–3 times or with

dendroid branching (Figure 31). Intramarginal vein mostly present, about 0.4–3 mm from edge at midpoint of the blade. Outer intramarginal vein present or invisible. Marginal ultimate venation mostly looped.

Detailed descriptions of leaf blades by species:

Many aspects of morphology relied heavily on Dawson (1999), but observed modifications are included.

Syzygium meorianum J.W. Dawson

Leaf morphology: Petioles 1–3 cm x 2–2.5 mm (length x width). Blades 9–13.5 x 3.5–7 cm, leathery; widely obovate to elliptic; base cuneate; apex obtuse, acute; margin flat to slightly revolute. Adaxial midvein flush; abaxial midvein projecting prominently. Adaxial surface shiny. Oil glands clearly visible on both sides.

Venation: Thicker secondary veins ca. 20–25 per side and mostly 3–8 mm apart; thinner intersecondary veins numerous on each side, usually one per intercostal area. Intramarginal vein 1–1.5 mm from the leaf edge at midpoint of the blade. Outer intramarginal vein visible, arching slightly as it connects adjacent intramarginal vein. Divergence of secondary veins from midvein consistently ca. 60 degrees. Areolas well-developed, triangular, quadrangular or regular in shape; ultimate veinlet in ultimate areolas branched 1–3 times. Tertiary venation reticulate or mixed. Marginal ultimate venation looped (Voucher: *McPherson 5712* [MO]).

Syzygium arboretum (Baker f.) J.W. Dawson

Leaf morphology: Petioles 2–3 mm x 1.5–2 mm wide. Blades 4–8 x 1.5–4 cm, ovate; base cuneate; apex rounded or sometimes retuse; margin wavy and revolute. Adaxial

midvein sulcate; abaxial midvein projecting prominently. Adaxial surface leathery and shiny. Oil glands indistinct on both sides.

Venation: Thicker secondary veins ca. 10–13 per side and mostly 2–5 mm apart; thinner intersecondary present, usually one per intercostal area. Intramarginal vein 0.7–1.1 mm from edge at midpoint of the blade. Outer intramarginal vein invisible. Divergence angle of secondary veins from midvein inconsistent, from ca. 40 degrees near apex to ca. 60–75 degrees at base. Areolas moderate developed, shape irregular, more or less variable in size. Ultimate veinlet in ultimate areolas branched 1–3 times. Tertiary veins mixed. Marginal ultimate venation looped (Voucher: *McPherson 17805* [MO]).

Syzygium austrocaledonicum (Seemann) Guillaumin

Leaf morphology: Petioles 1–1.6 cm x 0.8–1 mm. Blades 4–6 x 2–4 cm, obovate; base cuneate; apex acuminate; margin wavy and involute. Adaxial midvein sulcate; abaxial midvein projecting prominently. Adaxial surface leathery and very shiny. Oil glands typically visible but often indistinct.

Venation: Thicker secondary veins ca. 18–24 per side and mostly 1–3 mm apart; thinner intersecondary veins present, less than one per intercostal area. Intramarginal vein 0.5–1.1 mm from edge at midpoint of the blade. Outer intramarginal vein invisible. Divergence of secondary veins from midvein consistent, ca. 45 degrees. Areolas poorly developed, shape irregular, more or less variable in size. Ultimate veinlet in ultimate areolas branched 1–3 times. Tertiary veins ramified freely. Marginal ultimate venation absent (Voucher: *McPherson 17785* [MO]).

Syzygium balansae (Guillaumin) J.W. Dawson

Leaf morphology: Petioles 4–7 mm x 1.5–2.5 mm. Blades 4.5–7.5 x 3–4 cm, elliptic to obovate; base cuneate; apex acute; margin wavy and revolute; adaxial midvein sulcate; abaxial midvein projecting prominently. Adaxial surface leathery and shiny. Oil glands indistinct.

Venation: Thicker secondary veins ca. 9–12 per side and mostly 2–7 mm apart; thinner intersecondary veins present, less than one per intercostal area. Intramarginal vein 0.7–1 mm from edge at midpoint of the blade. Outer intramarginal vein 0.2–0.3 from the leaf edge at midpoint of the blade. Divergence angle of secondary veins from midvein not consistent, from ca. 60 degrees near apex to ca. 40 degrees at base. Areolas well developed, triangular, quadrangular or regular in shape. Ultimate veinlet in ultimate areolas with dendritic branching. Tertiary veins reticulate. Marginal ultimate venation looped (Voucher: *MacKee 20697* [MO]).

Syzygium boulindaense J.W. Dawson

Leaf morphology: Petioles 2–4 mm x 0.5–0.8 mm. Blades 1.3–2 x 0.8–1.3 cm, elliptic to obovate; base cuneate; apex acute or obtuse; margin revolute; adaxial midvein sulcate; abaxial midvein projecting prominently. Shiny on both sides. Oil glands indistinct.

Venation: Thicker secondary veins ca. 6–9 per side and mostly 1–2 mm apart; thinner intersecondary veins present, less than one per intercostal area. Intramarginal vein 0.4–0.9 mm from edge at midpoint of the blade. Outer intramarginal vein invisible. Divergence of secondary veins from midvein consistent, ca. 40 degrees. Areolas well developed, triangular, quadrangular or regular in shape. Ultimate veinlet in ultimate

areolas with dendritic branching. Tertiary veins reticulate. Marginal ultimate venation looped (Voucher: *Munz 568* [MO]).

Syzygium brongniartii J.W. Dawson

Leaf morphology: Petioles 2–7 mm x 1–1.5 mm. Blades 2.5–6.5 x 1.2–3 cm, obovate; base cuneate; apex slightly obtuse; margin involute; adaxial midvein sulcate; abaxial midvein projecting prominently. Adaxial surface shiny. Oil glands indistinct.

Venation: Thicker secondary veins ca. 9–13 per side and mostly 1–2 mm apart; thinner intersecondary veins present, usually one per intercostal area. Intramarginal vein 1.2–1.4 mm from edge at midpoint of the blade. Outer intramarginal vein invisible. Divergence of secondary veins from midvein consistent, ca. 45 degrees. Areolas well developed, triangular, quadrangular or regular in shape. Ultimate veinlet in ultimate areolas dendritic branching. Tertiary veins ramified. Marginal ultimate venation absent (Voucher: *McPherson 6564* [MO];).

Syzygium capillaceum (Brongniart & Gris) J.W. Dawson

Leaf morphology: Petioles ca. 3 mm x ca. 1.5 mm. Blades 3.5–6.5 x 2–3 cm, ovate to narrowly ovate; base rounded; apex acute or acuminate; margin wavy and revolute; adaxial midvein sulcate; abaxial midvein projecting prominently. Adaxial surface shiny. Oil glands generally visible on the underside of the leaf.

Venation: Thicker secondary veins ca. 20–22 per side and (2–) 3–7 mm apart; thinner intersecondary veins not prominent, usually less than one per intercostal area. Intramarginal vein ca. 1.1 mm from edge at midpoint of the blade. Outer intramarginal vein invisible. Divergence of secondary veins from midvein consistent, ca. 80 degrees. Areolas moderately developed, shape irregular, more or less variable in size. Ultimate

veinlet in ultimate areolas with dendritic branching. Tertiary veins mixed. Marginal ultimate venation looped (Vouchers: *McPherson 6144* [MO]).

Syzygium densiflorum Brongniart & Gris

Leaf morphology: Petioles 6–10 mm x 1–2 mm. Blades 6–10 x 3–5.5 cm, obovate to elliptic; base rounded to cuneate; apex acuminate; margin wavy and revolute; adaxial midvein sulcate; abaxial midvein projecting prominently. Adaxial surface leathery, shiny. Oil glands indistinct.

Venation: Thicker secondary veins ca. 27–30 per side and mostly 2–5 mm apart; thinner intersecondary veins faint, usually less than one per intercostal area. Intramarginal vein 1.1–1.3 mm from edge at midpoint of the blade. Outer intramarginal vein invisible. Divergence of secondary veins from midvein consistent, ca. 80 degrees. Areolas moderately developed, shape irregular, more or less variable in size. Ultimate veinlet in ultimate areolas branched 1–3 times. Tertiary veins reticulate or mixed. Marginal ultimate venation looped (Voucher: *McPherson 1688* [MO]).

