Conclusions

This study has arisen from the need to identify material from Southeast Asia that has been generally placed within the *Rothmannia* complex. It has had to consider doubts on the taxonomic limits of *Rothmannia* raised by Bremekamp (1957), Keay (1958), Wong (1984) and Bridson & Verdcourt (1988), including the inclusion of African and Asiatic species together in the same genus.

9.1 Character survey through morphological, micromorphological and palynological studies: the recognition of specialized groups in the *Rothmannia* complex

A survey of various characters (including general morphology, lower leaf surface micromorphology and palynology) prior to undertaking the cladistic analyses showed that only two somewhat distinct groups could be easily recognized within the *Rothmannia* complex. The two groups referred to include *Rothmannia* s.s. and *Kochummenia*, as follows.

(i) *Rothmannia* s.s.

This coherent group comprises the African type species and an alliance of eight species, i.e., *R. annae*, *R. capensis*, *R. fischeri* (3 subsp.), *R. hispida*, *R. lateriflora*, *R. libisa*, *R. librechtsiana*, *R. octomera*, and *R. ravae*. This group is easy to recognise through a combination of characters: truly solitary flowers terminating the flowering branches (and lack of bracteoles on the flower-bearing axis); right-contorted corolla
lobes; and Type I pollen characterised by reticulate (or sometimes microreticulate) pollen sexine, generally narrow ectocolpi, and presence of granules or luminal processes within pollen lumina. Two of the characters, i.e., right-contorted corolla lobes and pollen granules or luminal processes, are apparently uncommon within the Gardenieae or Rubiaceae (see Robbrecht, 1988 and Johansson, 1987). Hence, the characterisation of the group by such a combination of characters suggested that the group was rather distinct within the *Rothmannia* complex (indeed, this group should define the genus, if doubts arise as to the correct application of the name *Rothmannia* to the entire complex).

(ii) *Kochummenia*

*Kochummenia*, accepted as a closely related genus of *Rothmannia* (and formerly placed in *Rothmannia* by Bremekamp, 1957) has a branch system and leaf arrangement as in other members of *Rothmannia*. However, its two known species and a third unnamed species form a coherent group that differs significantly from other taxa in the *Rothmannia* complex by several characters, i.e., a subhypocrateriform corolla with long linear lobes, and anthers inserted at the basal part of the corolla tube. In terms of lower leaf surface micromorphological characters, *Kochummenia* can be distinguished by its unique pattern of anticlinal wall outlines of epidermal cells that are deeply sinuated, i.e., waves with very large amplitudes (Type C).

Two aberrant taxa, *R. macrophylla* and *R. globosa*, were also found. They are considered aberrant because of variance from other members of the complex in a very distinctive character: the possession of branch leaves in pairs, not (as in other members of the complex) having the branch leaves in 3-leaf clusters (based on the approximation of a 2-leaf node and a 1-leaf node). Besides this, each taxon also has further deviating characters. *R. macrophylla* has typically 2-node primary branches terminated by an
inflorescence, with subsequent higher-order branching typically absent. Its branch leaves are in a pair at the proximal node but are completely vestigial at the distal node. Among Malesian species of the complex, it is also the only taxon with infundibular corollas, long anthers (20–25 mm long), large pollen and wide ectocolpus. The African \textit{R. globosa} is also distinguishable from the rest of the \textit{Rothmannia} complex by a non-modal branch development, where each branch segment that terminates in an inflorescence comprises a variable number of (2–5–many) nodes (unlike the regular binodal branch modules of other \textit{Rothmannia} species). No characteristic leaf reduction is found in this species. \textit{R. globosa} also has a granular lower leaf cuticular ornamentation, which is unique within the entire complex.

The rest of the \textit{Rothmannia} species (from Africa, Asia and SW Pacific) are difficult to group in any way. Generally, they have basically dichasial cymes (rarely so much reduced as to bear just a solitary flower, whence the flower-bearing axis bears bracteoles homologous to those subtending branches in a cyme) and left-contorted corolla lobes. These are very general characters found in the Gardenieae and, indeed, any flowering plant group, and so cannot by themselves be considered unifying characters for a generic group.

