

---

# 16 Matters of Scale: Dealing with One of the Largest Genera of Angiosperms

*J. A. N. Parnell*

Department of Botany, School of Natural Sciences,  
Trinity College Dublin, Ireland

*L. A. Craven*

Australian National Herbarium, Centre for Plant Biodiversity Research,  
CSIRO Plant Industry, Canberra, Australia

*E. Biffin*

Division of Botany and Zoology, Australian National University,  
Canberra, Australia

## CONTENTS

16.1	Introduction .....	252
16.1.1	Introduction to the Myrtaceae and <i>Syzygium</i> .....	252
16.1.2	<i>Syzygium</i> : Derivation and Matters of Size .....	253
16.1.3	<i>Syzygium</i> : Ecology, Distribution and Other General Information .....	255
16.1.4	<i>Syzygium</i> : Taxonomy and Differential Morphological Characteristics .....	256
16.2	Taxonomic History .....	256
16.2.1	Nineteenth Century .....	256
16.2.2	Twentieth Century .....	260
16.3	Current Research .....	261
16.3.1	Morphological, Developmental and Chemical Studies .....	261
16.3.2	Molecular Sequence Studies .....	262
16.3.3	Floristic Studies .....	265
16.3.4	Breeding Biology .....	266
16.4	Future Prospects .....	267
	Acknowledgements .....	270
	References .....	270

## ABSTRACT

*Syzygium*, with about 1,200 species, is one of the largest generic groupings of Myrtaceae. Conventionally, it is considered to be taxonomically difficult due to its previous confusion with another large genus of the family (*Eugenia*), the seeming lack of 'good' diagnostic characters, and the uncertainty as to the delimitation of genera within the *Syzygium* complex per se. Current divergent taxonomic approaches are discussed, and the taxonomic history of *Syzygium* is summarised.

Present research includes floristic and reproductive biological studies, and active studies into morphological, anatomical and molecular aspects are in progress. The structural, ecological and biological diversity of the group, together with its economic and biodiversity significance, point to *Syzygium* being a challenging but rewarding subject for future research.

## 16.1 INTRODUCTION

This chapter aims to bring together past and present taxonomic and systematic research on the very large and taxonomically perplexing angiosperm genus *Syzygium* Gaertner (Myrtaceae) and to outline and stimulate further work; therefore, it is both retrospective and prospective. We show that *Syzygium* poses many problems, including its delimitation as a genus, documentation of its species and understanding of many aspects of its biology. Nevertheless, we suggest that ongoing floristic and phylogenetic studies have the potential to significantly improve our current understanding of the genus.

### 16.1.1 INTRODUCTION TO THE MYRTACEAE AND SYZYGIIUM

The Myrtaceae are a mostly Southern hemisphere family of moderate size, containing between 130 and 155 genera and 3,675 and 5,000 species<sup>1-7</sup>. Despite its modest size, the family poses a disproportionately large number of complex taxonomic problems evident at many levels in the taxonomic hierarchy, for example, concepts at and above species level within *Eucalyptus* L'Hér.<sup>8</sup> and within *Syzygium*<sup>9-12</sup>, or the separation of *Syzygium* from *Eugenia* L.<sup>13</sup>. McVaugh<sup>14</sup> described the species of American Myrtaceae as "distressingly alike in aspect and in most individual characters, making identification and classification of both genera and species a correspondingly difficult and tedious matter". It is evident that species of South East Asian *Syzygium* fall into this category and are not generally clear and easy to distinguish, but Craven<sup>9</sup> suggests that Australian-Papuan and New Caledonian species are.

Within the Myrtaceae two unequally sized subfamilies were recognised by Niedenzu<sup>15</sup>: the Leptospermoideae and Myrtoideae. The Myrtoideae contain only 60 genera<sup>16</sup> but approximately two thirds (2,375-3,400) of the species known in the family<sup>6</sup>. These species occur in the New and Old World tropics, are mainly shrubs or trees of wet forests, usually have an inferior ovary and almost always possess opposite broad leaves and a fleshy indehiscent fruit. Niedenzu's<sup>15</sup> subfamilial divisions are convenient and still used<sup>16,17</sup>. However, several recent studies indicate that Niedenzu's classification<sup>15</sup> is unsatisfactory<sup>6,13,18,19</sup>. Johnson and Briggs developed an informal system of alliances and suballiances through cladistic analysis of a fairly large and comprehensive data set<sup>18,19</sup>. They concluded that Niedenzu's division<sup>15</sup> of the family on the basis of fruit characteristics was not phylogenetically supportable, as their alliances and suballiances crossed traditional subfamilial boundaries.

Wilson et al.<sup>20</sup>, based on *matK* sequence data but with a strong morphological and anatomical background, have proposed a classification containing two subfamilies and 17 tribes. They showed that *Syzygium* together with *Acmena* DC., *Acmenosperma* Kausel, *Anetholea* Peter G. Wilson and *Waterhousea* B. Hyland form a tribe (the Syzygieae Peter G. Wilson), with *Eugenia* L. in a separate tribe (the Myrteae DC.) along with a large number of other genera including *Myrtus* L., *Psidium* L., *Rhodamnia* Jack and *Rhodomyrtus* (DC.) Reich. This result reinforces the work of Johnson and Briggs<sup>19</sup> and Johnson et al.<sup>2</sup>. These latter workers discussed the two alliances of particular concern in this chapter, the *Acmena* and Myrtoideae s.s. alliances<sup>19</sup>, or more specifically, the *Acmena* and *Eugenia* alliances<sup>2</sup>. Traditionally these alliances were placed near one another in the fleshy fruited Myrtoideae, but they are far apart phylogenetically. Indeed, they could scarcely be much further apart in Johnson and Briggs's cladogram<sup>19</sup>, wherein the *Eugenia* alliance is in a clade which incorporates the *Leptospermum* alliance, whilst the *Acmena* alliance forms an altogether separate clade with, amongst others, the *Eucalyptus* alliance. However, in a later compromise classification both alliances are placed together in the subfamily

Myrtoideae<sup>2</sup>, now defined by Wilson et al.<sup>20</sup> to encompass more or less the entire Myrtaceae as previously recognised.

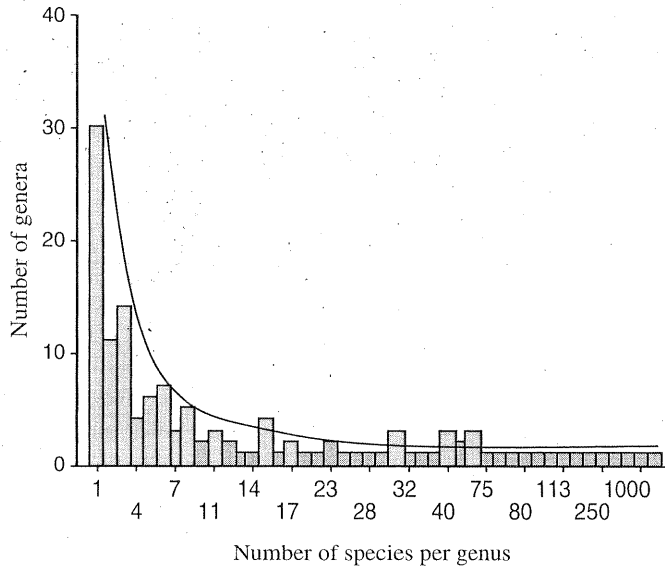
*Syzygium* and *Eugenia* are two of the most taxonomically confused genera in the Myrtaceae, and there are many other genera that have, at one time or another, been cleaved off from them or been reunited with them. Schmid<sup>13</sup> pointed out that there were about 35 generic names which have been or could be reduced to *Syzygium s.l.* and at least another 30 assignable to *Eugenia s.l.* Since Schmid's publication the number of segregates has increased with, for example, the description of *Waterhousea* B. Hyland and *Monimiastrum* A.J. Scott. In addition, several species have been placed within *Syzygium* on the basis that accurate subdivision or description of segregate genera is currently not possible (such as Craven<sup>9</sup>). Together, these genera form a 'vast array of more or less closely allied species' (Ashton<sup>21</sup>). This 'array', dominated by *Eugenia* and *Syzygium*, is very large. The standard printed work, *Index Kewensis*, has over 3,000 species listed under *Eugenia* and over 1,000 under *Syzygium*. Undoubtedly, this does not reflect the true balance in numbers of species between these genera when they are considered in the strict sense, as even now many authors prefer, because of historical precedent and because of the enormous number of consequent nomenclatural changes, to ignore the differences between them.

Schmid<sup>13</sup> provides a review of the status of *Syzygium s.l.* and makes clear why *Eugenia* and *Syzygium* were confused. Schmid's work summarises many of the relevant references and arguments, and is therefore not repeated here in detail. Essentially, Schmid showed that *Eugenia* and *Syzygium* were not closely related, differing most evidently in respect of the substitution of the transeptal vascular supply to the ovule of *Eugenia* with an axile one in *Syzygium*. Kochummen<sup>3</sup>, Kostermans<sup>22</sup> and others have criticised this work on the basis that very few species were studied; however, as contrary data have not been forthcoming, we accept Schmid's conclusions.

### 16.1.2 SYZYGIUM: DERIVATION AND MATTERS OF SIZE

*Syzygium* has long proved taxonomically difficult ever since its initial establishment with four species. Even the derivation of the name is unclear; the *Oxford English Dictionary*<sup>23</sup> indicates that the word *Syzygium* is most likely derived from the late Latin *syzygia* and hence from Greek (taken from *syn.* = together and *zygon* = yoke). In the case of the genus *Syzygium* this may indicate a reference to the paired arrangement of the leaves; however, this is not certain.

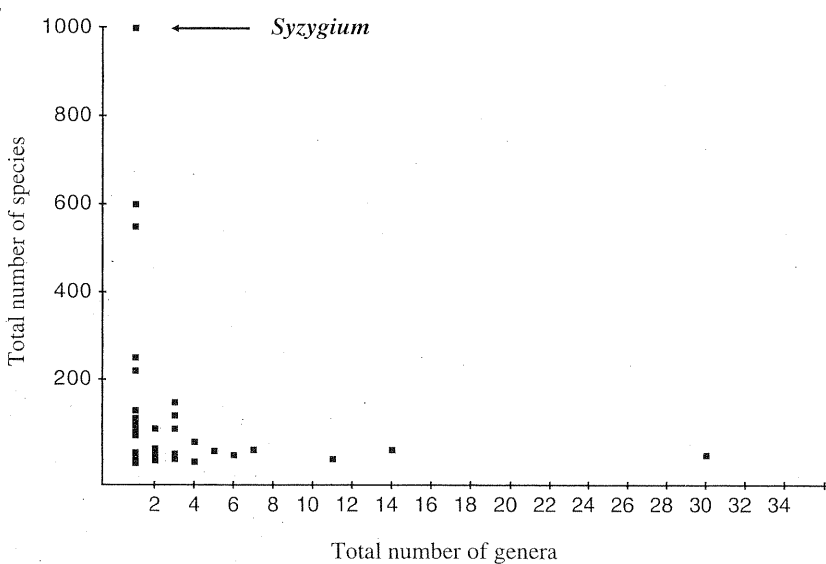
Some idea of the size of *Syzygium* relative to other members of the family in terms of numbers of species can be obtained from Figure 16.1 and Figure 16.2. Figure 16.1 shows that the Myrtaceae contains a large number of genera with very few species and very few genera with many species. This is typical of the 'hollow curve structure' discussed by Willis<sup>24</sup>, Minelli<sup>25</sup> and many others (see Hilu, *Chapter 11*) and which may, for obscure reasons, fit a fractal pattern<sup>26</sup>. Figure 16.2 shows that by far the largest genus in the Myrtaceae is *Syzygium*. As pointed out by Minelli<sup>25</sup> and Frodin<sup>27</sup>, *Syzygium* is clearly one of the very large genera of vascular plants. Frodin, utilising an estimate of 1,041 *Syzygium* species, places *Syzygium* sixteenth in his list of the 57 largest genera of flowering plants. However, estimating the number of species of *Syzygium* is difficult. The most up-to-date source, the International Plant Names Index (IPNI) (<http://www.ipni.org/index.html>), lists 1,507 specific epithets under *Syzygium*. To this current list of names must be added an estimate for those as yet undiscovered and, obviously, unnamed species. Work in Thailand<sup>28</sup> has shown that previously undescribed species form at least 6–7% of the total species number for that country, and work in Malaya<sup>3,29</sup> suggests that c. 33% of *Syzygium* species in that Flora may be unnamed. In addition, many validly described species await transfer to *Syzygium*. For example, based on Chantaranothai and Parnell<sup>28,30</sup>, up to 90% of specific epithets in *Syzygium* are derived from transfers from other genera. However, as a counter to these trends, which act to increase the number of available epithets, a large proportion (maybe as much as 90%) of the currently available species epithets under *Syzygium* are likely to be synonyms of other species within *Syzygium*. On the basis of these arguments, it appears that the reduction in the number of valid epithets due to synonymy may be



**FIGURE 16.1** Histogram and hand fitted trend line showing a plot of the number of genera against the number of species within each genus for the Myrtaceae.

balanced by the combination of the number of new species awaiting description and transfers into *Syzygium* of valid species wrongly placed in other genera. Conservatively, therefore, we estimate that the total number of species of *Syzygium* is likely to be more than 1,000 but less than 1,500. On this basis, *Syzygium* may be positioned higher up Frodin's<sup>27</sup> table than currently, possibly even within the top 10 largest plant genera in the world.