Syzygium kriegeri Guillaumin

Leaf morphology: Petioles 1.5–2 cm x 1.5–2.5 mm wide. Blades 6–9 x 2.5–5 cm, obovate; base attenuate or cuneate; apex rounded, obtuse; margin revolute; adaxial midvein sulcate; abaxial midvein projecting prominently. Adaxial surface leathery, shiny. Oil glands indistinct.

Venation: Thicker secondary veins ca. 21–26 per side and mostly 1–2 mm apart, thinner intersecondary veins not prominent, usually less than one per intercostal area. Intramarginal vein 1.1–1.4 mm from edge at midpoint of the blade. Outer intramarginal vein invisible. Divergence of secondary veins from midvein consistent, ca. 70 degrees.

Areolas moderately developed, shape irregular, more or less variable in size. Ultimate veinlet in ultimate areolas branched 1–3 times. Tertiary veins ramified. Marginal ultimate venation looped (Voucher: *McPherson 2679* [MO]).

Syzygium kuebiniense J.W. Dawson

Leaf morphology: Petioles 7–12 mm x 2–2.5 mm. Blades 5–8.5 x 2–3.5 cm, elliptic to oblanceolate; base cuneate; apex rounded, obtuse, or acute; margin revolute; adaxial midvein sulcate; abaxial midvein projecting prominently. Adaxial surface leathery, shiny. Oil glands indistinct (Dawson 1999).

Venation: Thicker secondary veins ca. 12–16 per side and mostly 1.7–2.1 mm apart, thinner intersecondary veins not prominent, usually less than one per intercostal area. Intramarginal vein faint. Outer intramarginal vein invisible. Divergence angle of secondary veins from midvein consistent, ca. 45 degrees. Areolas well developed, triangular, quadrangular or regular in shape. Ultimate veinlet in ultimate areolas with dendritic branching. Tertiary veins ramified. Marginal ultimate venation looped (Voucher: *McPherson 5052* [MO]).

Syzygium lateriflorum Brongniart & Gris

Leaf morphology: Petioles 5–10 mm x 0.8–1.5 mm. Blades 5–9.5 x 2–6 cm, obovate, oblancelate; base cuneate; apex acute; margin wavy and involute; adaxial midvein sulcate; abaxial midvein projecting prominently. Abaxial surface leathery, shiny. Small oil glands visible on abaxial leaf.

Venation: Thicker secondary veins ca. 29–32 per side and mostly 0.8–2 mm apart, thinner intersecondary veins not prominent, usually less than one per intercostal area. Intramarginal vein 0.4–0.6 mm from edge at midpoint of the blade. Outer intramarginal

vein invisible. Divergence angle of secondary veins from midvein consistent, ca. 60 degrees. Areolas moderately developed, shape irregular, more or less variable in size. Ultimate veinlet in ultimate areolas with dendritic branching. Tertiary veins reticulate or mixed. Marginal ultimate venation looped (Voucher: *McPherson 2275* [MO]).

Syzygium lecardii Guillaumin

Leaf morphology: Petioles 1.5–4 mm x 1–2 mm wide. Blades 2–8 x 1–4 cm, largely ovate to almost orbicular, or lanceolate; base cuneate, rounded, or cordate; apex rounded, obtuse, or acute; margin wavy and revolute slightly; adaxial midvein sulcate; abaxial midvein projecting prominently. Adaxial surface leathery, shiny. Oil glands indistinct.

Venation: Thicker secondary veins ca. 21–25 per side and mostly 2–5 mm apart, thinner intersecondary veins not prominent, usually less than one per intercostal area. Intramarginal vein 0.3–0.6 mm from edge at midpoint of the blade. Outer intramarginal vein invisible. Divergence of secondary veins from midvein inconsistent, ca. 60 degrees near apex to ca. 90–100 at base. Areolas well developed, triangular, quadrangular or regular in shape. Ultimate veinlet in ultimate areolas with dendritic branching. Tertiary veins reticulate. Marginal ultimate venation looped (Voucher: *MacKee 196* [MO]).

Syzygium macranthum Brongniart & Gris

Leaf morphology: Petioles 1–1.2 cm x 1.5–4 mm. Blades 5–14(–18) x 2.5–8.5 cm, obovate; base rounded or cuneate; apex obtuse to retuse, acuminate sometimes; margin wavy and revolute slightly; adaxial surface leathery, shiny; adaxial midvein sulcate; abaxial midvein projecting prominently. Adaxial surface leathery, shiny. Small oil glands visible on abaxial leaf.

Venation: Thicker secondary veins ca. 28–30 per side and mostly 1–2 mm apart, thinner intersecondary veins not prominent, usually less than one per intercostal area. Intramarginal vein 0.9–1.6 mm from edge at midpoint of the blade. Outer intramarginal vein invisible. Divergence of secondary veins from midvein consistent, ca. 65 degrees. Areolas moderately developed, shape irregular, more or less variable in size. Ultimate veinlet in ultimate areolas with dendritic branching. Tertiary veins ramified. Marginal ultimate venation looped (Voucher: *McPherson 4653* [MO]).

Syzygium micans Brongniart & Gris

Leaf morphology: Petioles 8–12 mm x 1–1.5 mm. Blades 3–5.5 x 1–2 cm, oblanceolate or obovate; base attenuate or cuneate; apex acuminate; margin revolute; adaxial midvein sulcate; abaxial midvein projecting prominently (needs to check). Adaxial surface leathery, shiny. Oil glands visible on abaxial leaf.

Venation: Thicker secondary veins ca. 15–17 per side and mostly 1–2 mm apart, thinner intersecondary veins not prominent, usually less than one per intercostal area. Intramarginal vein 0.5–0.7 mm from edge at midpoint of the blade. Outer intramarginal vein invisible. Divergence of secondary veins from midvein consistent, ca. 50–60 degrees. Areolas moderately developed, irregular shape, more or less variable in size. Ultimate veinlet in ultimate areolas branched 1–3 times. Tertiary veins reticulate or mixed. Marginal ultimate venation looped (Voucher: *MacKee 21918* [MO]).

Syzygium mouanum Guillaumin

Leaf morphology: Petioles 3–9 mm x 1.5–2.5 mm. Blades 4–10 x 2–4.5 cm, elliptic or obovate; base cuneate; apex rounded to obtuse; margin revolute; adaxial midvein

sulcate (however, Dawson reported it as projecting above); abaxial midvein projecting prominently. Adaxial surface leathery, shiny. Oil glands visible on both sides.

Venation: Thicker secondary veins ca. 13–16 per side and mostly 2–6 mm apart, thinner intersecondary veins not prominent, usually less than one per intercostal area. Intramarginal vein 1–2.4 mm from edge at midpoint of the blade. Outer intramarginal vein visible. Divergence of secondary veins from midvein consistent, ca. 30–45 degrees. Areolas well developed, irregular shape, more or less variable in size. Ultimate veinlet in ultimate areolas branched 1–3 times. Tertiary veins mixed. Marginal ultimate venation looped (Voucher: *McPherson 5437* [MO]).

Syzygium neocaledonicum (Seemann) J.W. Dawson

Leaf morphology: Petioles 4–55 mm x long 1–6 mm. Blades 9.5–25 x 2.5–7 cm, narrowly elliptic to lanceolate or obovate; base cuneate; apex rounded, acuminate sometimes; margin wavy and revolute slightly; adaxial midvein sulcate; abaxial midvein projecting prominently. Adaxial surface leathery, shiny. Oil glands indistinct.

Venation: Thicker secondary veins ca. 29–34 per side and mostly 1–5 mm apart, thinner intersecondary veins invisible. Intramarginal vein 0.6–0.9 mm from edge at midpoint of the blade. Outer intramarginal vein invisible. Divergence of secondary veins from midvein consistent, ca. 40–50 degrees. Areolas well developed, shape irregular, more or less variable in size. Ultimate veinlet in ultimate areolas branched 1–3 times. Tertiary veins mixed. Marginal ultimate venation looped (Voucher: *McPherson 5683* [MO]).