The lack of further clearly subdividing characters is, in itself, also quite interesting, as a significant number of taxa (41 species) are involved. Pollen characteristics appear to be much varied among these taxa. Some trends, perhaps noteworthy, although they remain difficult to interpret, at least within the scope of the present analysis. These are as follows:

(i) In Africa, the corollas are either infundibular or campanulate but never hypocrateriform (whereas in the Asian and SW Pacific species, the corolla are mostly hypocrateriform and only a small number are campanulate; the infundibular form is only found in one aberrant taxon, \textit{R. macrophylla}).
(ii) The majority of the African species tend to have relatively larger corolla compared to the Asian and SW Pacific species.

(iii) In Africa and mainland Asia (including the Andaman Islands), there are many (not all) species with speckled corolla throats (in the Malesian species, non-speckled corollas are the more common type).

(iv) In Africa many species have a reduced number of flowers per cyme (among the mainland Asian and Malesian species, most have a larger number of flowers per cyme).

(v) In Africa and mainland Asia, part or all of the inner corolla tube of most species is always hairy (in the Malesian species, a significant number has a glabrous inner corolla tube).

(vi) In Africa and mainland Asia, more species tend to have a style and stigma that are distinctly exsert from the corolla mouth (in the Malesian species, the style and stigma are typically included, and in some species the style and stigma are even much below the level of the anthers).

9.2 Inferences from, and inadequacies of, the cladistic analyses

Two cladistic analyses were made, the first examining the chloroplast trnQ-rps 16 intergenic spacer region of a very restricted number of taxa (limited by availability of, and opportunity for procuring, material) (see Chapter 7). This analysis demonstrated that representatives of the Rothmannia s.s. group (recognised in 9.1) were more closely related to the aberrant R. globosa (also from Africa) than the species of Rothmannia s.l. from Malesia. This suggests that the Malesian taxa are not likely to be congeneric with the type alliance, or Rothmannia s.s., although in its present state, the cladistic analysis,
by sheer exclusion of a wider range of known related genera of the Gardenieae, is not able to demonstrate clear relationships.

The other cladistic analysis utilised as many as possible of the characters derived from morphology, leaf surface micromorphology and palynology, and in effect also attempted to examine relationships among the many species within Rothmannia s.l. It included more species belonging to Rothmannia s.l. than the molecular analysis, including representatives from Malesia, Asia and Africa, as well as the other entities of the complex (Rothmannia s.s., Heinsenia, Kochummenia, and the two aberrant taxa mentioned). The somewhat expected results showed that the only clear terminal clustering was by the Rothmannia s.s. group and between both species of Kochummenia; all other species were not resolved. This indicated that the bulk of species now placed as Rothmannia s.l. could not be easily subdivided (although further character discovery, necessarily through studying even more cryptic features, could theoretically improve the analysis). At the same time, this analysis was not adequate for showing the potential generic alliances, again because its scope excluded a wider range of Gardenieae genera.

In spite of the limited interpretations possible, the cladistic analyses performed here can be taken to strongly suggest that the most fruitful possible approach to understanding the cladistic relationships of the Rothmannia complex, and the generic status of its members, is through a molecular study that includes a wider range of Gardenieae genera and a much wider sampling of the present study group. Although this is clearly what was not attempted in the present work, it represents a useful perspective for guiding subsequent analyses.

Thus, although it was not possible to demonstrate conclusive relationships among the taxa within the Rothmannia complex, several notions can be inferred from
both the morphological study together with the cladistic analyses performed. These include the following.

(i) *Rothmannia* is probably paraphyletic as currently circumscribed.

(ii) *R. macrophylla* and *R. globosa* are morphologically aberrant (and probably also taxonomically distinct) from the rest of the *Rothmannia* complex, although their relationship to these other elements within the *Rothmannia* complex is not clearly established.

(iii) the relationship of *Kochummenia* and *Heinsenia* to other elements in the *Rothmannia* complex cannot be established: with more evidence and a wider-scope molecular analysis, these may turn out to be either distinct, closely related genera, or simply part of a larger generic entity within the complex.