In summary of this section, *Syzygium* is an extremely large genus wherein many species await description.



**FIGURE 16.2** Frequency diagram of the total number of genera containing a certain number of species for the Myrtaceae.

### 16.1.3 *SYZYGium*: ECOLOGY, DISTRIBUTION AND OTHER GENERAL INFORMATION

*Syzygium* is an Old World genus with most species found in southern and South East Asia, Australia, Southern China, Malesia and New Caledonia. Fewer species occur in Africa, Malagasy, the Mascarenes and the remainder of the South Western Pacific islands, and there is one indigenous species each in Hawaii and New Zealand. Mostly, the species are found in rainforests, but they occur in nearly all vegetation types, from littoral communities at sea level through swamp, dry deciduous, bamboo, peat swamp, lowland, evergreen and montane forests, up to subalpine shrubberies. They also occur in open grassy savannah, gallery forest and heathland. Few species appear highly specialised in terms of their ecological requirements, but exceptions do occur with the rheophytic species and those species that occur obligately on ultramafic substrates. Gamage et al.<sup>31</sup> suggested that forest disturbance and hydrology were important environmental factors influencing the distribution of *Syzygium* in Sri Lanka and that leaf physiology and structure were related to each other and to shade tolerance and water use. Parnell<sup>12</sup>, using numerical methods, showed that Thai *Syzygium* could be divided into two morphologically definable groups: one widespread and lowland with larger, broader, longer petioled leaves with a wider midrib, secondary veins that are relatively close to each other, intramarginal veins relatively far from the margin, larger calyces, petals (and these have more gland dots), ovules and longer styles; the other, essentially only found above 1,000 m, containing many endemics and with the opposite suite of morphological characteristics. Whether this pattern is ecologically determined or not requires investigation.

Their habit ranges from canopy emergent trees to canopy trees, understorey trees, treelets, shrubs, rheophytes, and rarely even prostrate or semiscandent shrubs. Species mostly occur as scattered individuals but can be locally common. In rare cases, a species can be clonal, producing a patch of stems, but this may be restricted to savannah environments and be associated with frequent natural fires. Some species are widespread, such as *Syzygium grande* (Wight) Walpers which is relatively common throughout much of mainland South East Asia, and depending on how *Syzygium* is defined, *Cleistocalyx nervosum* (Roxb.) I.M. Turner (= *Cleistocalyx nervosus* (DC.) Kosterm. and *Syzygium nervosum* DC.) that occurs from southern and South East Asia-Southern China to Northern Australia, but there are many point endemics, for example *Syzygium kerrii* P. Chantaranothai and J. Parn.

Relatively little is known of the importance of *Syzygium* to other organisms, but it is highly likely the genus as a whole has high ecosystem significance. The often massed nectariferous flowers and typically fleshy fruit (Figure 16.4 and Figure 16.5) are food sources for a wide range of animals, from small insects through to large birds and primates. In one Thai study, 26% of hornbill nests located in 302 sample plots were in *Syzygium* (as *Eugenia*) trees, despite *Syzygium* representing only 3% of all large trees in these plots<sup>32</sup>.

A number of species are cultivated. One of the few that is economically important in world trade is *S. aromaticum* (L.) Merr. and L.M. Perry. It is the source of clove and clove oil and a vital component of the large Indonesian cigarette industry. In 2003, 59,328 tons of cloves were exported, these being worth US\$115,473,000<sup>33</sup>. Clove oil is one of the 20 most important essential oils in the world; one whose production value in 1993 was US\$7,000,000<sup>34</sup>. By contrast, although *S. polyanthum* (Wight) Walpers, the source of Indonesian bay leaf, is hugely important as a condiment in mainland South East Asia, it is scarcely traded on a world scale<sup>35</sup>. Several other species are of local commercial importance, being only sparsely traded. *Syzygium malaccense* (L.) Merr. and L.M. Perry (Malay apple) and *S. samarangense* (Blume) Merr. and L.M. Perry (Java apple), although very commonly cultivated as fruit trees in South East Asia, are almost unknown in world trade<sup>36</sup>. The potential for *S. aqueum* (Burm.f.) Alston (Jambu Air, water-, rose apple, etc.) to become a major crop is, however, considerable, as Taiwan market figures indicate<sup>37</sup>, and the commercial prospects for several other little known species, for example, *S. maraca* Craven and Biffin<sup>11</sup> or *S. rubrimolle* B. Hyland<sup>38</sup>, also appear good. Equally, medicinal prospects for species in the genus appear high. The bark of *S. jambos* (L.) Alston provides effective antimicrobial activity<sup>39</sup>, as have the essential oils of a number of other species<sup>40</sup>. For a genus with so many tree

species, *Syzygium* is not regarded as a major timber resource. Lemmens<sup>4</sup> indicates that only small amounts of the locally important timber Kelat (a South East Asian trade name that covers timber produced by a number of species of *Syzygium*) are exported. Eddowes<sup>41</sup> classed water gum (the Papua New Guinea trade name for *Syzygium* timber) as a major exportable hardwood, although it does not comprise a large proportion of the timber exported<sup>4</sup>.

To summarise this section, *Syzygium* is a widespread Old World genus of considerable ecological and economic importance and therefore, pragmatically, a predictive taxonomic classification will be of wide utility.

#### 16.1.4 *SYZYGIUM*: TAXONOMY AND DIFFERENTIAL MORPHOLOGICAL CHARACTERISTICS

Taxonomically important features of *Syzygium* at species level include leaf size and shape, venation, inflorescence position, flower shape and size and fruit colour and size (Figure 16.3 to 16.5).

Various characteristics have been used to distinguish species of *Syzygium*. For example, Ashton's key to *Syzygium* in Sri Lanka<sup>21</sup> makes extensive use of characters of the leaf, in particular its size and shape, the number of veins and the number of intramarginal veins, but makes almost no mention of floral characteristics. Kochummen<sup>3</sup> also makes almost no use whatsoever of floral characters, preferring instead features of the leaf (notably its shape, size and the number of veins). By contrast, Chantaranothai and Parnell working in Thailand<sup>28</sup>, Kostermans working in Sri Lanka<sup>22</sup>, Hartley and Perry working in Papuasias<sup>42</sup>, Craven and Matarczyk working in Australia<sup>43</sup> and Chen and Craven working in China<sup>44</sup>, make extensive use of floral characters. These characters include the shape of the hypanthial cup and pseudostipe, size of calyx lobes, number of gland dots on the corolla, number and size of the stamens and style, ovule and placentation features, as well as the number of intramarginal veins and the number of secondary veins and inflorescence position. Parnell's analysis of Thai *Syzygium*<sup>12</sup> demonstrated that many morphological features show overlap between species or groups of species and are therefore 'traits' (that is, features which may assume the value observed in either of the groups being investigated). However, there are some non-overlapping features (at least in terms of mean values) which do not, or cannot by definition, overlap and are not polymorphic and which can be termed 'characters'. Most authors working on *Syzygium* have failed to rigorously separate traits and characters. In mitigation, we note that Stevens<sup>45</sup> suggests that such separation may, for many features, be more subjective than absolute.

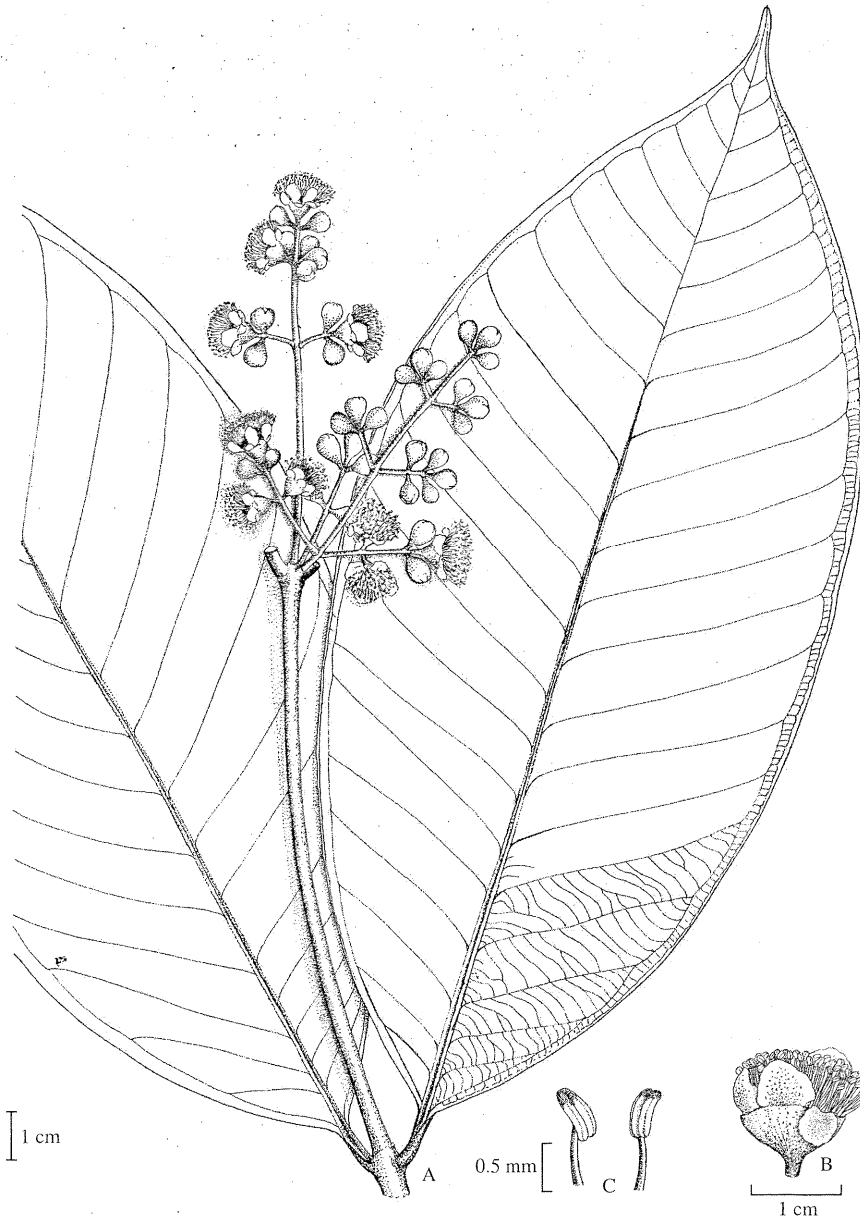
In summary of this section, both vegetative and floral features have been stressed by different authors as being taxonomically important in *Syzygium*. Such features are either traits or characters; rigorous investigation and definition of these features is awaited.

