Part One:

General Introduction
CHAPTER 1

INTRODUCTION

1.1 Background

1.1.1 A little-studied genus in a rich floristic region

Malesia is a natural phytogeographic area or floristic region that constitutes the Sunda Shelf (Malay Peninsula, Sumatra, Java and Borneo), Wallacea (the Philippines, Celebes, the Lesser Sunda Islands and the Moluccas) and the Sahul Shelf (New Guinea) as subunits (Van Welzen et al., 2005). It is considered one of the richest tropical rainforest regions that harbours c. 10% of the world’s flora (Whitmore, 1985). Its north-western extent includes the north of the Thai-Malaysian border with some of the southern provinces of peninsular Thailand. The northernmost limit is between Taiwan and the Philippines, while to the south, the Malesian region includes New Guinea just north of Australia, and to the eastern boundary New Guinea and some neighbouring islands (including the Bismarck Archipelago but not the Louisiades and the Solomons) are also included (Van Steenis-Kruseman, 1950 and later works by Van Welzen et al., 2005). Within this very rich region, the Rubiaceae are one of the most diverse groups. Many of the genera are poorly studied and are in need of revision (Puff & Wong, 1993). One of these genera, *Rothmannia* Thunb., distributed from Africa to Asia and the SW Pacific, is considered taxonomically problematic.

*Rothmannia*, placed within the tribe Gardenieae and Ixoroideae subfamily (Robbrecht, 1988), was first described in 1776 by Thunberg after Dr Georgius Rothman...
(1739–1778), a Swedish physician and botanist. Its type species is the South African *R. capensis* Thunb.

As of 2005, a total of 73 published binomials for *Rothmannia* have been documented in IPNI (International Plant Names Index), whereas 70 binomials have been documented in World Checklist Rubiaceae up to 2007, representing taxa from tropical and subtropical Africa, the Seychelles, Myanmar, Indo-China, Thailand, the Andaman Islands, South China, the Malay Peninsula, Java, Sumatra, Borneo and Papua New Guinea. Out of these, nine binomials have been described for parts of Malesia (Fagerlind, 1943; Bremekamp, 1957; Tirvengadum, 1983; Wong, 1984, 1989) (see also Puff & Wong, 1993). Although Wong (1984) reviewed the whole assemblage of *Randia* s.l. for Peninsular Malaysia and segregated *Rothmannia* as a distinct genus, a complete revision for Malesia has not been made. Recent checklists, such as Puff & Wong (1993), Coode et al. (1996), and Beaman & Anderson (2004) recognised the existence of unnamed or improperly understood taxa in *Rothmannia*.

1.1.2 **Taxonomic uncertainties in Rothmannia**

The delimitation of *Rothmannia* has been superficial and contentious. In the past, *Rothmannia* species have been placed under *Randia* s.l., e.g., *Randia* sect. *Euclinia* in De Candolle (1830), Hooker (1873) and Schumann (1891), including in floras and checklists by Oliver (1877), Hooker (1880), King & Gamble (1903), Merrill (1921), Ridley (1923), Pitard (1923), Hutchinson & Dalziel (1931), Craib (1932), Masamune (1942) and Backer & Bakhuizen (1965). Sometimes, *Rothmannia* species have also been placed in *Gardenia* s.l., e.g., *Gardenia* sect. *Rothmannia* in Endlicher (1838), Hooker (1873) and Schumann (1891), and also in floras and checklists by Miquel (1856), Merrill (1921) and Masamune (1942). The inclusion of such species in *Randia* s.l. and *Gardenia* s.l. was arbitrarily based on characters such as bilocular
ovaries in defining ‘Randia’ and unilocular ovaries in ‘Gardenia’, and also placental position. Fagerlind (1943) was the pioneer in demonstrating the heterogeneity of Randia through the use of characters including branching patterns and pollen grain features. As a consequence, he re-established three genera, including Rothmannia and made several new combinations in Rothmannia.

Various authors have accepted Rothmannia as a distinct genus among the African species of this complex, including Keay (1958), Hepper & Keay (1963), Hallé (1970), Dyer (1975), Bridson & Verdcourt (1988), Palgrave (1988), Somers & Robbrecht (1991) and Sonké & Simo (1996). A New Guinea species was recombined as Rothmannia macromera (Lauterb. & K.Schum.) Fagerl. by Fagerlind in 1943. Likewise, a number of Asiatic species have been described or recombined in Rothmannia, in Bremekamp (1957) for Laos, Indo China; Yamazaki (1970) for East Asia, Tirvengadum (1982, 1983) for South and Southeast Asia, Wong (1987, 1989) for Malaysia, Shui et al. (2003) for South China.

Although Rothmannia has been accepted generally by most taxonomists as an entity distinct from the rest of the Randia-Gardenia complex or Randia s.l., a more thorough analysis taking into account both the African and Asiatic species has not been carried out and the limits of the genus itself have been somewhat arguable, as demonstrated through the work of Bremekamp (1957), Keay (1958), Wong (1984) and Bridson & Verdcourt (1988). Keay (1958) pointed out the occurrence of two types of corolla aestivation within the African species, i.e., corolla lobes contorted to the right in the type species and its allies, and corolla lobes overlapping to the left in the other species. Wong (1984) considered that this kind of variation (right and left contortion of corolla lobes) occurs in Alstonia R.Br. (Apocynaceae) and may have some value in distinguishing infrageneric groups. He recommended a critical examination of both the African and Asiatic Rothmannia species to better understand their relationships, as well
as to confirm characters that are generically important. Additionally, Wong (1984) also concluded that there did not appear to be a single corolla shape for distinguishing Rothmannia as a whole. This can be seen by the variable corolla form, ranging from infundibular, campanulate to salverform (=hypocrateriform) (Wong, 1984; Bridson & Verdcourt, 1988) found among the species.