### 9.3 Taxonomic implications from the present study

Given the indications and circumstances summarised in sections 9.1 and 9.2, the following taxonomic approach appears judicious, until a wider-scope molecular analysis is in place:

(i) the African type species and its alliance with right-contorted corolla lobes are a closely related group that may be considered as *Rothmannia* in its strict sense (*Rothmannia* s.s.) when such clarity is required;

(ii) all the rest of the other *Rothmannia* with left-contorted corolla lobes from Africa and Asia (including SW Pacific) should still be referred to *Rothmannia* in a wide sense (*Rothmannia* s.l.);

(iii) *R. globosa* and *R. macrophylla*, aberrant within the complex, are maintained with their present names until subsequent study demonstrates generic relationships within the entire complex more clearly;
(iv) the genera *Heinsenia* and *Kochummenia* will continue to be accepted as they are validly described and already in much use in the literature; any potential changes will again have to await clearer indications from subsequent work.

With the above approach in mind, the Malesian taxa are treated as *Kochummenia* (3 species) and *Rothmannia* s.l. (18 species) (taxonomic enumeration in Chapter 8). In order to fulfill the needs of impending taxonomic inventories (such as the regional tree flora projects), and because it is likely that the clearer resolutions required would take a somewhat longer time to obtain, the recognition of five new species, 11 new combinations, and one new variety in *Rothmannia* s.l. is provisionally made.

### 9.4 Some biogeographical interpretations

It is not possible at this time to speculate on the biogeographical relationships of the various elements within *Rothmannia* s.l. Within Malesia, however, the distributional patterns of individual species, or taxa such as *Kochummenia*, show some interesting features.

#### (i) Narrow endemics

These are species or taxa restricted to only one or few sites in a small geographical range (Primack, 1993). The species in this category could be confined to a particular forest type within a restricted locality. Such species would be vulnerable to extinction with severe disturbance or habitat loss, and so are of special conservation concern.

Examples of this category include four species from New Guinea, one from the Philippines, and three from Peninsular Malaysia. The New Guinea species are only known in restricted areas within one Province each, and their distributions do not overlap (see Fig. 84 in Chapter 8). *R. kassamensis* was recorded from Kassam Pass in
the Kainantu subdistrict in a vegetation described by Damas (1998) as montane altitudinal zone, at 1000–1400 m, in the Eastern Highlands Province. *R. macromera* was recorded mainly from lower montane forest dominated by *Araucaria* species (750–1060 m) in the Morobe Province. *R. papuana* is represented by only three collections thus far and found in the seasonally dry evergreen lowland rain forest, to c. 70 m altitude, within the “Central Province Monsoon Forests” (Saulei & Beehler, 1993) in the Central Province. *R. uvarioides* has been found only in disturbed hill forests to 125 m elevation, within the “Sepik Alluvial Lowland Forests” (Saulei & Beehler, 1993) in the East Sepik Province.

In the Philippines, *R. leytensis* is known from only four specimens collected from Leyte, all collected around 1914–1923. Its extinction cannot be ruled out, because of over-exploitation of forests for logging and agriculture from the early 1950s until mid-1970s (Primack & Corlett, 2005).

*Kochummenia stenopetala* is found only in a few localities in Perak state in Peninsular Malaysia. The other two species, *K. parviflora* and *K. sp. 1*, have only so far been documented in the state of Terengganu, also in Peninsular Malaysia. All appear to be from primary and secondary lowland and hill dipterocarp forests, where logging damage often contributes to severe habitat modification, hence this genus should be considered of special conservation concern.

(ii) **Endemics common within an island**

Examples of this category include the New Guinean *R. anisophyloides*, recorded from lowland forests to 900 m in the Provinces of Madang, Northern, East Sepik and Central in Papua New Guinea, and Windowoi Mountain in West Irian Jaya Province, Irian Jaya. Another New Guinean species, *R. nigrescens*, was recorded from lowland
to hill forests, on ultrabasic and volcanic soils, to 730 m in the Madang, Morobe, Western, Milne Bay, Southern, Northern, Central and East Sepik Provinces.