### 16.2 TAXONOMIC HISTORY

As might be expected with such a species rich and geographically widespread group, many authors have contributed to our taxonomic, morphological, anatomical and floristic understanding of *Syzygium s.l.* Its taxonomic history has been discussed by Schmid<sup>13</sup>, Parnell<sup>12</sup> and Craven<sup>9</sup>, and only the more significant publications are detailed in this section.

#### 16.2.1 NINETEENTH CENTURY

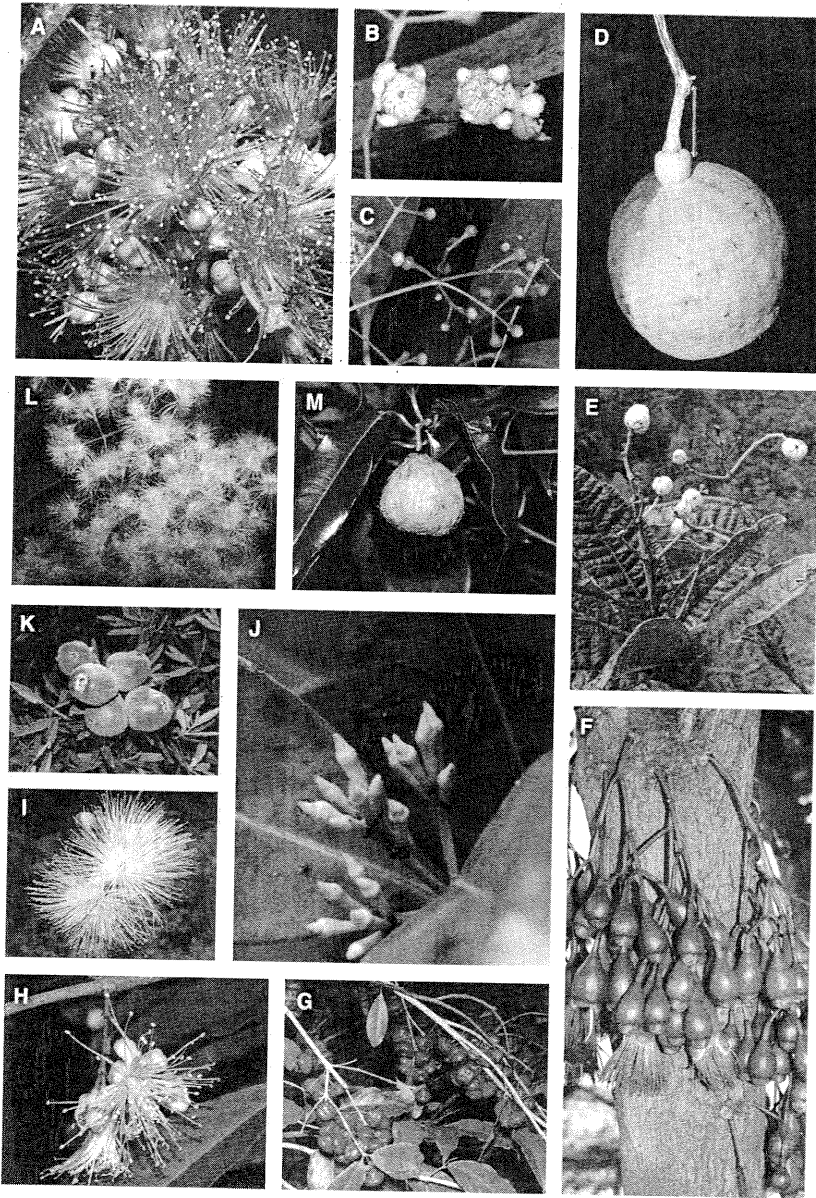
Some of the species later included in *Syzygium* were known to pre-Linnaean authors, and Linnaeus treated the species then known to him under *Caryophyllus* L., *Eugenia* and *Myrtus*<sup>46</sup>. Plant classifications in the eighteenth century were not always intended by their authors to reflect natural relationships, and it was not until the early nineteenth century that more natural systems were commonly adopted. This taxonomically higher-level work was stimulated by the need to accommodate the many unusual plants being discovered in Africa, the Americas, South and East Asia and



**FIGURE 16.3** Illustration of *Syzygium pergamentaceum* (King) P.Chantaranothai and J.Parn. Drawing shows (A) opposite leaves each with two intramarginal veins and inflorescence, (B) hypanthial cup, petals and gland dots on the petals and (C) stamens. (Reproduced from Chantaranothai and Parnell<sup>28</sup> with permission.)

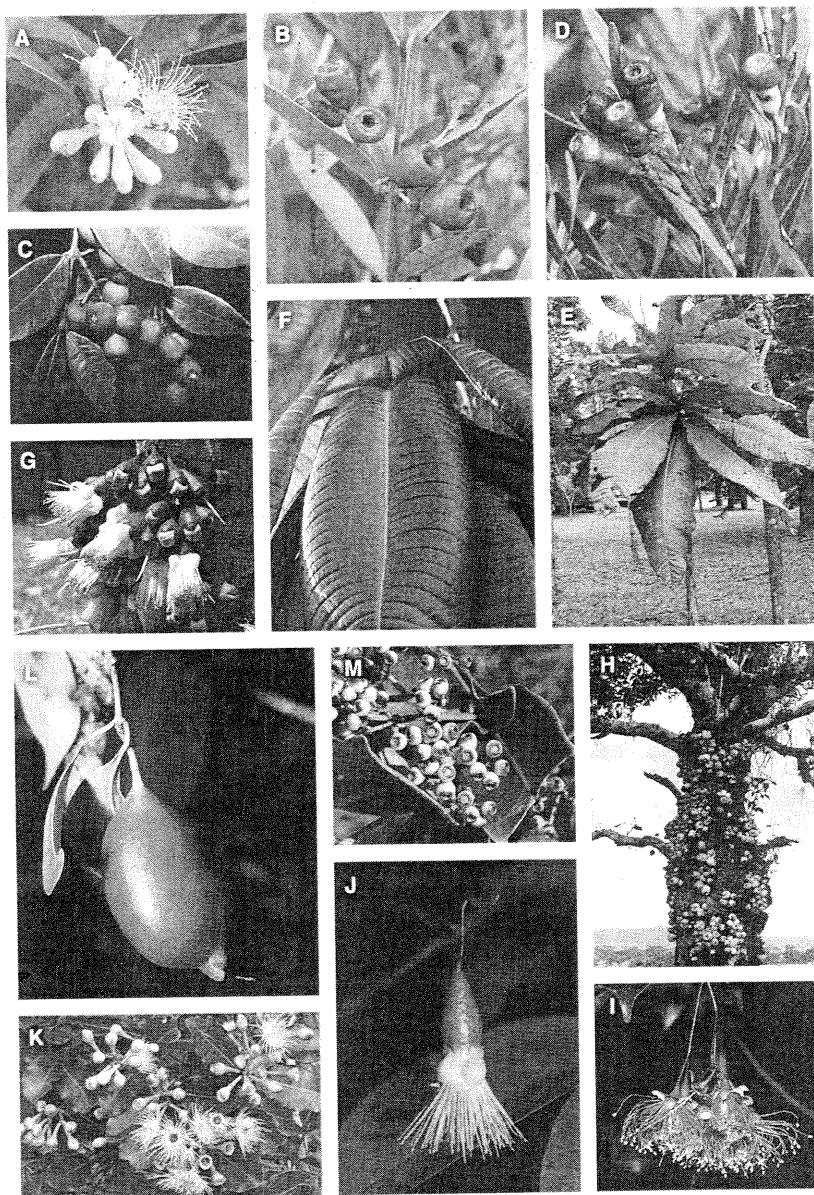
Australasia. For Myrtaceae, the work of De Candolle<sup>47</sup> stands out as the most comprehensive classification of the early nineteenth century. De Candolle<sup>47</sup> placed the fleshy fruited, one to few large seeded species in one of five genera: *Acmena*, *Caryophyllus*, *Eugenia*, *Jambosa* Adans. and *Syzygium*. The New World species were accommodated by De Candolle<sup>47</sup> in *Eugenia* and the Old World species classified in one of the remaining four genera.

Wight<sup>48</sup> proposed the merging of the five genera recognised by De Candolle<sup>47</sup> into one on the basis that the floral features demonstrated continuous variation, the internal structure of the flowers



**FIGURE 16.4** (A colour version of this figure follows page 240) Flowers and fruit of species of the *Syzygium* group. (A) Flowers of *Syzygium malaccense* (L.) Merr. and L.M. Perry; (B–D) flowers, inflorescence and fruit, respectively, of *Acmena* cf. *divaricata* Merr. and L.M. Perry; (E) fruit of *Piliocalyx bullatus* Brongn. and Gris; (F) buds and flowers of *Syzygium longifolium* (Brongn. and Gris) J.W. Dawson; (G–H) fruit and flowers, respectively, of *Syzygium aqueum* (Burm. f.) Alston; (I) flowers of *Syzygium jambos* (L.) Alston; (J) buds (note calyptras) of *Syzygium kuebiniense* J.W. Dawson; (K) fruit of *Syzygium rubrimolle* B. Hyland; (L–M) flowers and fruit, respectively, of *Syzygium glenum* Craven. (Reproduced with permission from G. Sankowsky (A–D, G, H, K–M), L. Craven. (F, I) and E. Biffin (J).)





**FIGURE 16.5** (A colour version of this figure follows page 240) Flowers, fruit and foliage of species of the *Syzygium* group. (A–B) buds and flowers, and fruit, respectively, of *Acmenosperma pringlei* B. Hyland; (C) *Syzygium wilsonii* subsp. *cryptophlebium* (F. Muell.) B. Hyland; (D) fruit of *Syzygium elegans* (Brongn. and Gris) J.W. Dawson; (E–G) habit, young leaves, and buds and flowers, respectively, of *Syzygium acre* (Pancher ex Guillaumin) J.W. Dawson; (H) fruit of *Syzygium cormiflorum* (F. Muell.) B. Hyland; (I) flowers of *Syzygium boonjee* B. Hyland; (J) flower of *Syzygium* sp.; (K) flowers of *Syzygium balansae* (Guillaumin) J.W. Dawson; (L) fruit of *Syzygium maraca* Craven and Biffin; (M) young fruit of *Syzygium* sp. (Reproduced with permission from A. Ford (A–B), G. Sankowsky (C, H, I, L), E. Biffin (D), L. Craven. (E–G, K, M) and J. Dowe (J).)

and structure of the fruit were very uniform, and the habit of the plants themselves was generally uniform. Wight did acknowledge the practical difficulty of not having some taxonomic substructure for such a species rich genus as *Eugenia* had now become. Therefore, he recognised each of the five genera he had merged into *Eugenia* as subgenera using the same epithets. Wight's solution for classifying all the large seeded species also had the effect of stabilising nomenclature, and from the comment made by Bentham<sup>49</sup>, this appeared to be one consideration for adoption of the same taxonomy by Bentham and Hooker<sup>50</sup> in their influential *Genera Plantarum*. Meanwhile researchers, mainly Dutch botanists working in the Malesian region, were continuing to describe new species in *Jambosa* and/or *Syzygium* (for example, Blume<sup>51</sup> and Miquel<sup>52</sup>). As more novel morphological variation was encountered, new genera were also described from Malesia and the South West Pacific (for example, *Acicalyptus* A. Gray, *Aphanomyrtus* Miq., *Clavimyrtus* Blume, *Cleistocalyx* Blume, *Cupheanthus* Seem., *Pareugenia* Turrill and *Piliocalyx* Brongn. and Gris.). Where the various segregate genera were known to Bentham and Hooker<sup>50</sup>, they were all reduced to *Eugenia* in *Genera Plantarum* and therein assigned to one of the three sections they recognised, sect. *Jambosa*, sect. *Syzygium* or sect. *Eugenia*. Although Bentham and Hooker's circumscription of *Eugenia* was followed by many taxonomists for over 100 years, it was not universally accepted.

