

Comprehensive Summaries of Uppsala Dissertations  
from the Faculty of Science and Technology 676



# Phylogenetic Studies in the Euasterids II

*with Particular Reference to  
Asterales and Escalloniaceae*

BY

JOHANNES LUNDBERG



ACTA UNIVERSITATIS UPSALIENSIS  
UPPSALA 2001

Dissertation for the Degree of Doctor of Philosophy in Systematic Botany presented at Uppsala University in 2002

### **Abstract**

Lundberg, J. 2001. Phylogenetic studies in the Euasterids II with particular reference to Asterales and Escalloniaceae. *Acta Univ. Ups. Comprehensive Summaries of Uppsala Dissertations from the Faculty of Science and Technology* 676. 38 pp. Uppsala. ISBN 91-554-5191-8.

The present study is concerned with the evolutionary relationships among the Euasterids II, a group of angiosperms that includes the orders Apiales, Aquifoliales, Asterales, and Dipsacales together with several small, poorly known families yet unplaced as to order.

Parsimony analysis of nucleotide sequence data from the chloroplast genes *atpB*, *ndhF* and *rbcL* together with morphological data are used to construct a phylogeny of the order Asterales, which in the present sense includes 11 families and more than 26 000 species. It is argued that Rouseaceae should be expanded to include also Carpodetaceae (and thus contain four genera), and that *Donatia* should be re-merged with Stylidiaceae. The present study also strongly supports that the sister taxon to the largest plant family, Asteraceae (Compositae), is the small South American Calyceraceae. A new addition to Asterales is *Platyspermation* (formerly in Escalloniaceae).

Using the recently developed Bayesian approach to phylogenetic reconstruction, in combination with a dataset consisting of the *atpB*, *ndhF* and *rbcL* nucleotide sequences, a resolved and fairly well supported phylogeny of the Euasterids II was reconstructed. Based on this analysis, and furthermore supported by morphological characters, the South Hemispheric family Escalloniaceae is recircumscribed to include the monogeneric families Eremosynaceae, Tribelaceae and Polyosmaceae, and in this new circumscription it includes seven genera. The formerly escalloniacean member *Quintinia*, together with the monogeneric families Paracryphiaceae and Sphenostemonaceae, is argued to constitute a monophyletic family Paracryphiaceae *sensu lato*, supported by several morphological characters.

*Johannes Lundberg, Department of Systematic Botany, EBC, Norbyvägen 18D, SE-752 36 Uppsala, Sweden*

© Johannes Lundberg, 2001

ISSN 1104-232X

ISBN 91-554-5191-8

Printed in Sweden by Uppsala University, Tryck & Medier, Uppsala 2001

The thesis is based on the following papers<sup>1</sup>, which will be referred to in the text by their respective Roman numerals:

- I. J. LUNDBERG AND K. BREMER. A phylogenetic study of the order Asterales using one morphological and three molecular data sets. *Manuscript* tentatively accepted for publication in *International Journal of Plant Sciences*.
- II. J. LUNDBERG. 2001. The Asterales affinity of the Mauritian *Roussea* (Rousseaceae). *Botanical Journal of the Linnean Society* **137**: 267-276.
- III. J. LUNDBERG. Polyosmaceae. *Manuscript* tentatively accepted for publication in K. Kubitzki (ed.): *The Families and Genera of Vascular Plants*.
- IV. J. LUNDBERG. Escalloniaceae. *Manuscript* tentatively accepted for publication in K. Kubitzki (ed.): *The Families and Genera of Vascular Plants*.
- V. J. LUNDBERG. A well resolved and supported phylogeny of Euasterids II based on a Bayesian inference, with special emphasis on Escalloniaceae and other incertae sedis. *Manuscript*.

Published and accepted papers are reproduced with the publishers' kind permission.

---

1. Of the 71 nucleotide sequences sequenced for this study, J. Lundberg did 32. All the analyses presented in the thesis are designed and conducted by him. In the first paper J. Lundberg did all morphological and molecular work and analyses. He also prepared the manuscript. K. Bremer initiated and supervised the study and took part in finalising the manuscript.