In Borneo, *R. ridsdalei* and *R. pseudoternifolia* var. *hispida* occur in all territories. *R. ridsdalei* occurs typically on hill to lower montane forests, to 1550 m in Sabah and Sarawak but may also be found in lowland forests in Brunei and Kalimantan, whereas *R. pseudoternifolia* var. *hispida* is found in primary and secondary forests in the lowlands and hill forests, including *kerangas* forests and seasonal flood-plain areas (e.g., fresh-water swamp forests), to 580 m altitude. In Sulawesi, *R. forsteniana* can be found in the Provinces of North, Central, Gorontalo and South, in primary and disturbed forests from lowlands to lower montane forests around 1050 m, on limestone, clayey, volcanic or alluvial soils.

(iii) Taxa widespread across two or more major islands

Examples include *R. grandis*, *R. merrillii*, *R. sundaensis*, *R. schoemannii*, *R. macrophylla*, and *R. pseudoternifolia* var. *pseudoternifolia*. *R. macrophylla*, although endemic to West Malesia, is common and widespread in all states in the Peninsular Malaysia, also found in Singapore and the Jambi, Central Sumatra, Riau and Riau Islands Provinces in Sumatra. It grows commonly in primary lowland to hill dipterocarp forest, in secondary forests, and even in swampy areas, to 1200 m altitude. *R. pseudoternifolia* var. *pseudoternifolia* occurs in a variety of habitats (lowlands, hill forests, lower montane forests, *kerangas* forests, limestone and seasonal flood-plain areas (e.g., fresh-water swamp forests) in all territories in Borneo and only in the Riau and Riau islands Provinces in Sumatra.

There are also examples of species in the *Rothmannia* complex that reflect so-called floristic provinces (specialised phytogeographical patterns) discussed by other authors (e.g., Corner, 1960; Wong, 1998).
(i) “Riau Pocket”

This floristic province was recognised by Corner (1960) and discussed by Wong (1998). The area defined by this province lies within the Sunda Shelf, typically including Central Sumatra, and the Riau islands, the eastern and southeastern part of the Malay Peninsula, and northwest Borneo. The distribution of *R. grandis* conforms to this pattern and has been recorded frequently in swamps, including peat swamp and *kerangas* forests, also in Dipterocarp forest, along ridges, to 1200 m in Peninsular Malaysia, Sumatra and Southwest and South Borneo. These areas have been connected in the past during the Pleistocene period during which time the sea-level dropped. Hence, species distributed only within these regions are surmised to have their range presently fragmented by increased sea levels.

(ii) “The seasonal Asiatic-Australasian intrusion”

The seasonal Asiatic-Australasian intrusion is shown in *R. merrillii*, a species distributed in the Philippines (East and South Luzon, Mindoro, Palawan, Negros, Panay and the smaller islands such as Sibuyan, Guimaras, Calamian group, Golo and Semirara) and also in Sabah (commonly in the north and north-eastern part and also western part, up to Beaufort)—in other words, the more distinctly seasonal parts of Malesia or drier parts within a generally wetter region more towards the equator from these. *R. schoemannii* also occurs in the seasonal areas of Myanmar, Thailand and Java, and similarly "intrude" along corridors of drier or similar climatic conditions into Peninsular Malaysia and Sumatra.
9.5 Suggestions for future work

A wider-scope molecular analysis of the entire complex, and also including a wider array of genera belonging to the Gardenieae, is a priority. This would allow better resolution of genera within the tribe, and justifiable generic groups within the complex.

Besides using just one region of the chloroplast gene, it would seem more justifiable to use different gene regions or perhaps, other genes to compare results. This could also be combined with a morphological cladistic analysis to assess its congruence in both data sets.

Some species are not completely documented, for instance, mature fruits of *Rothmannia macromera* and *R. uvarioides* from New Guinea and *R. graciliflora* from the Philippines are not yet known. Additionally, two insufficiently known species, *R.* sp. 1 and *R.* sp. 2, both from Peninsular Malaysia, lack flowering material for proper identification. Hence, better and more complete material is needed.

In terms of conservation, efforts should be taken in procuring living material (e.g., wildings, seedlings or cuttings) of rare and endemic species of *Rothmannia* s.l. and also *Kochummenia* for conservation purposes and future investigations.