Syzygium ngoyense (Schlechter) Guillaumin

Leaf morphology: Petioles 2.5–4 mm x 0.8–0.9 mm. Blades 1.5–2.4 x 0.8–1.6 cm, obovate; base cuneate; apex rounded; margin revolute; adaxial midvein sulcate; abaxial midvein projecting prominently. Adaxial surface leathery, shiny. Oil glands indistinct.

Venation: Thicker secondary veins ca. 10–13 per side and mostly 1–1.4 mm apart, thinner intersecondary veins not prominent, usually less than one per intercostal area. Intramarginal vein 0.5–0.6 mm from edge at midpoint of the blade. Outer intramarginal vein invisible. Divergence of secondary veins from midvein consistent, ca. 40–50 degrees. Areolas moderately developed, shape irregular, more or less variable in size. Ultimate veinlet in ultimate areolas branched 1–3 times. Tertiary veins mixed. Marginal ultimate venation looped (Voucher: *MacKee 22503* [MO]).

Syzygium pancheri Brongniart & Gris

Leaf morphology: Petioles 3–8 mm x 1–2.5 mm. Blades 3–8.5 x 2–4.5 cm, obovate to elliptic; base cuneate; apex rounded, acute; margin revolute, wavy sometimes; adaxial midvein sulcate; abaxial midvein projecting prominently. Adaxial surface leathery, shiny. Oil glands indistinct.

Venation: Thicker secondary veins ca. 15–17 per side and mostly 1.6–2.5 mm apart, thinner intersecondary veins not prominent, usually less than one per intercostal area. Intramarginal vein 0.8–1.1 mm from edge at midpoint of the blade. Outer intramarginal vein invisible. Divergence of secondary veins from midvein consistent, ca. 30–40 degrees. Areolas moderately developed, shape irregular, more or less variable in size. Ultimate veinlet in ultimate areolas with dendritic branching. Tertiary veins mixed. Marginal ultimate venation looped (Voucher: *McPherson 5018* [MO]).

Syzygium poyanum J.W. Dawson

Leaf morphology: Petioles 8–14 mm x 1–2 mm. Blades 4–12 x 2.5–6 cm, ovate to elliptic; base cuneate; apex rounded, acute sometimes; margin flat, wavy sometimes; adaxial midvein sulcate; abaxial midvein projecting prominently. Adaxial surface leathery, shiny. Oil glands clearly visible above.

Venation: Thicker secondary veins ca. 15–19 per side and mostly 1.9–2.4 mm apart, thinner intersecondary veins not prominent, usually less than one per intercostal area. Intramarginal vein 1.1–1.4 mm from edge at midpoint of the blade. Outer intramarginal vein very thin, not continuous. Divergence of secondary veins from midvein not consistent, ca. 40 degrees near apex to ca. 60 degrees at base. Areolas well developed, shape irregular, more or less variable in size. Ultimate veinlet in ultimate areolas with dendritic branching. Tertiary veins reticulate. Marginal ultimate venation looped (Voucher: *MacKee 14539* [MO]).

Syzygium propinquum (Guillaumin) J.W. Dawson

Leaf morphology: Petioles not present (leaves sessile); blades 3.5–15 x 2–6 cm; ovate to lanceolate; base rounded or cordate; apex rounded, acute sometimes; margin revolute; adaxial midvein sulcate; abaxial midvein projecting prominently. Adaxial surface leathery, shiny. Oil glands indistinct.

Venation: Thicker secondary veins ca. 11–13 per side and mostly 1.9–2.5 mm apart, thinner intersecondary veins not prominent, usually less than one per intercostal area. Intramarginal vein 0.9–1.4 mm from edge at midpoint of the blade. Outer intramarginal vein barely if at all visible. Divergence angle of secondary veins from midvein consistent, ca. 30–45 degrees. Areolas well developed, shape irregular, more or less variable in size.

Ultimate veinlet in ultimate areolas with dendritic branching. Tertiary veins mixed. Marginal ultimate venation looped (Voucher: *MacKee 42729* [MO]).

Syzygium rivulare Viellard ex Guillaumin

Leaf morphology: Petioles 1.5–2.5 mm x 0.8–1 mm. Blades 2.5–4 x 0.7–1.7 cm, ovate to elliptic, oblanceolate sometimes; base cuneate; apex rounded, acuminate sometimes; margin flat; adaxial midvein sulcate; abaxial midvein projecting prominently. Adaxial surface leathery, shiny. Oil glands indistinct.

Venation: Thicker secondary veins ca. 15–18 per side and mostly 1.5–2.1 mm apart, thinner intersecondary veins not prominent, usually less than one per intercostal area. Intramarginal vein 0.4–0.6 mm from edge at midpoint of the blade. Outer intramarginal vein invisible. Divergence of secondary veins from midvein consistent, ca. 20–30 degrees. Areolas well developed, shape irregular, more or less variable in size. Ultimate veinlet in ultimate areolas with dendritic branching. Tertiary veins mixed. Marginal ultimate venation looped (Voucher: *MacKee 14259* [MO]).

Syzygium schistaceum J.W. Dawson

Leaf morphology: Petioles 6–12 mm x 1.5–2 mm. Blades 6–17 x 1.5–4 cm, lanceolate; base cuneate, rounded, cordate sometimes; apex acuminate; margin flat; adaxial midvein sulcate; abaxial midvein projecting prominently. Adaxial surface leathery, shiny. Oil glands indistinct.

Venation: Thicker secondary veins ca. 17–24 per side and mostly 1.8–2.1 mm apart, thinner intersecondary veins invisible. Intramarginal vein 0.7–0.9 mm from edge at midpoint of the blade. Outer intramarginal vein invisible. Divergence angle of secondary veins from midvein consistent, ca. 30–40 degrees. Areolas moderately developed, shape

irregular, more or less variable in size. Ultimate veinlet in ultimate areolas with dendritic branching. Tertiary veins reticulate. Marginal ultimate venation looped (Voucher: *MacKee 37109* [MO]).

Syzygium schlechterianum Hochr.

Leaf morphology: Petioles 2–4 mm x 0.5–0.8 mm. Blades 1.5–2.7(–4) x 0.6–1.2– (2) cm, obovate to oblanceolate; base cuneate; apex acute or acuminate; margin revolute; adaxial midvein sulcate; abaxial midvein projecting prominently. Adaxial surface leathery, shiny. Oil glands indistinct or visible below.

Venation: Thicker secondary veins ca. 9–12 per side and mostly 1–2 mm apart, thinner intersecondary veins not prominent, usually less than one per intercostal area. Intramarginal vein 0.8–1.1 mm from edge at midpoint of the blade. Outer intramarginal vein invisible. Divergence angle of secondary veins from midvein consistent, ca. 30–40 degrees. Areolas moderately developed, shape irregular, more or less variable in size. Ultimate veinlet in ultimate areolas with dendritic branching. Tertiary veins mixed. Marginal ultimate venation looped (Voucher: *MacKee 19071* [MO]).

Syzygium tenuiflorum Brongniart & Gris

Leaf morphology: Sessile or petioles less than 1 mm x 0.8 mm. Blades 0.9–2.6 x 0.8–1.7 cm, broadly ovate to orbicular; base cordate; apex rounded, acute or sometimes acuminate; margin flat to sometimes wavy; adaxial midvein sulcate; abaxial midvein projecting prominently. Adaxial surface chartaceous, shiny. Oil glands visible on both sides.

Venation: Thicker secondary veins ca. 11–13 per side and mostly 1.2–2.2 mm apart, thinner intersecondary veins not prominent, usually less than one per intercostal area.

Intramarginal vein 0.9–1.2 mm from edge at midpoint of the blade. Outer intramarginal vein visible. Divergence of secondary veins from midvein consistent, ca. 20–40 degrees. Areolas moderately developed, shape irregular, more or less variable in size. Ultimate veinlet in ultimate areolas with dendritic branching. Tertiary veins reticulate. Marginal ultimate venation looped (Voucher: *MacKee 37715* [MO]).