## CONTENTS

<b>Introduction</b>	5
<b>Asterales: an inside view and a new analysis with Bayesian inference</b>	5
Material and Methods	6
Results	7
Discussion	7
Campanulaceae and Rouseaceae	7
Pentaphragmataceae: an enigmatic family	11
The Core Asterales	11
The MGCA: A four-family clade	12
The sister to Asteraceae	12
<i>Donatia</i> and Stylidiaceae, a reunion	12
Three enigmatic families and an unexpected newcomer	13
<b>Asterales: an outside view</b>	14
What, if anything, is Escalloniaceae	14
The paraphyly of <i>Escallonia</i>	22
Apiales and Dipsacales	23
Paracryphia, Sphenostemon, and <i>Quintinia</i>	24
<b>A synopsis of the classification of Euasterids II</b>	26
<b>A note regarding model based inference of phylogeny</b>	27
Bayesian inference--a short introduction	27
<b>Svensk sammanfattning</b>	30
<b>References</b>	33
<b>Tack!</b>	37

## INTRODUCTION

Systematics is a historical science. It aims to reconstruct and interpret a very peculiar history, that of evolutionary relationships of organisms through time. The backbone of much systematics is the reconstructed phylogeny of the organisms under study. Close to systematics, and sometimes included, stand biogeography, biochemistry, morphology, molecular evolution, ecology etc. The systematist often utilises information from these fields, and the phylogenies reconstructed can be used to gain a new and hopefully better and deeper understanding also in these other fields. It is an iterative process, which is part of our strive to understand better the world around us as well as our position in it.

The systematist does not only work with different related sciences, but also at different levels in the tree of life. It is thus possible to construct relationships between populations of the same species, or to reveal the relationships between the domains of life, or virtually anywhere inbetween. Put into a time scale, the evolutionary relationships reconstructed can deal with events that happened the last 10 000 years, or with relationships reaching back as far as to the very origin of Life itself on Earth, about 4 billion years ago.

In my own work I have tried to reconstruct and understand evolutionary events that took place approximately within the last 100 million years, and I have been working with groups of plants normally recognised at a family or order level. The focus of my research has been the order Asterales, and I have tried to reconstruct the evolutionary history of Asterales, as well as to put it into relation to its closest relatives among the Euasterids II.

I will in this **Comprehensive Summary** try to give a brief summary of my work and to put it into perspective.

## ASTERALES: AN INSIDE VIEW AND A NEW ANALYSIS WITH BAYESIAN INFERENCE

Asterales, one of the most species rich orders of all Angiosperms with more than 26,000 known species, are totally dominated by the largest of all flowering plant families Asteraceae (Compositae)<sup>1</sup>. This is in a way unfortunate, as this family have been dominating the research and focus of this order, and their peculiarities (like flowers in condensed heads and one-seeded dry, indehiscent fruits with their specialised dispersal apparatus, as well as its rather unique chemistry, dominated by the presence of a variety of polyacetylenes and sesquiterpene lactones) have many times been put forward as an argument to isolate Asteraceae, rather than to relate them to other plants (e.g. Takhtajan, 1997). In many taxonomic systems, Asteraceae have even been placed as the sole member of Asterales, while their presumed close relatives have been dispersed in several other orders.

---

<sup>1</sup> It must be admitted, though, that the orchidologists often consider the orchids Orchidaceae as the largest family of all, while the synantherologists of course are of an opposing opinion.

As here circumscribed, Asterales comprise eleven families, about 1 700 genera, and more than 26 000 species. This is also virtually the same circumscription as the one used by the Angiosperm Phylogeny Group (APG, 1998).

The phylogeny of Asterales was the focus of **Paper I**, in which I combined a morphological matrix with the three matrices of the nucleotide sequences from the chloroplast genes *atpB*, *ndhF*, and *rbcL*. In order to be able to analyse all these characters simultaneously I did a cladistic analysis. Late in the work it turned out that the published *rbcL*-sequence of *Cyphia elata* (GenBank accession number L18796; Cosner, Jansen and Lammers, 1994) that I used probably represents a *rbcL*-pseudogene. When the presumed *rbcL*-pseudogene was either removed or replaced by a newly sequenced *rbcL* gene from *C. rogersii*, *Cyphia* moved from a basal position as sister group to the rest of Campanulaceae (see, e.g., **Paper II**) to a more orthodox position as sister taxon to the Nemacladioideae—Lobelioideae clade (thus confirming the results obtained by Demker, 1998). Although the analysis with the substituted *Cyphia rbcL* sequence resulted in only six most parsimonious trees, much of the basal branching in Asterales was unfortunately totally unresolved. As the focus of **Paper I** was the major relationships within Asterales, and not the intra-familial phylogenies, the analysis proceeded without *Cyphia*, and, when *Cyphia* was removed from the analysis, two most parsimonious trees were obtained, with the only ambiguity within the out-group. In view of these findings, it must be stressed that the phylogenetic relationships of Campanulaceae and their closest relatives that have been obtained in previously published analyses using the presumed *rbcL*-pseudogene should be taken with some care (Cosner et al., 1994; Gustafsson et al., 1996; Backlund and Bremer, 1997; Bremer and Gustafsson, 1997; Gustafsson and Bremer, 1997; Kårehed et al., 1999; Savolainen et al., 2000b; **Paper II**).