Late in the century, Niedenzu's account of Myrtaceae was published in *Die Natürlichen Pflanzenfamilien*<sup>15</sup>. This work is similar to that of De Candolle<sup>46</sup> in that *Eugenia* is retained for the New World species (with a very few Old World species that clearly were part of this grouping) and the very great majority of the Old World species were assigned to four other genera. The Old World genera he recognised were *Acicalyptus*, *Jambosa* (including *Cleistocalyx* among others), *Piliocalyx* and *Syzygium* (including *Acmena* among others). The narrower generic concepts for the *Eugenia* group were welcomed by those taxonomists of the following century who believed Bentham and Hooker's broad circumscription<sup>50</sup> to be unsatisfactory.

In summary of this section, Bentham and Hooker's 'all in one' concept of genus<sup>50</sup> provided nomenclatural stability but was, by the end of the nineteenth century, often deemed unsatisfactory.

### 16.2.2 TWENTIETH CENTURY

As noted above, the word *Syzygium* is believed to refer to a joining or yoking together, but the derivation is unclear. If nothing else the genus certainly has two yoked histories, as twentieth-century authors can be grouped into two schools of thought as to its classification. One school used the all-inclusive Bentham and Hooker concept of a single genus, *Eugenia*, and the other school accepted *Eugenia* for the New World centred species and differing numbers of genera for the Old World syzygioid species. Typically, the latter taxonomic school recognised *Syzygium*, *Acmena*, *Cleistocalyx* and often *Jambosa*, with some additionally recognising *Acicalyptus*, *Acmenosperma*, *Cupheanthus* and *Piliocalyx* for some South West Pacific species. The twentieth-century champion of the *Eugenia* school in the Indo-Pacific was Henderson, who published a comprehensive account of the species occurring in the Malay Peninsula<sup>53</sup>. In this work, Henderson arranged the Malayan species in four sections: *Acmena*, *Cleistocalyx*, *Fissicalyx* and *Syzygium*, the latter of which he split into five groups. His circumscription of sect. *Syzygium* included the concepts of *Caryophyllus*, *Jambosa* and *Syzygium* that had been adopted by previous workers at genus or subgenus level.

Of the authors advocating the recognition of separate genera for the syzygioid species, the most significant have been Merrill and his coworker Perry. These two authors published accounts of *Acmena* and *Cleistocalyx*<sup>54,55</sup>, floristic treatments of *Syzygium* and its allies for Indo-China, China and Borneo<sup>56-58</sup>, and important contributions on the Papuanian<sup>59</sup> and Philippine<sup>60</sup> species. Interestingly, Merrill had accepted more genera than just *Acmena*, *Cleistocalyx* and *Syzygium* early in his career but moved to a more conservative position when he was most active floristically. Relatively late in his career he returned to the narrower generic position and recognised *Acmena*, *Aphanomyrtus*, *Caryophyllus*, *Cleistocalyx*, *Pareugenia*, *Syzygium*, *Tetraeugenia* Merrill and tentatively *Jambosa*<sup>60</sup>.

Investigations of *Syzygium* and *Eugenia* by other researchers in the second half of the century have contributed significantly to the debate. Ingle and Dadswell<sup>61</sup> studied the wood anatomy of Myrtaceae in the South West Pacific and concluded that the *Eugenia s.l.* species sampled fell into two distinct groups. A few species agreed anatomically with the New World species of *Eugenia s.s.* but the majority were distinct from these and comprised species of *Acmena*, *Cleistocalyx* and *Syzygium*. Pike<sup>62</sup> found that pollen morphology supported the conclusions of Ingle and Dadswell<sup>61</sup>. Pike further noted that the pollen of the *Eugenia s.s.* species examined resembled that of the subtribes Myrtinae and Myrciinae, a finding of significance in the light of the recent work of Wilson et al.<sup>20</sup>, in which *Eugenia* and *Syzygium* are placed in different tribes, that is, Myrteae and Syzygieae, respectively.

Floral anatomical investigations by Schmid<sup>13</sup> provided strong evidence that *Eugenia s.s.* and the *Syzygium* group were not as closely related as believed by many earlier workers. Schmid<sup>13</sup> considered that neither *Eugenia* nor *Syzygium* were directly ancestral to the other and that their divergence occurred long ago. This view was supported by the phylogenetic analysis of morphological and anatomical data by Johnson and Briggs<sup>19</sup>. This study indicated that *Eugenia* formed a clade with other Myrtoideae genera (for example, *Austromyrtus* (Nied.) Burret, *Myrcia* DC. ex Guill., *Myrtus* and *Psidium* L.), whereas *Syzygium* was in a clade with *Acmena* and other Old World species remote from the Myrtoideae *s.s.* clade. Leaf anatomy has been studied in Malay Peninsula species of *Eugenia* sects. *Acmena*, *Cleistocalyx*, *Fissicalyx* and *Syzygium* by Khatijah et al.<sup>63</sup>. The results supported the recognition of sect. *Acmena* but not of sects. *Cleistocalyx* and *Fissicalyx*, which were found to be similar to sect. *Syzygium*. Haron and Moore<sup>64</sup> in a study of leaf micromorphology of Old and New World *Eugenia s.l.* species, that is, species referable to *Syzygium* and *Eugenia s.s.*, found that there were differences in foliar features between the two groups.

In summary of this section, twentieth-century authors have either adopted Bentham and Hooker's 'all in one' concept of genus<sup>50</sup> or accepted *Eugenia* for the New World centred species and varying numbers of genera for the Old World syzygioid species.

### 16.3 CURRENT RESEARCH

Research into the distinction between *Eugenia s.s.* and the *Syzygium* group has not been the focus of current studies; that the two groups are amply distinct appears to be an accepted fact by all current workers as shown above.

#### 16.3.1 MORPHOLOGICAL, DEVELOPMENTAL AND CHEMICAL STUDIES

Current supraspecific work on *Syzygium* and its allies has centred on developing an understanding of the relationships between and within the genera. Phenetic and phylogenetic analysis of morphological data derived from Thai species of *Acmena*, *Cleistocalyx* and *Syzygium* provided support for the taxonomic reinstatement of *Jambosa* at some level but did not give strong resolution to other possible taxonomic groups<sup>12</sup>. Pollen studies of Thai *Syzygium* did not support any known taxonomic groupings of the species, although the pollen of the jambosoid species tended to be larger, suggesting that there might be differences in the breeding biology of the studied species<sup>65</sup>.

Floral development has been studied in one species of *Acmena* and one species of *Syzygium* by Belsham and Orlovich<sup>66</sup>. Development of the hypanthium in *Acmena* was similar to that in some dry-fruited Myrtaceae but the androecial development was similar to that of the fleshy-fruited *Luma* A. Gray, whereas the reverse was the case in the *Syzygium* studied. Unfortunately, the number of species examined was small and further work is warranted. The distribution of polyhydroxyalkaloids (PHAs) in 217 species of Myrtaceae was studied by Porter et al.<sup>67</sup>, but the taxonomic significance of PHAs in the *Syzygium* group appears inconclusive, and further work may be required.

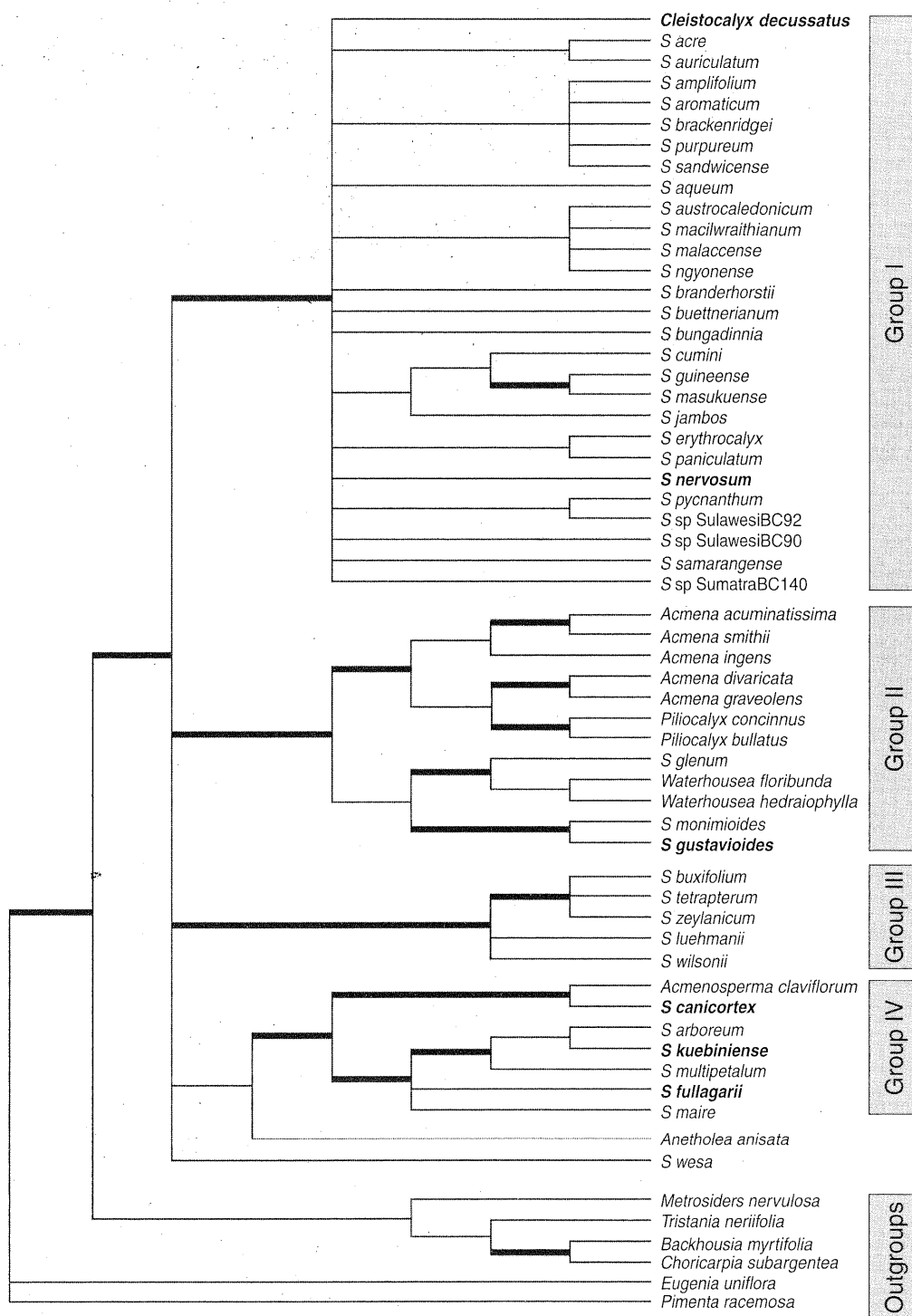
Khatijah et al.<sup>63</sup>, on the basis of 25 Malesian species surveyed, showed that Henderson's<sup>53</sup> groups 2 and 3 within *Syzygium* have paracytic stomata, whilst those in his group 4 are anisocytic; further investigation of this promising line of research has yet to be undertaken. The intrusive material present in the seeds of *Acmena*, *Acmenosperma* and *Piliocalyx* is an intriguing phenomenon. Hartley and Craven<sup>68</sup>, in studies on *Acmena*, reported that the intrusive tissue was of placental origin. Work in progress by Biffin indicates that the tissues in *Acmena* may be derived from the chalaza and be homologous with tissues that surround the seed in several species of *Syzygium* s.s. The embryology of the *Syzygium* group is another area of research that may be of systematic significance. Both unitegmic and bitegmic ovules have been observed<sup>69,70</sup>, and this promising work is being continued.