Syzygium tripetalum Guillaumin

Leaf morphology: Petioles 1.5–4 mm x 1.5–2 mm. Blades 2–6.5 x 1.2–2.8 cm, obovate; base cuneate; apex obtuse; margin revolute; adaxial midvein sulcate; abaxial midvein projecting prominently. Adaxial surface chartaceous to leathery, shiny. Oil glands indistinct or visible below.

Venation: Thicker secondary veins ca. 19–24 per side and mostly 1–3 mm apart, intersecondary veins present, usually one (sometimes more than one) per intercostal area. Intramarginal vein 0.8–1.3 mm from edge at midpoint of the blade. Outer intramarginal vein invisible. Divergence of secondary veins from midvein consistent, ca. 70–80 degrees. Areolas well developed, shape irregular, more or less variable in size. Ultimate veinlet in ultimate areolas with dendritic branching. Tertiary veins mixed. Marginal ultimate venation looped (Voucher: *McPherson 2548* [MO]).

Syzygium wagapense Brongniart & Gris

Leaf morphology: Petioles 5–10 mm x 1–2 mm. Blades 4–10 x 2–4.5 cm, ovate to lanceolate; base cuneate or rounded; apex acute or acuminate; margin involute slightly; adaxial midvein sulcate; abaxial midvein projecting prominently. Adaxial surface leathery, shiny. Oil glands indistinct or visible below.

Venation: Thicker secondary veins ca. 13–16 per side and mostly 1–3 mm apart, thinner intersecondary veins not prominent, usually less than one per intercostal area. Intramarginal vein 1.2–1.4 mm from edge at midpoint of the blade. Outer intramarginal vein visible, 0.3–0.5 mm from edge at midpoint of the blade. Divergence angle of secondary veins from midvein consistent, ca. 70–80 degrees. Areolas well developed, shape irregular, more or less variable in size. Ultimate veinlet in ultimate areolas with dendritic branching. Tertiary veins reticulate or mixed. Marginal ultimate venation looped (Voucher: *McPherson 5588* [MO]).

Syzygium jaffrei J.W. Dawson

Leaf morphology: Petioles ca. 2 mm x 1 mm. Blades 3.5–6.5 x 2–3 cm, ovate to lanceolate; base cordate; apex acuminate; margin strongly wavy or revolute; adaxial midvein sulcate; abaxial midvein projecting prominently. Both sides shiny. Oil glands indistinct or sometimes visible.

Venation: Thicker secondary veins ca. 14–18 per side and mostly 2–6 mm apart, thinner intersecondary veins not prominent, usually less than one per intercostal area. Intramarginal vein 2.2–2.5 mm from edge at midpoint of the blade. Outer intramarginal vein invisible. Divergence angle of secondary veins from midvein not consistent, ca. 70 degrees near apex to ca. 90 at base. Areolas moderately developed, shape irregular, more or less variable in size. Ultimate veinlet in ultimate areolas with dendritic branching. Tertiary veins ramified. Marginal ultimate venation looped (Voucher: *Munz 4184* [MO]).