In an attempt to resolve the basal branchings, and to test the strange Phellinaceae-Argophyllaceae-Stylidiaceae relationship found in **Paper I** (see below), I also did a model-based phylogenetic analysis using Bayesian inference (see *A note regarding model based inference of phylogeny* below, or the review by Lewis, 2001, and references therein). In this analysis I chose to include *Cyphia* as a crude test of the validity of excluding the genus; if both analyses gave the same result regarding the phylogeny of the remaining taxa, it would indicate that the exclusion of *Cyphia* from the parsimony analysis did not influence the relationships of interest.

## Material and Methods

The lab work and the cladistic analysis is described under Material and Methods in **Paper I**, and will not be repeated here. The model-based analysis of Asterales (unpublished) used a Bayesian approach and the aligned nucleotide sequence data sets from **Paper I**, complemented with the *atpB*, *ndhF* and *rbcL* sequences from *Cyphia rogersii*. Thus the morphological data set (100 characters) and the *ndhF*-indel data set (8 characters) were removed prior to analysis. For the analysis MRBAYES (version 2.01; Huelsenbeck and Ronquist, 2001a,b) was used. Posterior clade probabilities were calculated under the General Time Reversible model with a gamma distribution of substitution rates over the sites plus a proportion of invariable sites (GTR +  $\Gamma$  + I). Two Metropolis-coupled Markov chain Monte Carlo with incremental heating temperature 0.2 were run for 100 000 generations and sampled every 100:th generation. The burning

in period was determined graphically, and the first 250 sampled trees were discarded. The posterior probabilities were estimated using the remaining trees.

## Results

The cladistic analysis in **Paper I** resulted in two most parsimonious trees (6398 steps; Fig. 1).

The Bayesian analysis gave a fully resolved tree (i.e., the monophyly of all clades was supported by a posterior probability of at least 50%). All but one of the major, inter-familial, clades were supported by at least 95% (Fig. 2). The single major clade receiving somewhat lower support (91%) is the sister group relationship between Stylidiaceae *sensu lato* and the MGCA clade (node 13 in Fig. 2). The position of Campanulaceae as sister group to Rouseaceae basal in Asterales, and that of *Pentaphragma* as sister taxon to the Core Asterales (node 14 in Fig. 2) was thus the same in both the maximum parsimony trees and in the Bayesian phylogeny, indicating that the exclusion of *Cyphia* from the cladistic analysis was appropriate.