In summary of this section, new morphological and anatomical analysis has brought forward promising characters that may be of considerable taxonomic importance. However, in the majority of cases, further analysis is needed before their significance can be adequately assessed.

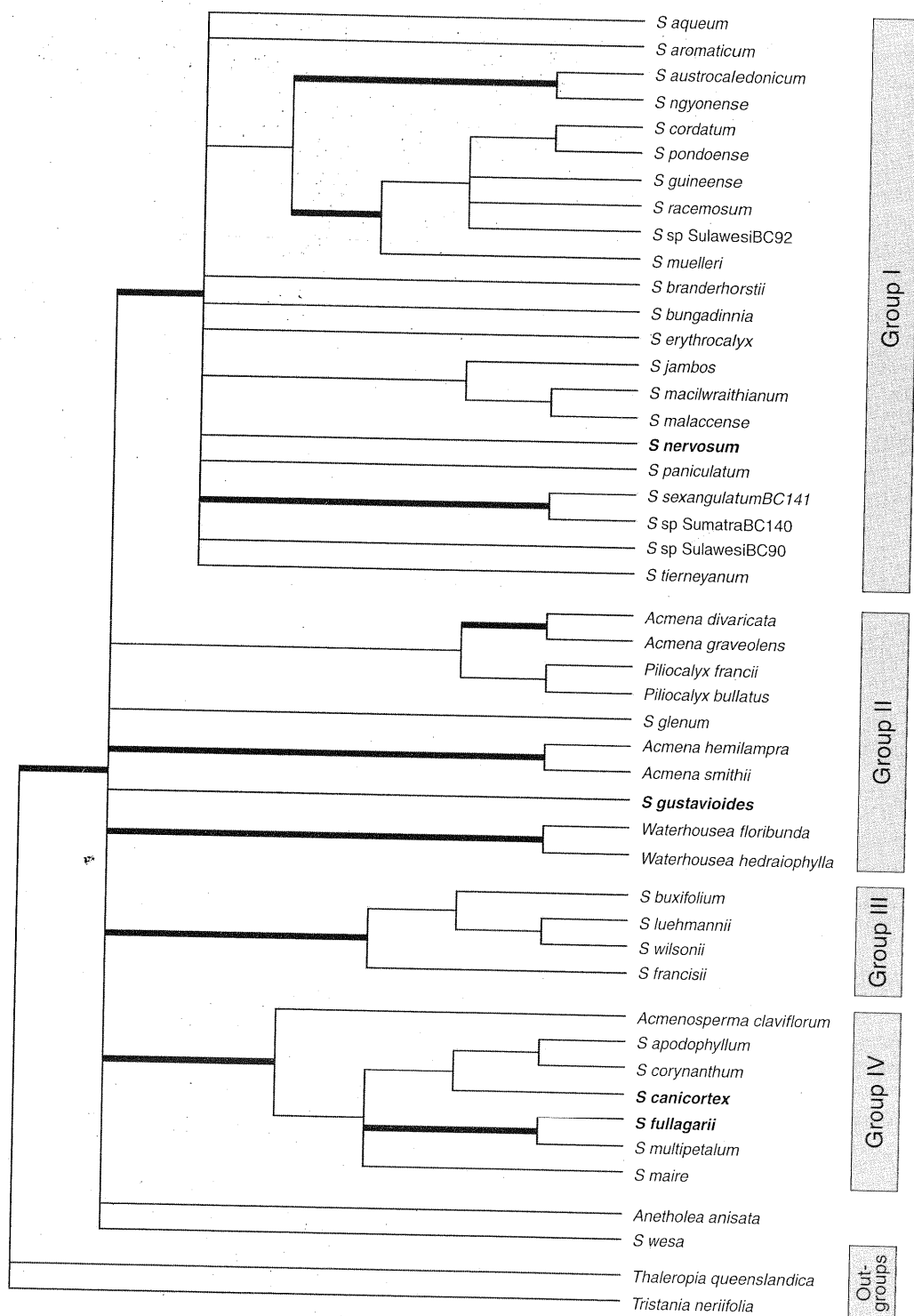
### 16.3.2 MOLECULAR SEQUENCE STUDIES

Harrington and Gadek<sup>71</sup> utilised sequence data from the internal transcribed spacers (ITS) and external transcribed spacer (ETS) of nuclear rDNA from 65 Australian and the one Lord Howe Island species of the *Syzygium* group. Their sample included species representative of *Acmena*, *Acmenosperma*, *Anetholea*, *Cleistocalyx*, *Syzygium* and *Waterhousea*, together with six unnamed species at that time not placed to genus<sup>71</sup>. The results of their analyses were not congruent with current taxonomic circumscriptions, indicating that the separation of the Old World genera into two groups, the *Acmena* suballiance and the *Syzygium* suballiance, proposed by Briggs and Johnson<sup>18</sup> was unjustified. There was also no support for the conventional concepts of *Acmena*, *Acmenosperma*, *Cleistocalyx*, *Jambosa*, *Syzygium* and *Waterhousea*, and *Anetholea* was also nested in *Syzygium*<sup>71</sup>. Biffin et al.<sup>72</sup> analysed cpDNA sequences from the *matK* and *ndhF* genes and the *rpl16* intron from 87 species of the *Syzygium* group. The sampling was comprehensive, covering the taxic and morphological diversity sampled by Harrington and Gadek<sup>71</sup>, with the addition of species from the South West Pacific that represented the generic concepts of *Acicalyptus* A. Gray, *Cupheanthus* Seem. and *Piliocalyx* Brongn. and Gris, a few species from Africa and Malesia and some widely cultivated species of uncertain geographic origin. As with the study by Harrington and Gadek<sup>70</sup>, there was no support for conventional concepts but there were some major clades that are being further investigated. It is possible that these clades may be 'cryptic', that is, not readily diagnosed morphologically, and future directions for research into this aspect are discussed by Biffin et al.<sup>73</sup>.

Figure 16.6 and Figure 16.7 are summaries of present knowledge as to the phylogeny of *Syzygium* s.l. inferred from analysis of molecular sequence data. The *Syzygium* s.l. species that were analysed to obtain these two trees are representative samples drawn from the genera accepted by various workers in recent times, that is, *Acmena*, *Acmenosperma*, *Anetholea*, *Cleistocalyx*, *Piliocalyx*, *Syzygium* and *Waterhousea*. Figure 16.6 shows a strict consensus tree derived from combined *ndhF* and *matK* data. Four well supported clades are evident with two species, *Anetholea anisata* Peter G. Wilson and *Syzygium wesa* B. Hyland, each comprising a monospecific lineage that is not well supported as members of any of these clades. *Jambosa* and *Syzygium*, as it is traditionally circumscribed, species are in Group I; this clade therefore includes the very great majority of species of the complex and has a correspondingly large geographic range. Group II, comprising *Acmena*, *Piliocalyx* and *Waterhousea* species, along with *Syzygium gustavioides* (F.M. Bailey) B. Hyland, *S. glenum* Craven and *S. monimioides* Craven, is characterised by the majority of its species possessing intrusive material within the cotyledons. *Syzygium gustavioides* and *S. monimioides*, however, differ in that they have seeds typical of *Syzygium* s.s. Groups III and IV and may equate to Henderson's Groups 4 and 5, respectively, of his *Eugenia* sect. *Syzygium*<sup>53</sup>. *Acmenosperma claviflorum* (Roxb.) Kausel, a member of Group IV, has intrusive material in the cotyledons as in many Group II species, but it is not yet known if the tissues are homologous. Work is in progress to identify practical macromorphological features that can be used to support the recovered clades and in classification.



**FIGURE 16.6** Strict consensus tree of 10,000 trees derived from a combined *ndhF*, *matK* and *rpl16* dataset from a representative sampling of *Syzygium s.l.* Bold branches have BS  $\geq$  90%; length 877; CI = 0.831; RI = 0.829. Names in bold indicate species referable to *Cleistocalyx* sensu Merrill and Perry<sup>54</sup>.



**FIGURE 16.7** 50% bootstrap consensus tree for the ITS data set from a representative sampling of *Syzygium* s.l. Data analysed under parsimony with transversions receiving four times the weight of transition substitutions. Bold branches have BS  $\geq 90\%$ . Names in bold indicate species referable to *Cleistocalyx* sensu Merrill and Perry<sup>54</sup>.

The ITS data set shows a strong bias towards transition substitutions (CT, AG), and the tree (Figure 16.7) was derived with transversion substitutions receiving four times the weight of transitions. The ITS data provides moderate to strong support for clades consistent with Groups I, III and IV in the chloroplast data, although Group II is not resolved as monophyletic, and the relationships of *Anetholea* and *S. wesa* are also unresolved. It is important to note, however, that areas of disagreement between the ITS and chloroplast data are only weakly, or are not statistically supported in the ITS data, consistent with the hypothesis that these data are uninformative regarding some relationships within *Syzygium s.l.*, rather than suggesting an alternative, conflicting resolution. For instance, we note that, at moderate to high levels of sequence divergence, transition substitutions are saturated (that is, there is a high probability of unobserved substitutions occurring at some nucleotide positions), and as such, the historical signal may be obscured by 'noise'. On the other hand, congruence between our data sets increases our confidence in the recognition of Groups I, III and IV. Additional lines of evidence, including further sequences of nuclear DNA and from morphology, will be required to confidently resolve relationships of the 'acmenoid' taxa (Group II), *S. wesa* and *Anetholea*.

In summary of this section, molecular data have suggested that current, largely morphologically derived, generic characterisations are flawed.

### 16.3.3 FLORISTIC STUDIES

Floristic activity is presently high, and several projects have been completed recently or are underway (Table 16.1). This type of research is both undervalued and underfunded. In large part, the current advances made in molecular studies by Harrington and Gadek<sup>71</sup> and Biffin et al.<sup>72,73</sup> are an undeniably vital component in exploring the evolution and relationships of this large genus. Their foundations were built upon the knowledge of the morphological diversity occurring in Australia and Melanesia that is encapsulated in the revisionary and floristic studies of Hyland<sup>38</sup>, Smith<sup>74</sup>, Dawson<sup>75</sup> and Craven and Matarczyk<sup>42</sup>. Despite such activity, coverage is far from even and still utterly inadequate in a number of countries. For example, Utteridge<sup>76</sup>, in relation to a checklist of woody plants of Sulawesi, states: "This highlights how some groups, for example *Syzygium* (Myrtaceae), are badly in need of specialist systematic work. For example, only four species of *Syzygium* are recorded in the checklist, but approximately 350 un-named collections are listed".