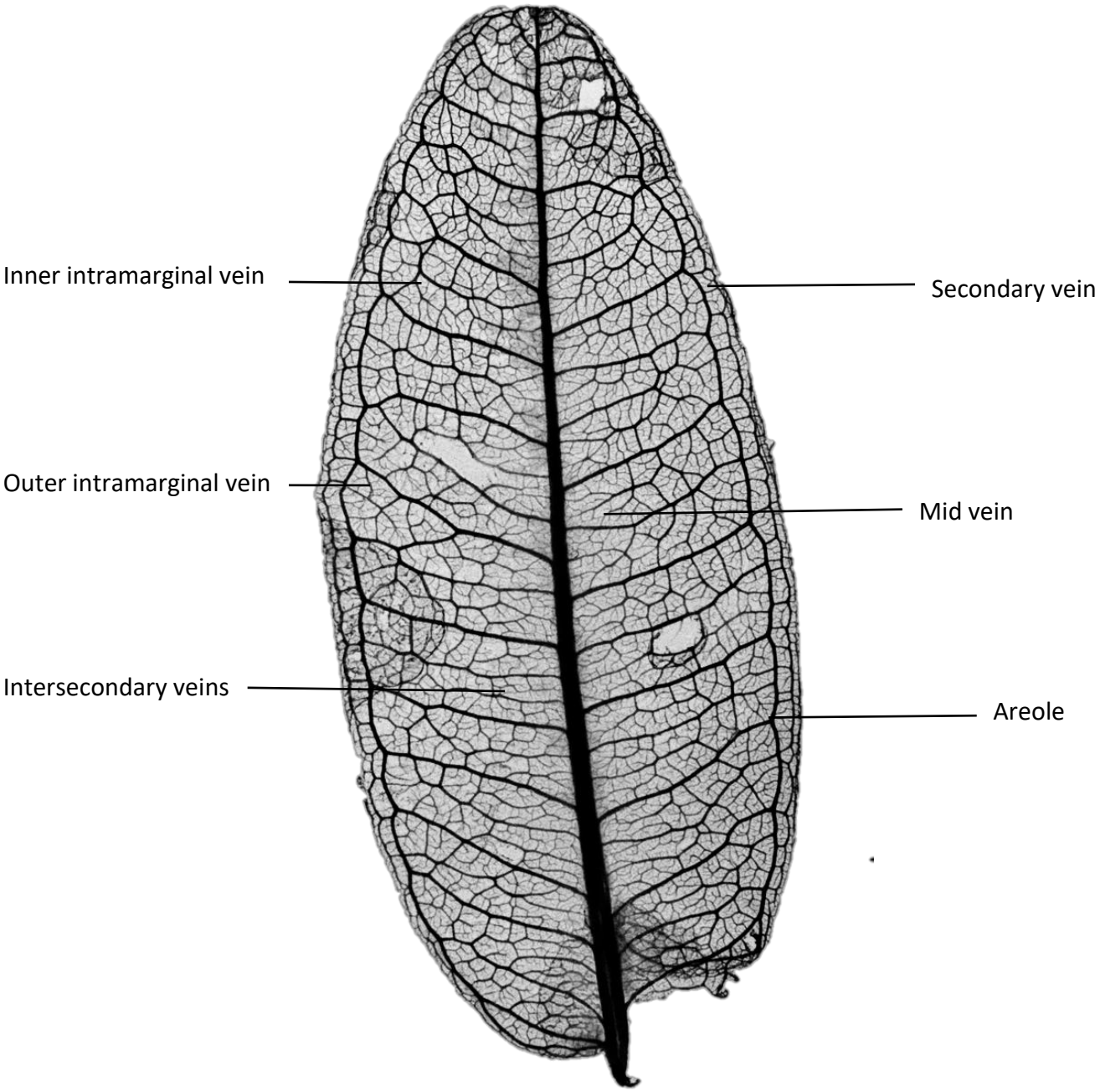
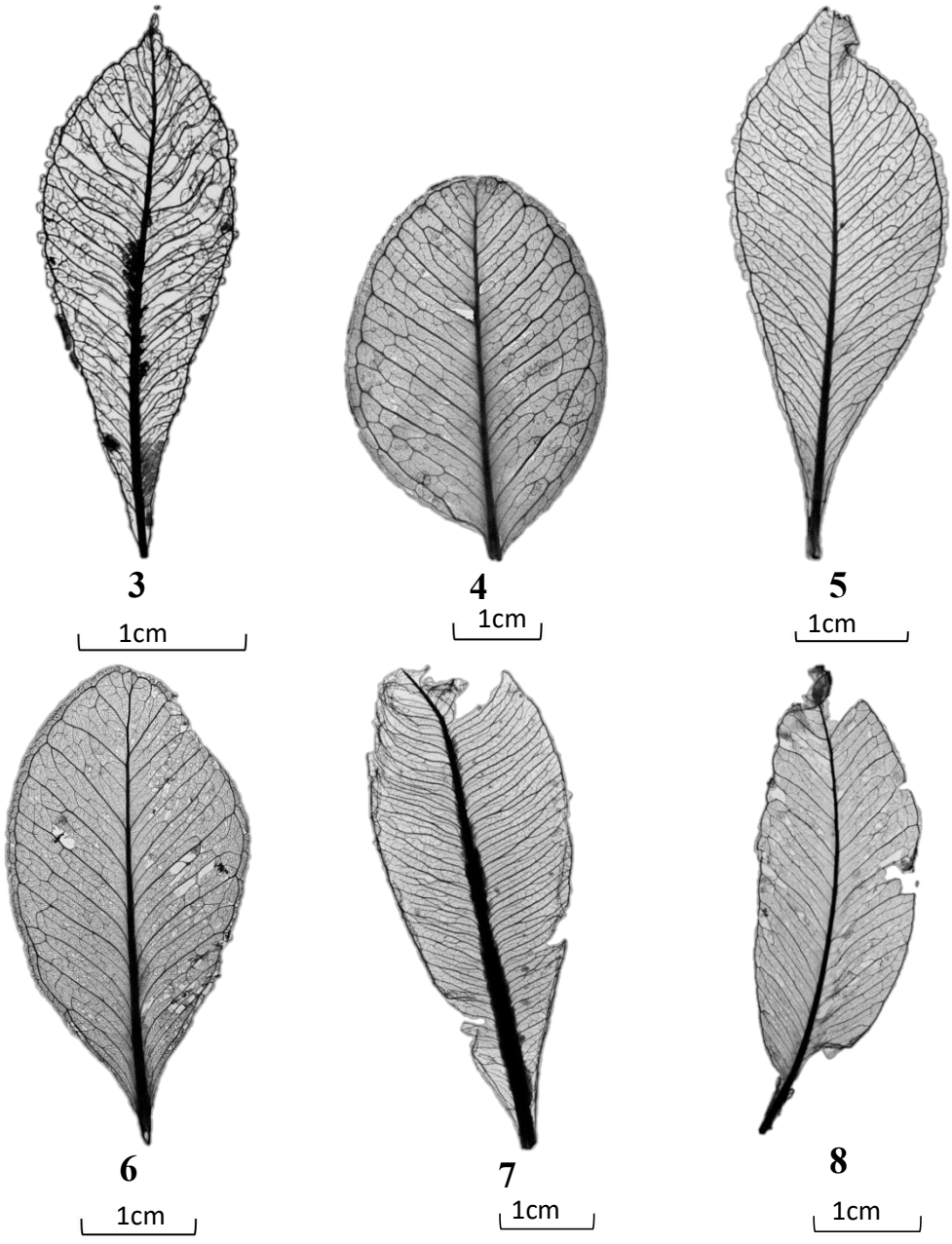
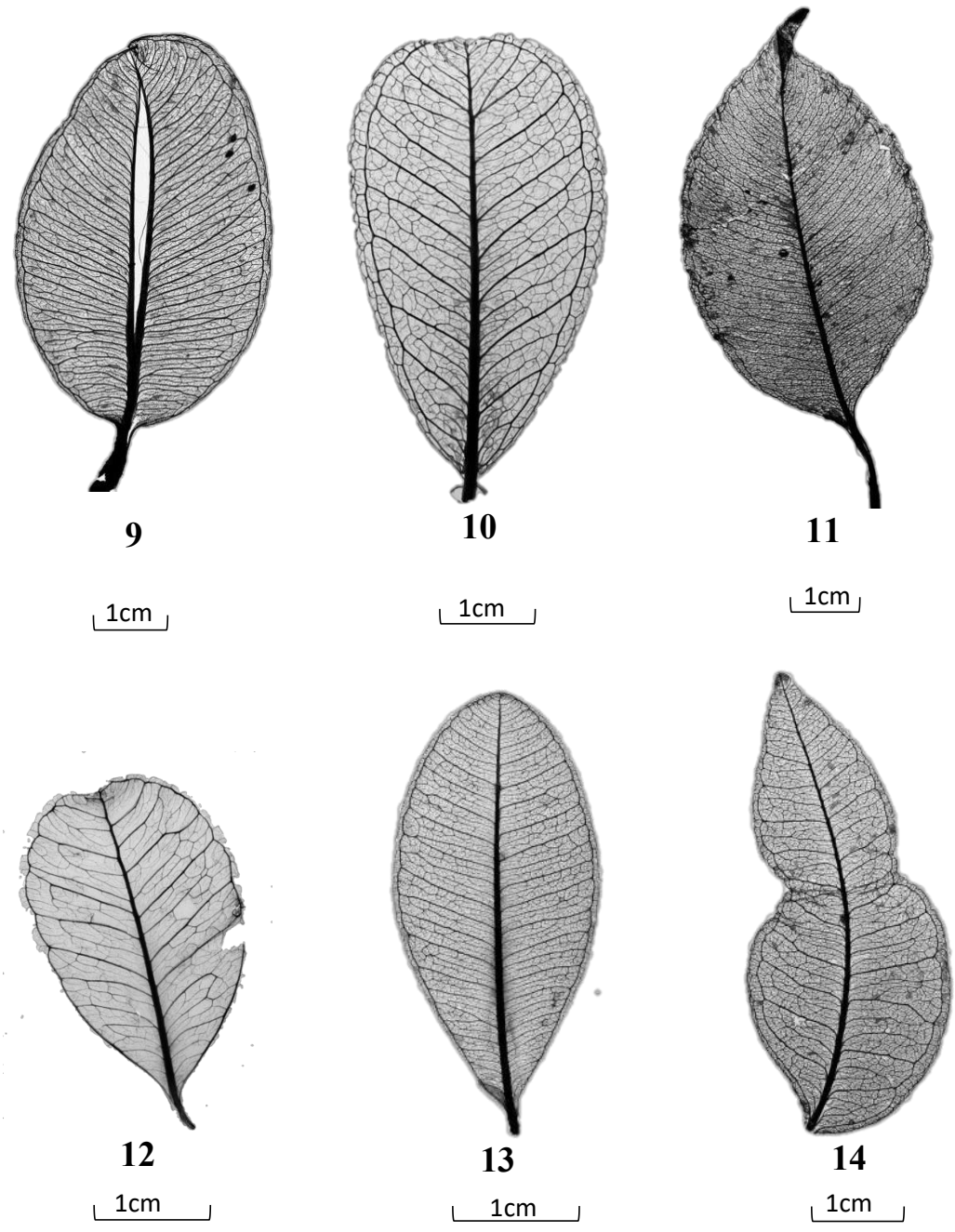