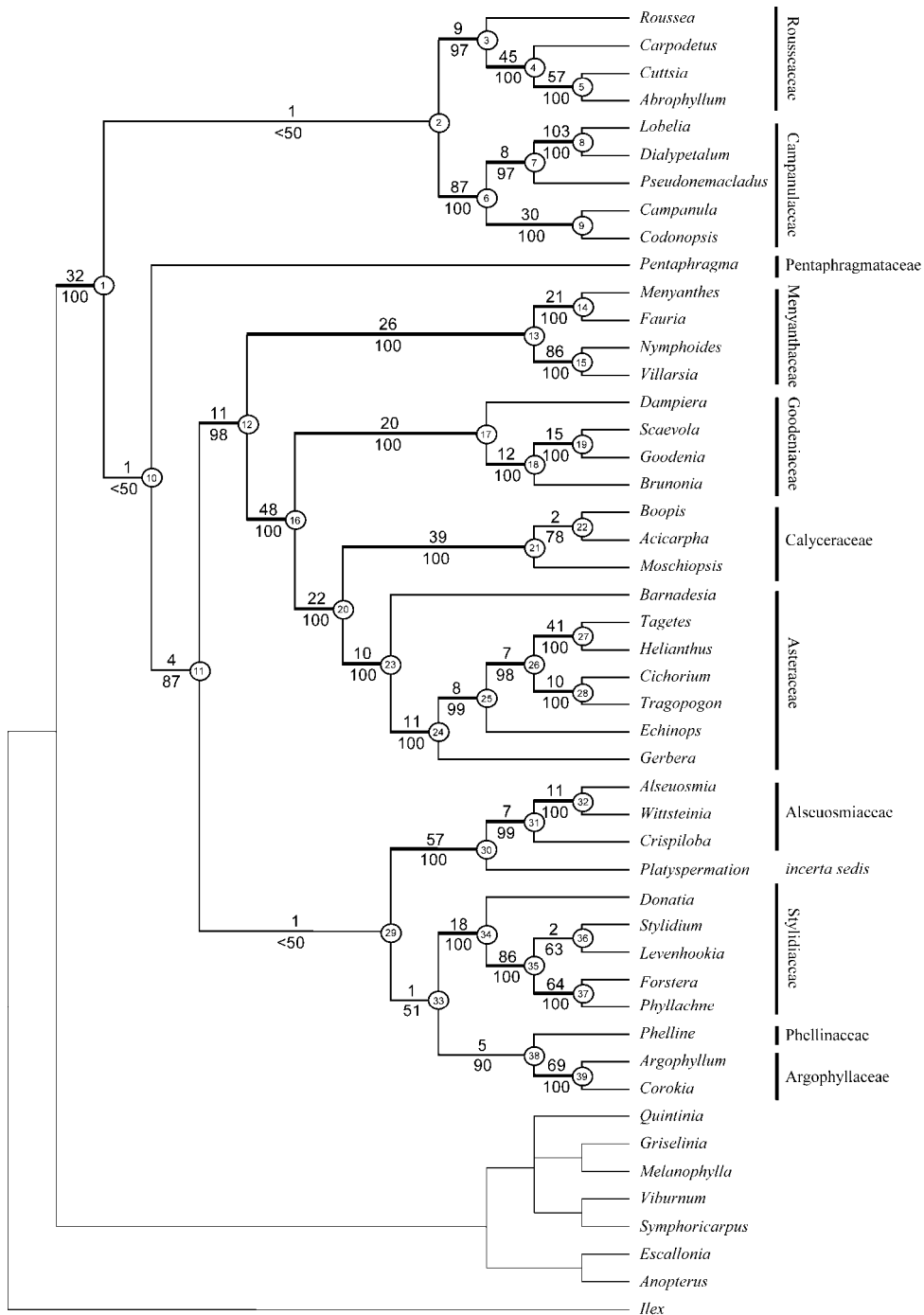
## Discussion

The result from the Bayesian analysis (Fig. 2) of the Asterales matrix is promising. With the exception of the placement of Stylidiaceae *sensu lato*, and some internal relationships within this family, its topology is identical to the parsimony tree (Fig. 1). The posterior probabilities for the monophyly of the clades are generally higher than the jackknife resampling percentages indicate. Furthermore, the support for the alternative position of Stylidiaceae *s.l.* as the sister group to the Phellinaceae-Argophyllaceae clade in the maximum parsimony tree receives very low support (Bremer support = 1, Jackknife < 50%), while the more realistic position of Stylidiaceae *s.l.* (see discussion below) as sister group to the Core Asterales has a posterior probability of 91%.

### Campanulaceae, Rouseaceae

The basalmost branching in Asterales seems to be between a clade consisting of the small family Rouseaceae and Campanulaceae, and the rest of Asterales. Although the support for this branching using maximum parsimony is rather low (**Paper I**), it receives a very high posterior probability (100%).