TABLE 16.1

Current and Recently Published Floristic Research in *Syzygium s.l.*

Region	Project	Status	Author(s)
Australia	Revision	Completed	Hyland <sup>38</sup>
	Flora of Australia	Completed (in press)	Craven and Matarczyk <sup>43</sup>
East Africa	Flora of Tropical East Africa	Completed	Verdcourt <sup>84</sup>
Fiji	Flora of Fiji	Completed	Smith <sup>74</sup>
Mascarenes	Flore des Mascareignes	Completed	Scott <sup>83</sup>
Sri Lanka	Flora of Ceylon	Completed	Ashton <sup>21</sup>
	Revision	Completed	Kostermans <sup>22</sup>
Thailand	Flora of Thailand	Completed	Chantaranothai and Parnell <sup>28</sup>
New Caledonia	Flora de la Nouvelle-Calédonie	Part completed, balance in preparation	Dawson <sup>75</sup>
Borneo	Tree Flora of Sabah and Sarawak	In preparation	Ashton <sup>86</sup>
China	Flora of China	In preparation	Chen and Craven <sup>44</sup>
Papuasias	Revision	In preparation	Craven <sup>87</sup>
Indo-China	Flora du Cambodge du Laos et du Viêt nam	Initiated	Parnell and Chantaranothai <sup>85</sup>

There are significant impediments to floristic and systematic research on *Syzygium*. The group is badly undercollected in many parts of its geographic range. Parnell<sup>77</sup> showed that the distribution of even the most common species of Thai *Syzygium* showed significant false gaps, which could be filled in by subsequent collecting, a process that has not yet been even closely approached in Thailand (and therefore most of South East Asia). Furthermore, Parnell et al.<sup>78</sup> showed that Thailand was severely undercollected, with a low collecting density and low rate of collecting activity. Such undercollecting is typical of most countries where *Syzygium* is native. In addition to this lack of floristic survey, *Syzygium* species are infrequent flowerers, and nonflowering material is generally abhorred by tropical collectors, as usually it cannot be named to species. Therefore, even when areas are thoroughly sampled over a one- to two-year period, species are passed over. Another limitation is due to the inadequate representation in herbaria of the reproductive stages necessary for complete descriptions and key preparation, for rarely does a species carry both flowers and fruit at the same time. Other limitations equally applicable to all plant groups but especially critical for groups of exceptional size are that the world's herbaria are understaffed and that the largest are located, through historical accident, in Europe<sup>79-82</sup>. The major collections are therefore removed from the centres of diversity of *Syzygium*, and this does not aid field study. Current projects that will result in the easier exchange of data through imaging will mitigate this problem.

Despite the research activity described in Table 16.1, there are a number of countries or areas where no adequate floristic account exists or is realistically projected, including the Philippines, Sulawesi and Sumatra. Areas where much further detailed work is needed include Peninsular Malaysia, Kalimantan and the Andaman and Nicobar Islands, and these therefore could form the focus for involvement of new workers on the genus. The presence of novel taxonomic data retrievable only from the above areas cannot be ruled out. Such data, if it exists, could have a dramatic impact on the structure of any phylogenetic hypothesis.

In summary of this section, current floristic activity is high, but nevertheless there are significant gaps, which may be of evolutionary significance.

#### 16.3.4 BREEDING BIOLOGY

The breeding biology of *Syzygium* is underinvestigated, and this is a considerable impediment to understanding the delimitation and evolution of its species. Nic Lughadha and Proença<sup>16</sup> review the literature for the Myrtoideae and show that dichogamy is likely in *Syzygium* and that bird and mammal pollination occurs, with nectar being the primary reward. Boulter et al.<sup>88</sup> show that *S. sayeri* (F.M. Muell.) B. Hyland is visited for its nectar both during the day and at night by a wide range of pollinators, including bats, birds, bees, wasps, moths, thrips and the occasional ant or spider. Hopper<sup>89</sup> observed that the majority of interflower movements of pollinators on *S. tierneyanum* (F. Muell.) Hartley and L.M. Perry were within the same plant. Lack and Kevan<sup>90</sup> found that *S. syzygioides* (Miq.) Merr. and L.M. Perry was self-incompatible; consequently the spatial arrangement of flowering trees and pollinator behaviour become issues in maintaining reproductive success. Boulter et al.<sup>88</sup> indicate that *S. sayeri* is xenogamous, with low self-compatibility and moderate levels of outcrossing. Chantaranothai and Parnell<sup>91</sup> record that visitor numbers to *S. jambos*, *S. megacarpum* (Craib) Rathakr. and N.C. Nair and *Syzygium samarangense* (Blume) Merr. and L.M. Perry 'See-nak', are often very low, although Free<sup>92</sup> indicates that there are no reports that pollination is inadequate in *S. aromaticum* (as *Eugenia caryophyllus* Bullock and Harrison). Taken as a whole, these data do not conclusively indicate whether inbreeding or outbreeding is the norm in *Syzygium*. It may be that part of the complexity of structure and species richness of the genus is a result of inbreeding. Chantaranothai and Parnell<sup>91</sup> showed that three breeding systems may operate in *Syzygium*. All species tested, *S. samarangense* 'See-nak', *S. jambos*, *S. formosum* (Wall.) Masam. and *S. megacarpum*, showed self-compatibility; *S. samarangense* also showed enhanced seed set through self pollination, and it and *S. jambos* exhibited nonobligate apomixis with both fruits and seeds having the potential to develop without fertilisation.



Free<sup>92</sup> indicated that *S. aromaticum* may be a nonobligate apomict. The data in Boulter et al.<sup>88</sup> indicate that *S. sayeri* may be able to act as an agamosperm, but that agamospermy is very much less successful in terms of successfully pollinated buds than outcrossing. A further complication is the inconsistent exhibition of adventitious polyembryony in certain species, for example *Syzygium cumini* (L.) Skeels, wherein it is combined with reportedly varying levels of polyploidy<sup>16</sup>.

There are no data on the frequency of occurrence of apomixis, nor varying ploidy levels, nor the frequency of adventitious embryony in *Syzygium*. Nevertheless, it is clear that the description of species based on few collections, when combined with a very low collecting rate and density over much of the range of *Syzygium*, and the potential for apomixis and ploidy variation might result in the false delimitation of many taxa as new species which are, at best, microspecies. As far as we are aware, the suggestion that a significant number of microspecies may exist in *Syzygium* is novel.

The anthers in many *Syzygium* species have conspicuous, although small, glands associated with the connective which appear secretory. In addition, the petals of *Syzygium* are also often glandular. Discussion of the function, if any, of these glands in *Syzygium* is almost nonexistent, and details of the chemical composition of the glands' secretions is unknown. However, the secretions are clearly variable in quantity and — probably — composition and function; and gland density has been used as a taxonomic characteristic (Chantaranothai and Parnell<sup>28</sup>). Their further study may offer novel taxonomic data and insights on breeding biology as has been suggested for another Myrtaceous genus, *Verticordia* DC. (Ladd et al.<sup>93,94</sup>).

In summary of this section, the breeding biology of *Syzygium* is underinvestigated. Various systems ranging from inbreeding to outbreeding occur, and the lack of information on their frequency of occurrence and distribution is a considerable impediment to understanding the delimitation and evolution of species in the genus.

## 16.4 FUTURE PROSPECTS

We have shown that *Syzygium* has never been revised as a unit at species level outside of the nineteenth century and have also shown that current estimates of phylogeny suggest that *Syzygium* comprises several well supported clades. Whether or not these clades are indicative that *Syzygium* is nonmonophyletic is dependent upon one's delimitation of that genus per se. In addition, we have shown that there is considerable floristic activity dealing with *Syzygium*, by definition on a regional basis, and we are confident that the genus is simply too large to facilitate a worldwide species-level monograph. We acknowledge that current activity will leave significant unexplored geographical gaps. Especially in a university, but also in a research institution, monographic activity on the scale needed is likely to be unsustainable, as high performance indicators are difficult to maintain when undertaking a monograph. We do not wish to rehearse, yet again, arguments contrasting monographs with floras but are aware that current regional work in *Syzygium* has the potential to produce inchoate accounts that do not mesh with each other, and that to some extent this has already occurred. We believe that this is undesirable, but admit that it is nevertheless almost inevitable, as the only practical way forward at species level is a regional one. To mitigate the detrimental potential of local working, we believe that a World Wide Web-based site for workers on *Syzygium* might stimulate interest and simplify exchange of material and ideas. Such a site would clearly interdigitate with the activities of the Flora Malesiana project (the majority of species of *Syzygium* occur in the Malesian region) and the initiative coordinated by the Royal Botanic Gardens Kew, U.K., which aims to produce a world checklist of Myrtaceae.

There are many species new to science awaiting description within *Syzygium s.l.* At present, there are two main approaches taken to the placement of such species. Craven<sup>9</sup> favours placement of all such new species, which are of course always described on the basis of morphology, in *Syzygium s.l.* The core argument advanced here is that to split off anomalous variation will necessarily lead to the splitting of *Syzygium* into a plethora of genera, and that these will be both

ambiguous and impossible to recognise without both flower and fruit. In addition, Craven implies that novel data, especially molecular data, are likely to suggest splitting of *Syzygium* in unforeseen ways which will then allow the erection of robust, phylogenetically defined genera, and that it is unwise to set up new genera in the interim. Based upon a synthesis of the presently available molecular and morphological evidence, however, Craven and Biffin consider that the species under discussion constitute a single, natural group, and that all should be classified in *Syzygium* with an infrageneric classification that reflects the evolutionary relationships of the constituent clades. By contrast, Parnell believes that the inclusion of the majority of new species within an expanded concept of *Syzygium* might make it more polyphyletic and overstretch the genus boundaries. He argues that knowledge of phylogeny will always be imperfect and favours the erection of separate genera to accommodate such new species based on a sufficiency of current evidence. He believes that any degree of predictability which could be derived from the current classification will be diluted by cramming all the currently split off genera (for example, *Acmena*, *Acmenospermum*, *Cleistocalyx Piliocalyx* and *Waterhousea*) along with new, probably generically distinct taxa, into an ever-expanding *Syzygium*. Neither Craven's nor Parnell's methodology eliminates the necessity for future species transfer between genera — rather, both admit that it will be necessary — however, they have not agreed which procedure will be minimally disruptive, producing the smallest number of intergeneric transfers. It does not appear that Article 34 of the International Code of Botanical Nomenclature<sup>95</sup> can be stretched to resolve this problem, as neither Craven or Parnell suggest that the species described are invalid, nor do they suggest that the new species might not belong to *Syzygium*.

This debate raises the question as to whether strict monophyly should be the overwhelming consideration for classification of such a species rich group, and if it is, how (that is, on what basis) it is to be established. Clearly, it is unlikely that sufficient numbers of strict monophyletic lineages can be established in the short to medium term in such a species rich, widespread and poorly known genus as *Syzygium*, where molecular data are limited and phylogenetically promising morphological data are still being discovered. However, if major clades can be identified, then the task of classifying the genus will be facilitated because researchers will be able to narrow down the number of species included in their studies. Despite attempts to utilise morphological data cladistically by Parnell<sup>12</sup> and Craven<sup>96</sup>, the lack of resolution suggests that, as in many other genera, morphology by itself will be inadequate for the task. It may be, as Olmsted and Scotland<sup>97</sup> argue, that molecular data offer 'more and better data' to reconstruct phylogeny. Results of analysis of the chloroplast *ndhF*, *matK* and *rpl16* data are summarised in Figure 16.6 and are generally congruent with the ITS data (Figure 16.7). The reliability of ITS data for phylogenetic reconstruction has been questioned by Álvarez and Wendel<sup>98</sup>, and Biffin<sup>99</sup> is presently investigating the utility of the nuclear encoded large subunit of RNA polymerase (*rpb2*) as a source of data for a second nuclear region. Whether general congruence is a sufficient measure indicating accurate reconstruction of phylogeny requires further debate.

Strict adherence to the concept of monophyly may also be operationally infeasible. Our work suggests that the variation patterns of *Syzygium* s.s. species in South East Asia and Australasia are different, that there are many species awaiting description and naming, and that a uniform species concept may, in part due to different breeding systems, be inapplicable. We believe that such basic descriptive is best undertaken in a phylogenetic framework. However it is clear that in *Syzygium*, although the overall framework is being developed as a result of the studies by Harrington and Gadek<sup>71</sup> and Biffin et al.<sup>72,73</sup>, the detail will take longer and requires much work. It is important that this work be undertaken for the extremely large *Jambosa-Syzygium* clade (Group I), not only because of its extreme size (c. 1,000 species are involved) but also because this group contains the economically important fruit and spice species. Although morphology may lack the strength of molecular sequence data for phylogenetics in *Syzygium*, it still has much to offer the *Syzygium* systematist. Apart from its obvious significance for identification, morphology will be important in characterising the clades recovered from analysis of sequence data.