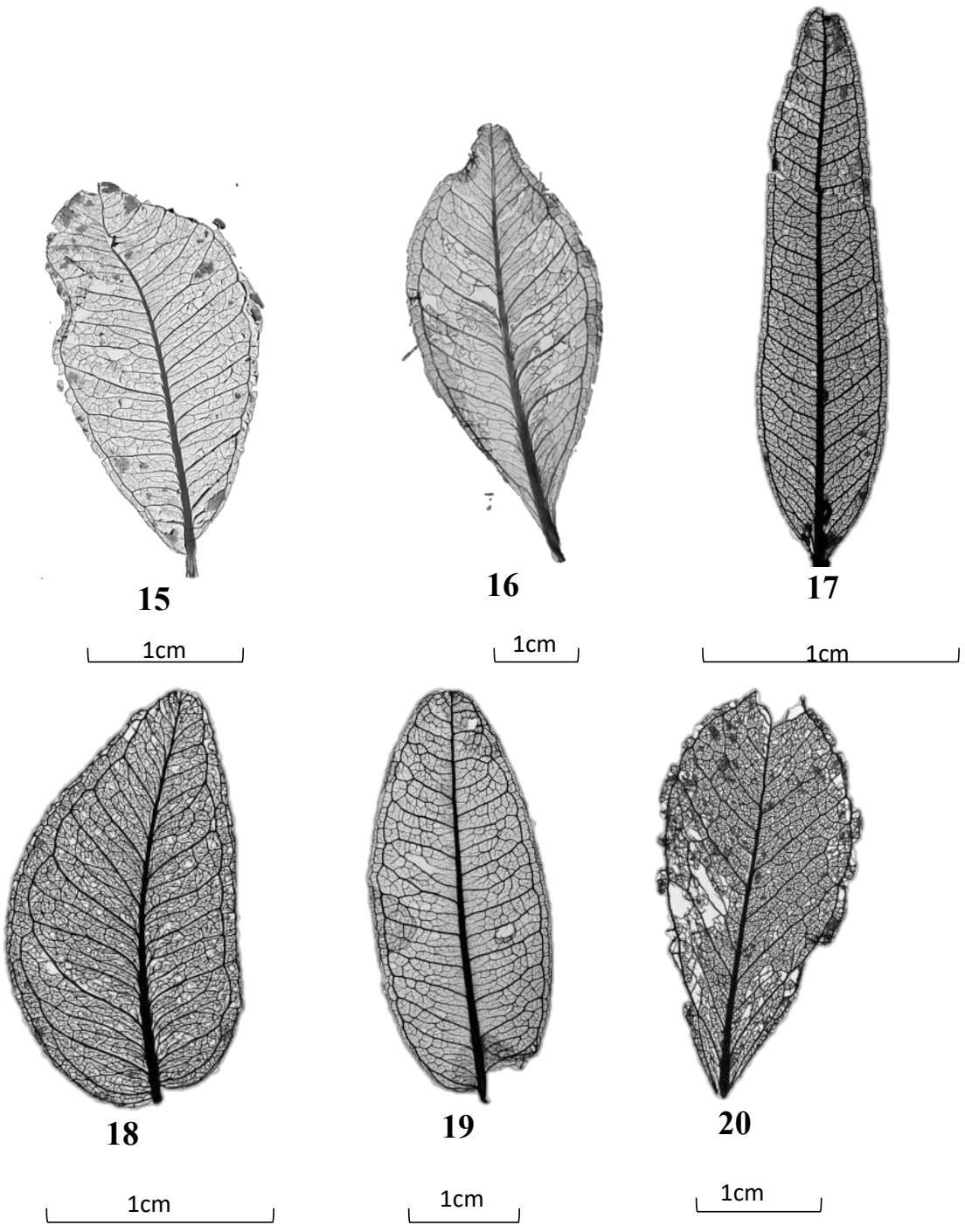
Figure 2. Leaf architectural characters illustration. Species: *Syzygium wagapense* (Voucher: *McPherson 5588* [MO]).



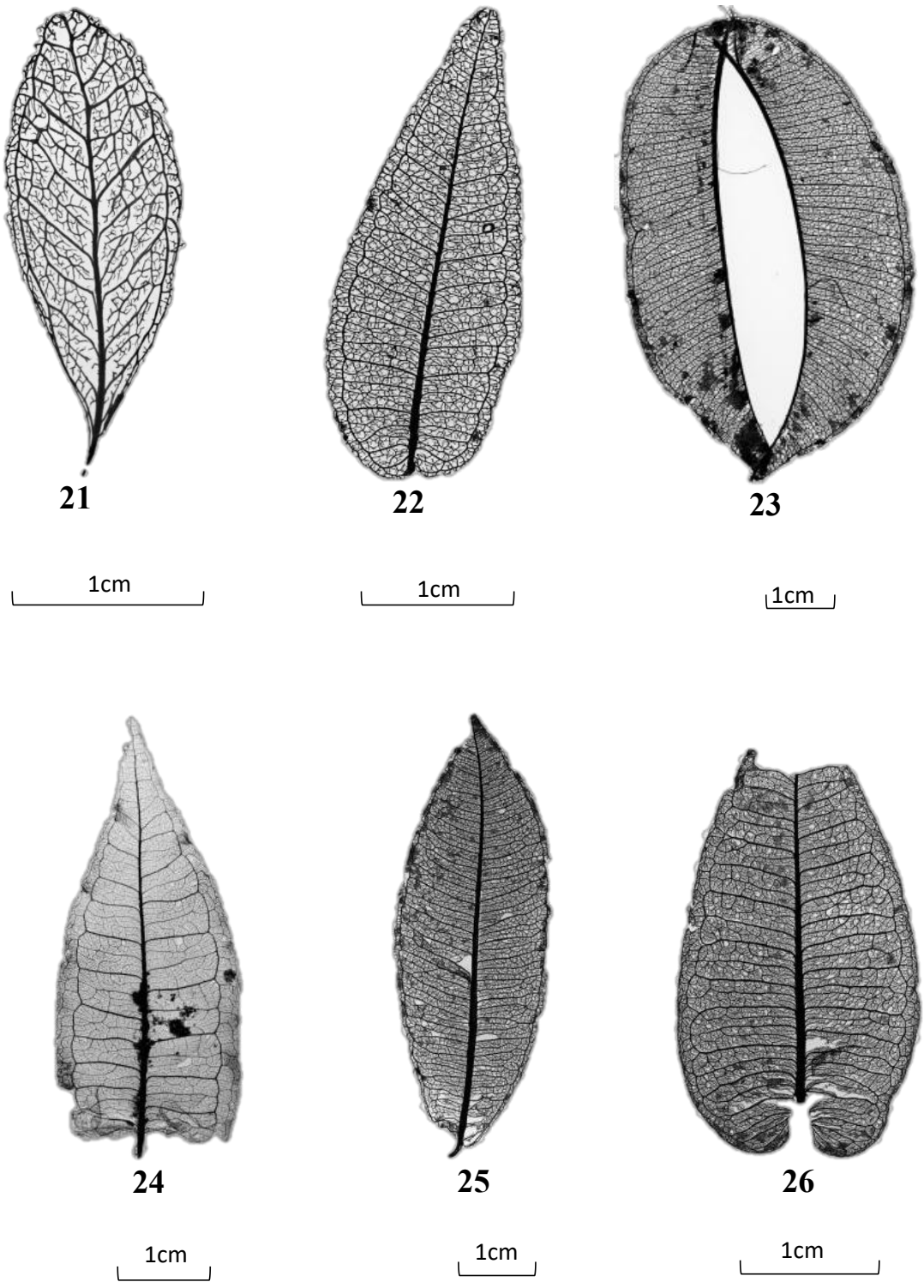
Figures 3-29. Leaf venation in *Syzygium.* 3. *S. micans*. 4. *S. arboreum*. 5. *S. austrocaledonicum*. 6. *S. brongniartii*. 7. *S. kriegeri*. 8. *S. kuebiniense* (For vouchers, see above).



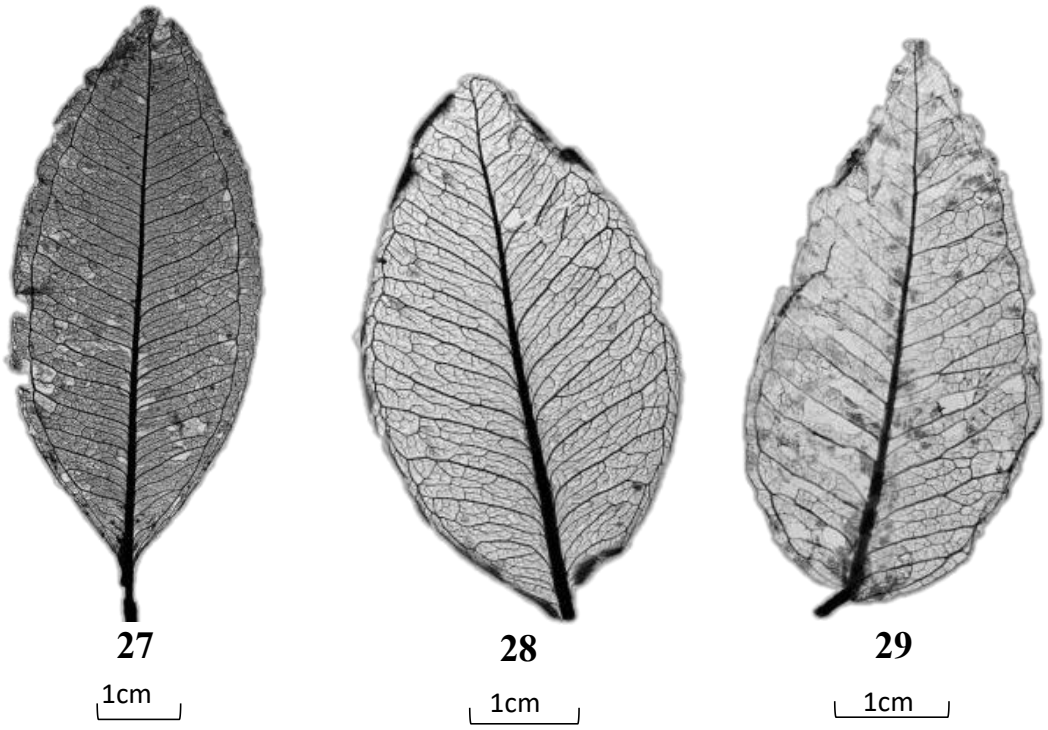
Figures 9-14. 9. *S.macranthum.* 10. *S.mouanum.* 11. *S.neocaledonicum*. 12. *S.ngoyense.* 13. *S.tripetalum.* 14. *S.poyanum* (For vouchers, see above).