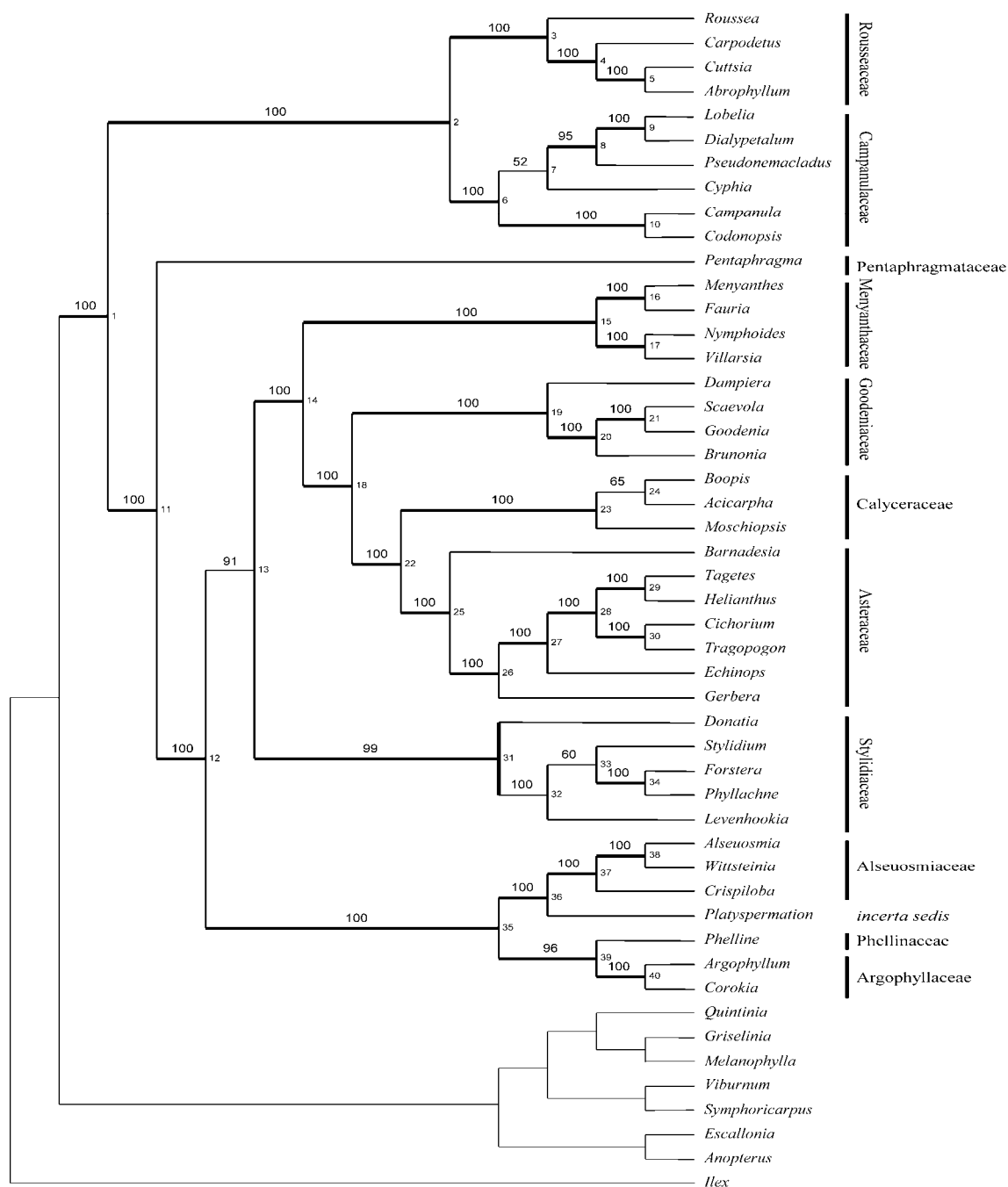
Rouseaceae have historically often been taken as a monotypic family, only consisting of the genus *Roussea*. The sole species, *liane Rousseau* (*R. simplex*; Fig. 3), is a climbing shrub or liana native to mountain forests of Mauritius, a small volcanic island in the Indian Ocean east of Madagascar. More often than not *Roussea* has been associated with two other genera, *Ixerba* and *Brexia*, and this alliance has in turn been regarded as associated with Engler's Saxifragaceae (e.g. Engler, 1928). Today, *Ixerba* seems to be included somewhere among the Eurosids (Koontz and Soltis, 1999; Savolainen et al., 2000b; Soltis et al., 2000) and *Brexia* is merged with Celastraceae of the Eurosids I (e.g. APG, 1998). *Roussea*, on the other hand, was shown to be a member of the Euasterids, and particularly the Asterales, by Soltis and Soltis (1997) and later also by Savolainen, Spichiger and Manen (1997), Soltis et al. (1997), Koontz and Soltis



**Figure 1.** Strict consensus cladogram summarising the two most parsimonious cladograms resulting from the combined analysis (morphological and *atpB*, *ndhF*, and *rbcL* nucleotide sequence data). The trees are 6398 steps long, with a consistency index (excluding uninformative characters) of 0.43, and a retention index of 0.57. The ingroup (Asterales) branch supports are indicated for each branch, with the Bremer support values above the branches, and the jackknife support (in %) below. Well supported branches (jackknife support >94% and Bremer support >5) are thicker than the less well supported.