If monophyly is not given prime place, then this raises the issue of what drives classification and nomenclature. We do not believe that historical precedent and convenience should be the sole pilots of classification. So, for example, we welcome the transfer of inappropriately placed species from *Eugenia* to *Syzygium*, as no rational systematist now argues that they are closely related. Unsatisfactory as it might seem, we believe that what will drive classification and nomenclature in *Syzygium*, and the segregation of related genera etc., will be similar arguments, essentially based on an 'unassailable mass' of evidence. We differ, however, in our consideration of what is sufficient mass. Guidance may well be provided by molecular data. Where phylogenetic trees of large genera constructed on the basis of a few exemplar species, or only a single gene, challenge currently accepted patterns, we certainly suggest that those patterns and their underlying causes are re-examined and the testing expanded. Taxonomic change should not be undertaken rashly. We have shown that DNA sequence data do offer new insights into *Syzygium*, especially at the higher levels; however, it is unclear at present how robust those insights are. Advances in phylogenetic reconstruction methods may be needed for large datasets which might derive from large groups such as *Syzygium*. One promising development is continuous jackknife function analysis<sup>100</sup>, and this appears unutilised for large datasets which might derive from large groups such as *Syzygium*. Its application may be an important tool allowing assessment of the stability of large group phylogenies and impartial assessment of the achievement of 'unassailable mass'.

Another difficulty is the question of whether locally distinctive species groups (for example, the Fijian species assigned to *Cleistocalyx*, the Papuan species of the *Syzygium furfuraceum* Merr. and L.M. Perry group and the trimerous New Caledonian species) should be given recognition at some level. If this is done, it is likely to result in a paraphyletic classification with a very large number of comparably ranked taxa that had to be established merely to 'balance' the classification. In part, we are here concerned with a conflict between the operability and utility of classifications and their predictability and monophyly. In general, we accept the thrust of the letter coordinated by Nordal and Stedje<sup>101</sup> which advocates the acceptance of paraphyletic taxa (at least for Floras) and on this basis, there is no reason not to allow for the recognition of locally distinctive species groups.

Clearly, *Syzygium* is unusual in size and an obvious question is 'why is it so big?'. For example, we may want to know if there are any key innovations that can correlate with, or explain, diversification patterns (see Davies and Barraclough, *Chapter 10*; Hodkinson et al., *Chapter 17*). In some other large genera, there appears to be an uniting apomorphy of great importance in driving speciation; in *Solanum* it may be buzz pollination, in *Euphorbia* it may be the cyathium, in *Ficus* it may be the fig (i.e., the syconium), in the Compositae it may be either a specialised incompatibility mechanism linked to specialised pollination mechanisms or the development of chemical poisons. In *Syzygium* it may be invidious to single out only one key innovation; perhaps, it is better to consider *Syzygium's* combination of features as innovative.

Research areas that we believe will be personally rewarding to study, and which are important to pursue from the biodiversity perspective include the following:

- Resolving interrelationships of the 80–90% of the genus that comprises Group I (as defined on the basis of molecular analysis), that is the *Jambosa-Syzygium* s.s. clade. This will be a major task, given the sampling issues posed by the geographical distribution of the group, let alone the identification of suitable DNA sequence regions for analysis.
- Completing floristic surveys of the major regions not yet investigated adequately, especially Myanmar, Peninsula Malaysia, Kalimantan, Sulawesi and the Philippines.
- Developing an understanding of the biogeography of the major clades, especially of their prehistorical biogeography.
- Investigating the breeding systems to establish to what extent, if any, there are implications for taxonomy from factors such as apomixis, hybridisation and introgression.
- Studying evolutionary phenomena, such as r and K adaptive strategies.

- Examining novel, or understudied but promising, morphological characters, including stomatal type and especially those associated with characteristics of the placenta and ovule, including vascular anatomy, the development and types of intrusive tissue and the number of integuments.
- Examining the chemical composition of the secretions of the anther gland connective and petals.
- Determining the factors, including 'key innovation(s)', that drive diversification of *Syzygium*.

In conclusion, we regard the size of *Syzygium* as a positive, even though we acknowledge there are caveats on logistical grounds, as it offers opportunities for the initiation of major and stimulating research projects well into the twenty-first century and beyond. The enormous structural diversity embodied in the plants themselves, their habit, foliage, their often highly attractive flowers and fruit, their manifestly diverse ecology and wide geography, their biotic and abiotic interactions with other animals including man, all ensure that exciting and meaningful research is limited only by money and imagination.

## ACKNOWLEDGEMENTS

We wish to thank various agencies and individuals whose data and support have contributed to this chapter. John Parnell thanks the EU for support under the Marie Curie Scheme for various post-doctoral fellows and under the Human Capital and Mobility Scheme, the Trinity Trust and Trinity College Dublin (TCD) for sponsorship of various postgraduate students, especially Professor Pranom Chantaranothai, and all of the herbaria, especially TCD and all others listed in their publications, without whose collections and support this chapter would have been unconstructible. Lyn Craven and Ed Biffin acknowledge support from the Pacific Biological Foundation, CSIRO and ANU, and the many individuals and institutions who generously have provided material, information and field and other assistance. Ed Biffin holds an ABRIS Postgraduate Scholarship from the Australian Biological Resources Study and a Scholarship from the Australian National University.

## REFERENCES

1. George, A.S., Myrtaceae, Family description, in *Fl. Australia* 19, George, A.S., Ed., Australian Government Publishing Service, Canberra, 1988, 1.
2. Johnson, L.A.S. et al., Myrtaceae, in *Flowering Plants in Australia*, Morley, B.D. and Toelken, H.R., Eds., Rigby, Willoughby, 1988, 175.
3. Kochummen, K.M., Eugenia, in *Tree Flora of Malaya* 3, Ng, F.S.P., Ed., Longman, London, 1995, 172.
4. Lemmens, R.H.M.J., *Syzygium*, in *PROSEA (Plant Resources of South East Asia) 5 Timber Trees: Minor Commercial Timbers*, Eds. Lemmens, R.H.M.J., Soerianegara I., and Wong, W.C., Backhuys, Leiden, 1995, 441.
5. Mabberley, D.J., *The Plant Book*, 2nd ed., Cambridge University Press, Cambridge, 1997.
6. Schmid, R., Comparative anatomy and morphology of *Psiloxylon* and *Heteropyxis*, and the subfamilial and tribal classification of Myrtaceae, *Taxon*, 29, 559, 1980.
7. Craven, L.A., Myrtaceae of New Guinea, in *Ecology of Papua*, Conservation International, in press.
8. Chippendale, G.M., *Eucalyptus*, in *Fl. Australia* 19, George, A.S., Ed., Australian Government Publishing Service, Canberra, 1988, 1.
9. Craven, L.A., Unravelling knots or plaiting rope: what are the major taxonomic strands in *Syzygium* sens. Lat. (Myrtaceae) and what should be done with them? in *Taxonomy: The Cornerstone of Biodiversity Proc. Fourth Fl. Males. Symp.*, Saw, L.G., Chua, L.S.L., and Khoo, K.C., Eds., Forest Research Institute, Malaysia, Kuala Lumpur, 2001, 75.
10. Craven, L.A., Four new species of *Syzygium* (Myrtaceae) from Australia, *Blumea*, 48, 479, 2003.
11. Craven, L.A. and Biffin, E., *Anetholea anisata* transferred to, and two new Australian taxa of, *Syzygium* (Myrtaceae), *Blumea*, 50, 157, 2005.

12. Parnell, J., Numerical analysis of Thai members of the *Eugenia-Syzygium* group (Myrtaceae), *Blumea*, 44, 351, 1999.
13. Schmid, R., A resolution of the *Eugenia-Syzygium* controversy Myrtaceae, *Amer. J. Bot.*, 59, 423, 1972.
14. McVaugh, R., The genera of American Myrtaceae: an interim report, *Taxon*, 17, 354, 1968.
15. Niedenzu, F., Myrtaceae, in *Die Natürlichen Pflanzenfamilien* 3, Abteilung 7, Engler, A. and Prantl, K., Eds., Engelmann, Leipzig, 1893, 57.
16. Nic Lughadha, E. and Proença, C., A survey of the reproductive biology of the Myrtoideae Myrtaceae, *Ann. Missouri Bot. Gard.*, 83, 480, 1996.
17. Hora, F.B., Myrtaceae, in *Flowering Plants of the World*, Heywood, V.H., Ed., Oxford University Press, Oxford, 1978, 161.
18. Briggs, B.G. and Johnson, L.A.S., Evolution of the Myrtaceae: evidence from inflorescence structure, *Proc. Linn. Soc. New South Wales*, 102, 157, 1979.
19. Johnson, L.A.S. and Briggs, B.G., Myrtales and Myrtaceae: a phylogenetic analysis, *Ann. Missouri Bot. Gard.*, 71, 700, 1984/5.
20. Wilson, P.G. et al., Relationships within Myrtaceae sensu lato based on a *matK* phylogeny, *Pl. Syst. Evol.*, 251, 3, 2005.
21. Ashton, P.S., Myrtaceae, in *A Rev. Handbook Fl. Ceylon* 2, Dassanayake, M.D., Ed., Balkema, Rotterdam, 1981, 403.
22. Kostermans, A.J.G.H., *Eugenia*, *Syzygium* and *Cleistocalyx* (Myrtaceae) in Ceylon, *Quart. J. Taiwan Mus.*, 34, 117, 1981.
23. Simpson, S.C. and Weiner, E.S.C., *The Oxford English Dictionary*, Book Club Associates for Oxford University Press, London, 1989.
24. Willis, J.C., *Age and Area*, Cambridge University Press, Cambridge, 1922.
25. Minelli, A., *Biological Systematics: The State of the Art*, Chapman and Hall, London, 1993.
26. Minelli, A., Fusco, G., and Sartori, S., Self-similarity in biological classifications, *Biosystems*, 26, 89, 1991.
27. Frodin, D.G., History and concepts of big plant genera, *Taxon*, 53, 753, 2004.
28. Chantaranothai, P. and Parnell, J., *Syzygium*, in *Fl. Thailand* 7, Santisuk, T. et al., Eds., Forest Herbarium, Royal Forest Department, Bangkok, 2002, 811.
29. Turner, I.M., Myrtaceae, in *A Catalogue of the Vascular Plants of Malaya: Gardens' Bull. Singapore*, 47, 370, 1995.
30. Chantaranothai, P. and Parnell, J., A revision of *Acmena*, *Cleistocalyx*, *Eugenia* s.s. and *Syzygium* (Myrtaceae) in Thailand, *Thai Forest Bull.*, 21, 1, 1994.
31. Gamage, H.K., Ashton, M.S. and Signhakumara, B.M.P., Leaf structure of *Syzygium* spp. (Myrtaceae) in relation to site affinity within a tropical rain forest, *Bot. J. Linn. Soc.*, 141, 365, 2003.
32. Poonswad, P., Nest site characteristics of four sympatric species of hornbills in Khao Yai National Park, Thailand, *Ibis*, 137, 183, 1995.
33. FAOSTAT, *Food and Agricultural Organisation Statistical Data*, <http://faostat.fao.org/faostat>, 2005.
34. Oyen, L.P.A. and Xuan, Dung, N., Introduction, in *PROSEA (Plant Resources of South East Asia) 19: Essential Oils*, Oyen, L.P.A. and Xuan Dung, N., Eds., Backhuys, Leiden, 1999, 15.
35. Sardjono, S., *Syzygium polyanthum* (Wight) Walpers, in *PROSEA (Plant Resources of South East Asia) 13: Spices*, de Guzman, C.C. and Siemonsma, J.S., Eds., Backhuys, Leiden, 1999, 218.
36. Panggabean, G., *Syzygium*, in *PROSEA (Plant Resources of South East Asia) 2: Edible Fruits and Nuts*, Oyen, L.P.A. and Xuan Dung, N., Eds., Backhuys, Leiden, 1992, 292.
37. Vinning, G. and Moody, T., Wax apple, in *A Market Compendium of Tropical Fruit*, RIRDC, Barton, ACT, 1997, 267.
38. Hyland, B.P.M., A revision of *Syzygium* and allied genera (Myrtaceae) in Australia, *Austral. J. Bot. Suppl. Ser.*, 9, 1, 1983.
39. Djado Djipaa, C., Delmée, M., and Quetin-Leclercq, J., Antimicrobial activity of bark extracts of *Syzygium jambos* (L.) Alston (Myrtaceae), *J. Ethnopharmacol.*, 71, 307, 2000.
40. Shafi, P.M., et al., Antibacterial activity of *Syzygium cumini* and *Syzygium travancoricum* leaf essential oils, *Fitoerapia*, 73, 414, 2002.
41. Eddowes, P.J., Water gum, in *Commercial Timbers Papua New Guinea: Their Properties and Uses*, Office of Forests, Port Moresby, 1977, 20.
42. Hartley, T.G. and Perry, L.M., A provisional enumeration of species of *Syzygium* Myrtaceae from Papusia, *J. Arnold Arb.*, 54, 160, 1973.