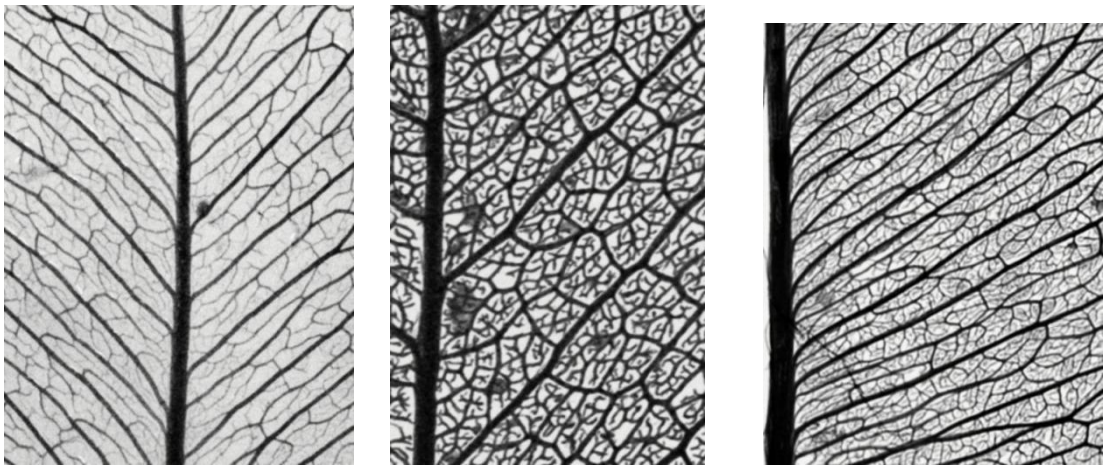
Figures 15-20. 15. *S.rivulare.* 16. *S.schistaceum.* 17. *S.schlechterianum.* 18. *S.tenuiflorum.* 19. *S.wagapense.* 20. *S.balansae* (For vouchers, see above).



Figures 21-26. 21. *S. boulindaense.* 22. *S. capillaceum.* 23. *S. densiflorum.* 24. *S. jaffrei.* 25. *S. lateriflorum.* 26. *S. lecardii* (For vouchers, see above).



Figures 27-29. 27. *S. meorianum*. 28. *S. pancheri.* 29. *S. propinquum* (For vouchers, see above).



Ramified

S. austrocaledonicum

(Voucher: *McPherson 17785*[MO])

Reticulate

S. balansae

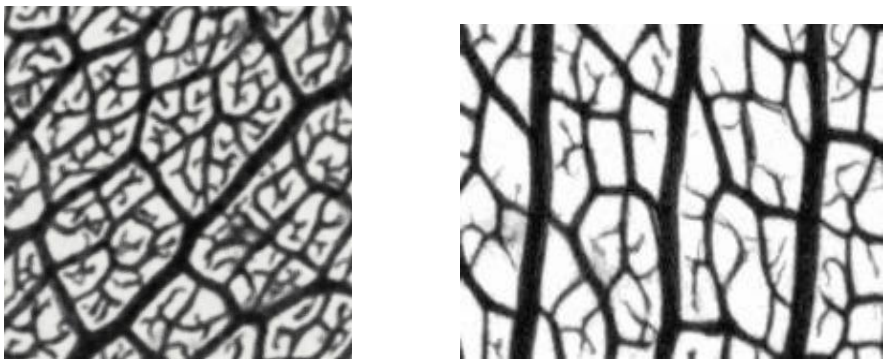
(Voucher: *MacKee 20697* [MO])

Mixed

S. macranthum

(Voucher: *McPherson 4653* [MO])

Figure 30. Three types of Teritiary venation. Left: Ramified venation. Center: Reticulate ventation. Right: Mixed venation.



S. balansae

(Voucher: *MacKee 20697* [MO])

S. densiflorum

(Voucher: *McPherson 1688* [MO])

Figure 31. Two types of areolas. Left: dendritic branching. Right: 1-3 branched.

3.2 Cluster analysis

Cluster analysis classified the samples into three large clusters.

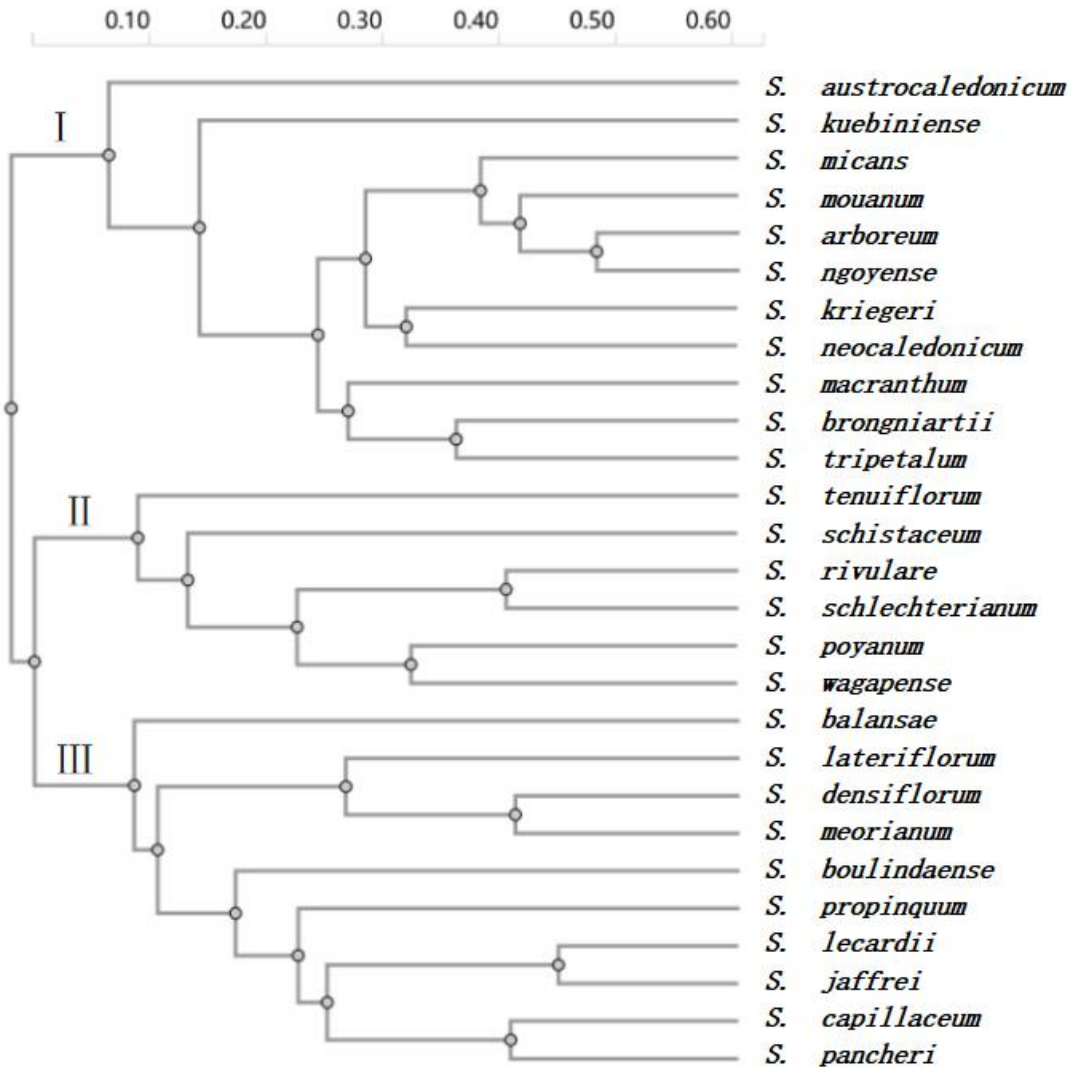


Figure 32. UPGMA dendrogram of selected species of New Caledonian *Syzygium* based on leaf architectural characters. The scale of overall similarity is above the dendogram.