There is also the need to consider the relationship between Rothmannia, Kochummenia K.M.Wong and Heinsenia K.Schum., which share some interesting characters. Heinsenia is a monotypic African genus that was placed by Robbrecht & Puff (1986) in its own tribe, Aulacocalyceae. Keay (1958) and Bridson & Verdcourt (1988) have pointed out that Heinsenia and Rothmannia share the same branching pattern and have similar corolla speckling (i.e., white with coloured spots inside). In a recent phylogenetic analysis using rbcL sequence data and a combined cladistic analysis using morphological and molecular data (Andreasen & Bremer, 2000), Heinsenia emerged as weakly associated with Rothmannia (the two emerging as a minor clade with poor bootstrap support). The African Aulacocalyx was also placed in the same tribe as Heinsenia by Robbrecht & Puff (1986), and in fact at some point, Heinsenia was placed as a synonym to Aulacocalyx by Petit (1962). Later, Heinsenia was even proposed as a subgenus of Aulacocalyx by Verdcourt (1981). Both these genera share similar characteristics in terms of small number of ovules, 1–2; embryo radicals that are superior; small number of seeds, (1–)2–4 per fruit and seed coats that are lacking or strongly reduced (Robbrecht & Puff, 1986). Nonetheless, only Heinsenia was included in the cladistic analyses in this thesis.

Kochummenia (endemic to Peninsular Malaysia) also has the same branch architecture as Rothmannia. However, in Kochummenia, the corolla form is tubular and the lobes are much longer than the tube, a feature unique to that genus (Wong, 1984; Robbrecht & Puff, 1986) whereas in Rothmannia the corolla can be campanulate,
infundibular and salverform, with broad lobes shorter than the tube. A phylogenetic study by Persson (1996), based on morphological characters, demonstrated Kochummenia as distinct from (the African species of) Rothmannia, but such a study including Asiatic Rothmannia species has not been available.

1.2 Scope of research and objectives

The present study includes a survey of characters of the African taxa, in particular, those most closely related to the type species, as well as other groups that have come to be called Rothmannia in mainland Asia and Malesia; the emphasis, however, is an updated taxonomic revision of the Malesian taxa. A detailed investigation of species from Asia and the SW Pacific region placed under Rothmannia and related generic names, e.g., Randia, Gardenia Ellis, Kochummenia, Porterandia Ridl. and indeterminate specimens of Rubiaceae was carried out in parallel with this. Besides surveying the macromorphological characters, it was thought prudent to investigate various micromorphological characters (lower leaf surface micromorphology and palynology). This was expected to yield further useful insight in comparing the type (African) alliance and other groups in Rothmannia, including the Asiatic (and Malesian) taxa.

This study serves to extend perspectives on the Rothmannia complex developed by past workers, including the morphology-based, Africa-centred phylogenetic analysis of Persson (1996). Although material collection towards a study based on molecular characteristics has begun, a good representation of the various groups is still elusive. With such a large geographical spread and number of taxa, it is unlikely that a comprehensive gathering of such material would be possible within a short time. Thus, the results of the present study would be useful in making various decisions on
plausible “operational taxonomic units” and hypotheses to be further tested in subsequent analyses using a more elaborate molecular analysis.

In brief, the objectives of the present study are as follows—

(i) to gather comparative data based on morphology and fine structure for a direct review of Asiatic (especially Malesian) taxa placed in or near Rothmannia against the type alliance and other species in Africa;

(ii) to consider a tenable framework for classifying the Rothmannia complex with limited analyses based on molecular and also morphological (including micromorphological) evidence; and

(iii) to revise and enumerate the Malesian taxa in this complex, contributing to both national and regional biodiversity inventory and conservation programmes.

Any study investigating generic limits within this group would require inclusion of a significant number of genera of the Gardenieae for comparison. Given that no proper documentation or review of characters have been carried out for the Malesian (and even mainland Asian) taxa placed in Rothmannia and the large number of taxa potentially involved, it was decided that this would be a worthwhile venture only after exploring the various elements forming the Rothmannia complex. This thesis, therefore, especially in Malesia, seeks clues toward a viable approach for resolving the problem in the longer term.

The thesis is presented in three parts. The first part forms the General Introduction that presents the taxonomic history, problems and scope and objectives of study for Rothmannia and its related genera (Chapter 1: Introduction); the past research on Rothmannia and its related genera (Chapter 2: Literature Review) and the materials and methods that were applied in the present study (Chapter 3: Materials and Methods).
The second part presents the results of studies based on macromorphology and some aspects on flower biology (Chapter 4), as well as micromorphological features (including lower leaf surface micromorphology (Chapter 5) and palynology (Chapter 6)). The final part of the thesis forms a tentative taxonomic framework for Rothmannia, incorporating results from the preceding Part Two. Three chapters are presented in this part. Chapter 7 concerns implications from cladistic analyses based on both molecular and morphological (macromorphological and micromorphological) characters. Chapter 8 drafts out a treatment of the Rothmannia complex and enumerates the taxa in Rothmannia s.l. in Malesia. The final synthesis forms Chapter 9 (Conclusions).