43. Craven, L.A. and Matarczyk, C.A., *Acmena*, *Acmenosperma*, *Eugenia*, *Syzygium*, *Waterhousea*, in *Fl. Australia*, Wilson, A., Ed., in press.
44. Chen, J. and Craven, L.A., Myrtaceae, in *Fl. China*, Zhengyi, W. Raven, P.H. and Deyuan, H., Eds., in press.
45. Stevens, P.F., On characters and characters states: do overlapping and non-overlapping variation, morphology and molecules all yield data of the same value, in *Homology and Systematics*, Scotland, R. and Pennington, T., Eds., Taylor and Francis, London, 2000, 80.
46. Linnaeus, C., *Species Plantarum*, Impensis Laurentii Salvii, Stockholm, 1753.
47. De Candolle, A.P., Myrtaceae, in *Prodr. Syst. Nat. Reg. Veg.* 3, Treuttel and Würz, Paris, 1828, 207.
48. Wight, R., Myrtaceae, in *Illustrations of Indian Botany* 2, American Mission Press, Madras, 1841, 6.
49. Benthams, G., Notes on Myrtaceae, *J. Linn. Soc., Bot.* 10, 101, 1869.
50. Benthams, G. and Hooker, J.D., Myrtaceae, in *Genera Plantarum* 1, Reeve and Co., London, 1865, 690.
51. Blume, C.L., Myrtaceae, in *Mus. Bot. Lugduno-Batavum*, Brill, Leiden, 1850, 66.
52. Miquel, F.A.W., Myrteae, in *Fl. Ned. Indië* 1, Post, Amsterdam, Post, Utrecht, Fleischer, Leipzig, 1855, 407.
53. Henderson, M.R., The genus *Eugenia* (Myrtaceae) in Malaya, *Gardens' Bull. Singapore*, 12, 1, 1949.
54. Merrill, E.D. and Perry, L.M., Reinstatement and revision of *Cleistocalyx* Blume (including *Acicalyptus* A. Gray), a valid genus of the Myrtaceae, *J. Arnold Arb.*, 18, 322, 1937.
55. Merrill, E.D. and Perry, L.M., A synopsis of *Acmena* DC., a valid genus of the Myrtaceae, *J. Arnold Arb.*, 19, 1, 1938.
56. Merrill, E.D. and Perry, L.M., On the Indo-Chinese species of *Syzygium* Gaertner, *J. Arnold Arb.*, 19, 99, 1938.
57. Merrill, E.D. and Perry, L.M., The Myrtaceae of China, *J. Arnold Arb.*, 19, 191, 1938.
58. Merrill, E.D. and Perry, L.M., The myrtaceous genus *Syzygium* Gaertner in Borneo, *Mem. Amer. Acad. Arts Sci.*, 18, 135, 1939.
59. Merrill, E.D. and Perry, L.M., Plantae Papuanae Archboldianae, IX, *J. Arnold Arb.*, 23, 233, 1942.
60. Merrill, E.D., Readjustments in the nomenclature of Philippine *Eugenia* species, *Phil. J. Sci.*, 79, 351, 1951.
61. Ingle, H.D. and Dadswell, H.E., The anatomy of the timbers of the South-west Pacific area, *Austral. J. Bot.*, 1, 353, 1953.
62. Pike, K.M., Pollen morphology of Myrtaceae from the South-west Pacific area, *Austral. J. Bot.*, 4, 3, 1956.
63. Khatijah, H.H., Cutler, D.F., and Moore, D.M., Leaf anatomical studies of *Eugenia* L. (Myrtaceae) species from the Malay Peninsula, *Bot. J. Linn. Soc.*, 110, 137, 1992.
64. Haron, N.W. and Moore, D.M., The taxonomic significance of leaf micromorphology in the genus *Eugenia* L. (Myrtaceae), *Bot. J. Linn. Soc.*, 120, 265, 1996.
65. Parnell, J., Pollen of *Syzygium* (Myrtaceae) from S.E. Asia, especially Thailand, *Blumea*, 48, 303, 2003.
66. Belsham, S.R. and Orlovich, D.A., Development of the hypanthium in *Acmena smithii* and *Syzygium australe* (*Acmena* alliance, Myrtaceae), *Austral. Syst. Bot.*, 16, 621, 2003.
67. Porter, E.A., Nic Lughadha, E., and Simmonds, M.S.J., Taxonomic significance of polyhydroxyalkaloids in the Myrtaceae, *Kew Bull.*, 55, 615, 2000.
68. Hartley, T.G. and Craven, L.A., A revision of the Papuan species of *Acmena* (Myrtaceae), *J. Arnold Arb.*, 58, 325, 1977.
69. Biffin, E., unpublished data, 2005.
70. Tobe, H., unpublished data, 2005.
71. Harrington, M.G. and Gadek, P.A., Molecular systematics of the *Acmena* alliance (Myrtaceae): phylogenetic analyses and evolutionary implications with reference to Australian taxa, *Austral. Syst. Bot.*, 17, 63, 2004.
72. Biffin, E., Craven, L.A., Crisp, M.D., and Gadek, P.A., Molecular systematics of *Syzygium* and allied genera (Myrtaceae): evidence from the chloroplast genome, *Taxon*, 55, 79, 2006.
73. Biffin, E. et al., Evolutionary relationships within *Syzygium* s.l. (Myrtaceae): molecular phylogeny and new insights on morphology, *Proc. Sixth Fl. Males. Symp.*, in press.
74. Smith, A.C., Myrtaceae, in *Fl. Vitiensis Nova* 3, Pacific Tropical Botanical Garden, Lawai, Hawaii, 1985, 289.
75. Dawson, J.W., Myrtaceae, Myrtoideae I: *Syzygium*, *Fl. Nouvelle-Calédonie*, 23, 1, 1999.
76. Utteridge, T., Review of checklist of woody plants of Sulawesi, Indonesia, *Blumea Supplement* 14, *Kew Bull.*, 59, 174, 2004.

77. Parnell, J., The conservation of biodiversity: aspects of Ireland's role in the study of tropical plant diversity with particular reference to the study of the flora of Thailand and *Syzygium*, in *Biodiversity: The Irish Dimension*, Rushton, B.S., Ed., Royal Irish Academy, Dublin, 2000, 205.
78. Parnell, J.A.N. et al., Plant collecting spread and densities; their potential impact on biogeographical studies in Thailand, *J. Biogeogr.*, 30, 1, 2003.
79. Parnell, J., European plant systematics and the European Flora, in *Systematics Agenda 2000: The Challenge for Europe*, Blackmore, S. and Cutler, D., Eds., Samara Publishing for the Linnean Society of London, London, 1996, 31.
80. Roos, M.C., Charting tropical plant diversity: Europe's contribution and potential, in *Systematics Agenda 2000: The Challenge for Europe*, Blackmore, S., and Cutler, D., Eds., Samara Publishing for the Linnean Society of London, London, 1996, 54.
81. Schram, F.R. and Los, W., Training systematists for the 21st century, in *Systematics Agenda 2000: The Challenge for Europe*, Blackmore, S., and Cutler, D., Eds., Samara Publishing for the Linnean Society of London, London, 1996, 89.
82. Walmsley, Baroness et al., *What on Earth?* House of Lords Select Committee on Science and Technology Third Report, London, <http://www.publications.parliament.uk/pa/ld200102/ldselect/ldsctech/118/11802.htm>, 2002.
83. Scott, A.J., *Syzygium*, in *Fl. Mascareignes* 92, Bosser, J. et al., Eds., MSIRI, Mauritius; ORSTOM, Paris; RBG, Kew, 1990, 28.
84. Verdcourt, B., *Syzygium*, in *Fl. Trop. East Africa*, Beentje, H.J., Ed., Balkema, Rotterdam, Brookfield, 2001, 67.
85. Parnell, J. and Chantaranothai, P., *Myrtaceae*, in *Fl. Laos, Cambodg. Viet.*, Vidal, J. and Hull, S., Eds., Muséum National d'Histoire Naturelle et Association Botanique Tropicale, Paris, in prep.
86. Ashton, P.S., *Myrtaceae*, in *Tree Fl. Sabah Sarawak*, Forest Research Institute, Malaysia, in prep.
87. Craven, L.A., *Syzygium* (Myrtaceae) in Papuasia, in prep.
88. Boulter, S.L. et al., Any which way will do: the pollination biology of a northern Australian rainforest canopy tree (*Syzygium sayeri*; Myrtaceae), *Bot. J. Linn. Soc.*, 149, 69, 2005.
89. Hopper, S.D., Pollination of the rainforest tree *Syzygium tierneyanum* (Myrtaceae) at Kuranda, Northern Queensland, *Aust. J. Bot.*, 28, 223, 1980.
90. Lack, A.J. and Kevan, P.G., On the reproductive biology of a canopy tree, *Syzygium syzygioides* (Myrtaceae), in a rain forest in Sulawesi, Indonesia, *Biotropica*, 16, 31, 1984.
91. Chantaranothai, P. and Parnell, J., The breeding biology of some Thai *Syzygium species*, *Trop. Ecol.* 35, 199, 1994.
92. Free, J.B., Myrtaceae, in *Insect Pollination of Crops*, 2nd ed., Academic Press, London, 1993, 383.
93. Ladd, P.G., Parnell, J.A.N., and Thomson, G., Anther diversity and function in *Verticordia* DC. (Myrtaceae), *Pl. Syst. Evol.*, 219, 79, 1999.
94. Ladd, P.G., Parnell, J., and Thompson, G., The morphology of pollen and anthers in an unusual myrtaceous genus (*Verticordia*), in *Pollen and Spores: Morphology and Biology*, Harley M.M., Morton C.M. and Blackmore S., Eds., Royal Botanic Gardens Kew, London, 2000, 325.
95. Greuter, W. et al., *Int. Code Bot. Nomenclature (Saint Louis Code)*, Koeltz Scientific Books, Königstein, 2000.
96. Craven, L.A., unpublished data, 2002.
97. Olmsted, R.G. and Scotland, R.W., Molecular and morphological datasets, *Taxon*, 54, 7, 2005.
98. Álvarez, I. and Wendel, J.F., Ribosomal ITS sequences and plant phylogenetic inference, *Mol. Phyl. Evol.*, 29, 417, 2003.
99. Biffin, E., unpublished data, 2005.
100. Miller, J.A., Assessing progress in systematics with continuous jackknife function analysis, *Syst. Biol.*, 52, 55, 2003.
101. Nordal, I. and Stedje, B., Paraphyletic taxa should be accepted, *Taxon*, 54, 5, 2005.