Table 3. Cluster groups based primarily on variations of leaf apex and leaf margin.

Taxon	Leaf apex	Leaf margin
Cluster I		
S. micans	acuminate	revolute
S. arboreum	obtuse	revolute
S. austrocaledonicum	acuminate	involute
S. brongniartii	obtuse	involute
S. kriegeri	obtuse	revolute
S. kuebiniense	obtuse	revolute
S. macranthum	obtuse	revolute
S. mouanum	obtuse	revolute
S. neocaledonicum	acuminate	revolute
S. ngoyense	obtuse	revolute
S. tripetalum	obtuse	revolute
Cluster II		
S. poyanum	acute	flat
S. rivulare	acuminate	flat
S. schistacem	acuminate	flat
S. schlechterianum	acute	involute
S. tenuiflorum	acute	flat
S. wagapense	acute	involute
Cluster III		
S. balansae	acute	revolute
S. boulindaense	acute	revolute
S. capillaceum	acute	revolute
S. densiflorum	acuminate	revolute
S. jaffrei	acuminate	revolute
S. lateriflorum	acute	involute
S. lecardii	acute	revolute
S. meorianum	acute	revolute
S. pancheri	acute	revolute
S. propinquum	acute	revolute

Chapter IV

Discussion

4.1 Comparion with Klucking's Results

Klucking (1988) summarized his results for Myrtaceae and *Syzygium* separately with dichotomous keys to groups of species based on leaf venation characters. He arranged the species of *Syzygium* into five groups based in large measure on the nature of the secondary venation (Klucking 1988). However, although his dichotomous key to the five groups contained long narrative descriptions of traits, the groups he recognized are vague. The differences between groups are subtle, and he did not use quantitative characters to distinguish the groups. As such, his overly descriptive statements ultimately are of limited use to compare with the results of the present study.

Klucking (1988) placed *Syzygium lateriflorum*, *S. macranthum*, *S. ngoyense*, *S. pancheri*, and *S. densiflorum* in his Group 3 and *S. wagapense* in his Group 4 based on the number of acrodromal veins. His species in Group 3 have one pair of acrodromal veins, whereas species in Group 4 have two pairs of acrodromal veins, which are similar to the results of this study. However, he interpreted the intramaginal veins as acrodromal veins, which most people do not (e.g., Wilson 2011). In other words, *Syzygium wagapense* is the only one among the New Caledonian species in his research that has two intramarginal veins, which nearly all researchers in Myrtaceae now refer to as inner-

intramarginal and outer intramarginal veins. The other five species he studied only have one intramaginal vein.

Furthermore, he divided the Group 3 into twenty-three subgroups, with *Syzygium lateriflorum*, *S. macranthum* in the first subgroup, *S. ngoyense*, *S. pancheri* in the twentieth subgroup, and *S. densiflorum* in the eleventh subgroup. The main difference between the first and the twientieth subgroups were the secondary veins of the same thickness as the intersecondary veins for the first subgroup, but secondary veins were recurved at the connection with the midvein for the twentieth subgroup. This reflects the results of the present study as well: the intersecondary veins of *S. ngoyense* and *S. pancheri* are thinner than the secondary veins, and also are recurved as they connect to the midvein. The difference of thickness of the intersecondary veins and secondary veins in *S. lateriflorum* and *S. macranthum* is minimal. In the eleventh subgroup the angle between the secondary and main veins is smaller than that of the other two subgroups. However, Klucking (1988) did not clearly distinguish between his recognition of small, moderate, and large, so his distinctions cannot be standardized and easily applied here.

My results show that the divergence of secondary veins from midvein of *Syzygium macranthum* is more acute than the other five species, which does not align with what Klucking (1988) indicated. In addition, my results show that the divergence of secondary veins from midveins is relatively consistent in *Syzygium meorianum*, *S. austrocaledonicum*, and *S. boulindaense.* In contrast, in *Syzygium balansae* the divergence angle in the distal portion of leaves is more acute than the angle in the proximal portion. *Syzygium brongniartii* and *S. austrocaledonicum* are the only two species studied here in which that marginal ultimate venation is irregular or invisible, a

character which can be of taxonomic value to distinguish among sterile (neither flowering nor fruiting) specimens of *Syzygium*.

The concentration of reagents used for this study differed for different species. A large number of preliminary clearings using variations of reagents and heating were required to determine the optimal concentration and time required. The quality and longevity of the leaves also were factors that affected the quality of the leaf clearing process. The general methods used in this project were mostly devised 45-70 years ago. Some of the leaf clearings were imperfect, but despite hundreds examined, Klucking (1988) also was unable to clear some leaves cleanly and consistently.

4.2 Cluster analysis

The two characters that seem to best separate the sampled species into three phenetic clusters were those of the leaf apex shape and leaf margin (Table 3). Fig. 32 shows that the Branch II contained the fewest sampled species. The characters that mostly support that group were an acute or acuminate leaf apex, whereas the primary character supporting of Branch I, the largest group, was (mostly) an obtuse leaf apex. The primary supporting character of leaf apex also supports Branch III, which includes a number of species intermediate between the other groups. However, each Branch has some species with an acuminate leaf tip.

Leaf margin traits also contributed to the clustering of the three Branches. In Branch II, most species had flat leaf margins, whereas a few had involute margins. In Branch III, the flat margins were not present, but the revolute trait was dominant, with fewer species showing involute margins.

The tertiary venation showed clustering similar to leaf apex and leaf margin. In Branch II the tertiary veins were dominated by reticulate and mixed character traits, whereas Branch III included some species with ramified venation. Branch I lacked reticulate venation but many species with ramified branch tips.

4.3 The taxonomic value of the leaf architecture in *Syzygium*

The phylogenetic study of Soh and Parnell (2011) of *Syzygium* focused on cross-sectional anatomy, not venation patterns of cleared leaves. In contrast, the present study focuses on leaf architectural characters of *Syzygium* in New Caledonia. The results here indicate that leaf architecture characters sometimes provide sufficient features to identify sterile specimens. In addition, the characters can potentially be useful taxonomically when combined with other sources of data.

In this survey, the leaf venation patterns of *Syzygium* species were relatively consistent. One character that showed no variation among the sampled New Caledonian species of *Syzygium* was brochidodromous venation, so this character is of no evident taxonomic value among the sampled species of *Syzygium.* Most species have brochidodromous venation with reticulate tertiary venation. The areoles (enclosed areas by tertiary venation) differ in size and are of irregular shapes; the marginal ultimate venation is looped. Differences occur in the areole size; the intramarginal vein; the number of secondary veins; the angle between secondary veins and primary vein; the distance between secondary veins; the presence of inner secondary veins and how they ramify; the presence of intramarginal vein; and the branching conditions of ultimate veinlet. Therefore, distinct differences of venation occur at the species level, which suggests possible value of venation characters for classification.

Further study of leaf venation patterns will be of value for future research of *Syzygium* due to the vastness of the genus and its poorly-studied situation.

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