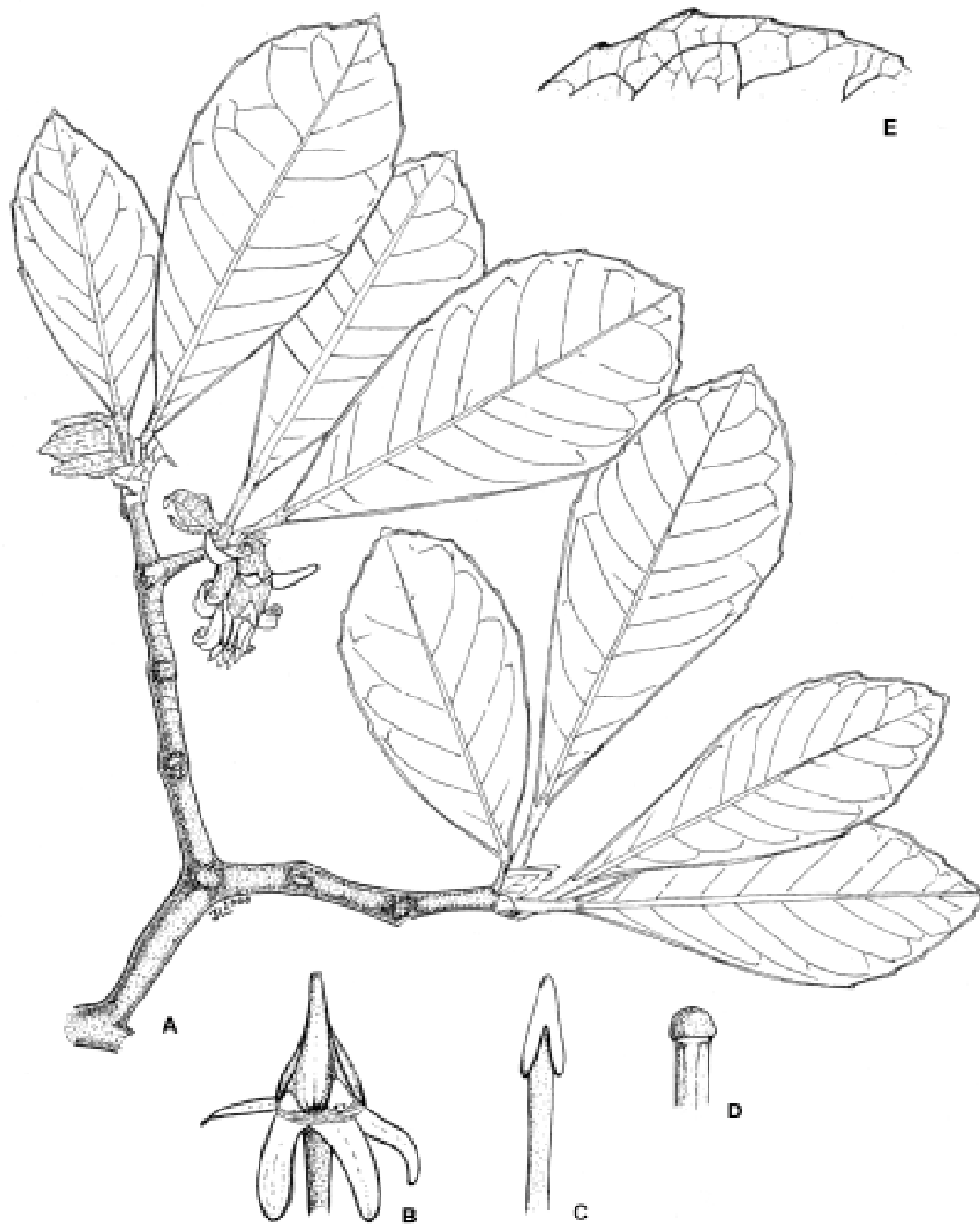
(1999), Savolainen et al. (2000a, b), and Soltis et al. (2000). Except for Savolainen et al. (2000b), all these analyses sampled Asterales too sparse to be able to identify the sister group of *Roussea* within the order, and none discussed its relations with the other





**Figure 2.** The phylogenetic tree derived from the Bayesian analysis of the DNA nucleotide sequence part of the Asterales matrix (the aligned *atpB*, *ndhF*, and *rbcL* nucleotide sequences). The posterior probability for the monophyly of the clades are given in %.

members of Asterales from a morphological and biogeographic point of view. In **Paper II** I tried to identify the sister group of *Roussea*, and also to find potential synapomorphies supporting the relationship. With a cladistic analysis of a molecular data set consisting of the chloroplast genes *ndhF* and *rbcL* for 20 Asteralean genera plus an additional five genera outside Asterales in the Euasterids II, I obtained two most parsimonious cladograms (differing only in relations within the non-Asteralean genera) and very high support values for a sister group relationship between *Roussea* and a clade consisting of *Carpodetus*, *Cuttsia* and *Abrophyllum* (previous to this study



**Figure 3.** ROUSSEACEAE. *Roussea simplex*. **A.** Flowering branch. **B.** Young fruit without petals. **C.** Stamen with anther. **D.** Stigma. **E.** Leaf margin. Drawing by J. Lundberg, modified from Paper II.

sometimes referred to as Carpodetaceae, e.g. Gustafsson and Bremer, 1997). Despite several striking differences, for example rather large sympetalous flowers in *Roussea* in contrast to the small choripetalous flowers of the other genera, and the peculiar

indumentum found on *Abrophyllum*, *Carpodetus*, and *Cuttsia*, not present in *Roussea*, there are some similarities that support a merging of Rouseaceae and Carpodetaceae into one family (which needs to be named Rouseaceae due to the priority of that name, first published in 1789 by Sir James Edward Smith, over Carpodetaceae, validly published in 1841 by Eduard Fenzl). Among these are the multilocular ovaries as well as stamens that are free from the rather thick petals. Of these traits, multilocular ovaries are also shared by Campanulaceae, particularly Campanuloideae, but as bilocular ovaries also are common among these taxa, an optimisation of the character still supports the multilocular (and multicarpellary) ovaries as a synapomorphy for Rouseaceae s.l. A stamen-corolla tube is also present in Goodeniaceae, Stylidiaceae s.l., Phellinaceae, and Argophyllaceae, but these occurrences are all most parsimoniously explained as independent acquisitions.

### **Pentaphragmataceae: An enigmatic family**

Pentaphragmataceae are a small family with a single genus, *Pentaphragma* of about 25 species showing a Malesian distribution. They are perennial, more or less succulent herbs. Wood anatomy has suggested a relationship with Begoniaceae (Airy Shaw, 1942), and the helicoid cymes are somewhat similar to the inflorescences of many Boraginaceae while the habit can resemble certain Gesneriaceae. Despite these peculiarities *Pentaphragma* has often been associated with Campanulaceae, sometimes even included within this family as a subfamily of its own (e.g. Schönland, 1889). This relationship has been questioned not only because of the dissimilarities mentioned above, but also because of differences in wood anatomy (Carlquist, 1997), pollen morphology (Dunbar, 1978), the arrangement and morphology of the nectaries (Vogel, 1998), and earlier phylogenetic analyses based on *rbcL* sequences (e.g. Cosner et al., 1994) or *ndhF* sequences (e.g. Jansen and Kim, 1996). Both the maximum parsimony analysis (**Paper I**) and the Bayesian analysis support a sister group relationship between *Pentaphragma* and the Core Asterales.

### **The Core Asterales**

Four major clades make up the core of Asterales: a large four-family clade containing the families Menyanthaceae, Goodeniaceae, Calyceraceae, and Asteraceae (the MGCA-clade); a small clade with the small family Alseuosmiaceae and the monotypic genus *Platyspermation*; a small clade with two families, Phellinaceae and Argophyllaceae; and the single family Stylidiaceae (including Donatiaceae). The two analyses (the maximum parsimony in **Paper I** and the Bayesian analysis presented here) differ with respect to the position of Stylidiaceae. In **Paper I** Stylidiaceae is the sister group to a clade with Phellinaceae and Argophyllaceae, while in the Bayesian analysis a sister group relationship between Stylidiaceae and a clade with Menyanthaceae, Goodeniaceae, Calyceraceae and Asteraceae (the MGCA clade) receives moderate posterior probability (PP 91%). The unorthodox position of Stylidiaceae as the sister taxon to the Phellinaceae-Argophyllaceae clade, and with Alseuosmiaceae-*Platyspermation* clade as the sister group to the Stylidiaceae-Phellinaceae-Argophyllaceae clade, receives only very low support (JK < 50%, BS = 1), and has not been found in any previously published analyses. Despite that the sister group relationship between Stylidiaceae and Phellinaceae-Argophyllaceae can be supported by a few morphological characters

(absence of a stamen-corolla tube, also encountered elsewhere in Asterales, and by crassinexinous pollen, a character only poorly known in the potential Alseuosmiaceae-*Platyspermatum*-Stylidiaceae-Phellinaceae-Argophyllaceae [“APAS“] clade) I am doubtful about this relationship, and rather believe that Stylidiaceae either is the sister group to a clade with Alseuosmiaceae, Arophyllaceae, Phellinaceae and *Platyspermatum* (this sister group relationship is supported by latrorse anthers and possibly also by the presence of chalazal endosperm haustoria) or the sister group to the MGCA clade (no potential morphological synapomorphies have been identified for this relationship, which is identified by the Bayesian analysis).

### **The MGCA: the Four-Family Clade**

A clade consisting of the families Menyanthaceae (formerly often placed in Gentianales; e.g. Takhtajan, 1987), Goodeniaceae, Calyceraceae and Asteraceae, has been identified earlier (e.g. Downie & Palmer, 1992; Lammers, 1992; Olmstead et al., 1992; Morgan & Soltis, 1993) and receives very high support also in my analyses of Asterales (**Paper I & II** as well as the Bayesian analysis). There are several morphological synapomorphies supporting this clade (**Paper I**): generally unilocular ovaries, absence of micropylar endosperm haustoria (Cosner et al., 1994), and a thick, multilayered integument (Inoue and Tobe, 1999).

### **The sister to Asteraceae**

There has been much controversy regarding the closest relatives of Asteraceae (see, e.g., the review by Gustafsson, 1996). With the introduction of molecular data sets in combination with cladistic analyses, the number of potential relatives has been drastically reduced, and lately only three serious candidates have been considered as the sister group to Asteraceae: the predominantly Australian family Goodeniaceae, the solely South American family Calyceraceae, and a clade consisting of these two families. Both the parsimony analysis (**Paper I**) and the Bayesian analysis give very strong support for a sister-group relationship between Calyceraceae and Asteraceae. This is also the biogeographically most plausible relationship, as the most plesiomorphic members of Asteraceae are native in South America. There are furthermore several morphological characters that support this sister group relationship: e.g. pollen with intercolpar concavities (Skvarla et al., 1977; Hansen, 1991, 1992; but see Zhao et al. 2000), flowers aggregated into compact heads surrounded by involucre bracts, calyx modified into a fruit dispersal apparatus, wood with libriform fibres (Carlquist and DeVore, 1998), and lateral petal veins not anastomosing with the midvein (Hansen, 1992).

### ***Donatia* and Stylidiaceae, a reunion**

*Donatia* is a small genus with two species, one native to Tierra del Fuego (subantarctic South America), and the other to Tasmania and New Zealand. In the 19th century *Donatia* was often included among the heterogeneous Saxifragaceae (e.g. Lindley, 1853; Agardh, 1858; Engler, 1890), but it was later transferred to the mainly Australian Stylidiaceae as a subfamily of its own (Mildbraed, 1908). Its history in Stylidiaceae was however to be short; a new monogeneric family was soon suggested (Chandler, 1911;

Skottsberg, 1915), and it has mostly since then been kept within Donatiaceae, although admittedly closely related to Stylidiaceae (e.g. Takhtajan, 1997). Both the maximum parsimony analysis (**Paper I**) and the Bayesian inference gave strong support for a sister group relationship between Stylidiaceae and *Donatia*, and this relationship is further supported by some important morphological synapomorphies: an imbricate petal bud aestivation, a reduced number of stamens, and extrorse anthers. Taking the consequences of this we suggest reemerging *Donatia* into a Stylidiaceae in Mildbread's (1908) sense. As Stylidiaceae, the trigger-plants, are a well defined clade itself supported by many morphological synapomorphies<sup>1</sup> and a restricted distribution (only a few shore plants are widespread outside Australasia) it will best be recognised as a subfamily consisting of four genera (see Laurent et al., 1999).

### Three Enigmatic Families and an Unexpected Newcomer

The relationship between the three small Australasian families Alseuosmiaceae, Argophyllaceae, and Phellinaceae has been treated in detail by Kårehed et al. (1999). These three families have in recent analyses consistently been grouped together in a monophyletic clade however with rather low support values (Backlund and Bremer, 1997; Gustafsson and Bremer, 1997; Kårehed et al., 1999; **Paper II**), and there has not been any unequivocal morphological or anatomical synapomorphies identified for this clade. Unfortunately, the three families are almost unknown chemically (with the exception of *Phelline*, from which many unusual alkaloids have been detected) and embryologically.

Alseuosmiaceae include four genera, *Alseuosmia* with about five species native to New Zealand (Merrett and Clarkson, 2000), *Wittsteinia* with two species in Australia and New Guinea, and the two monotypic genera *Periomphale* (New Caledonia; not included in **Paper I**) and *Crispiloba* (endemic to Queensland, Australia). There are several synapomorphies supporting the monophyly of Alseuosmiaceae (Kårehed et al., 1999) some of which also occurs in other parts of Asterales (e.g. sympetalous flowers, distinct petal wings, and epipetalous stamens) while others are more unique: the wood has a stem endodermis with well developed Casparian bandings, and there are living fibres storing starch at maturity.

Argophyllaceae contain only two genera; *Argophyllum* with about 15 species from tropical east Australia and New Caledonia, and *Corokia* with six species showing a wide South Pacific distribution. Also this family is well supported by morphological synapomorphies (Kårehed et al., 1999), e.g. a stomatal apparatus where the guard cells are raised above the surrounding epidermis, presence of T-shaped multicellular hairs, and petals with corolline ligules (although other kinds of petal appendages are also found in Alseuosmiaceae).

The third family, Phellinaceae, are monogeneric with the single genus *Phelline* (c. 10 species) endemic to New Caledonia. Their monophyly is well supported by several morphological synapomorphies (Kårehed et al., 1999), among other the unisexual flowers, superior ovaries, sessile stigma, guard cells with outer and inner stomatal

---

<sup>1</sup> Among the more peculiar synapomorphies for the trigger plant's are the stamens and that style that formes a column, which in several species is irritable: when the pollinating insect comes into contact with the bent column, it will suddenly and with great force release and plunge down to the insect body—hence the family's English name—and the insect is thus powdered with pollen from the anthers at the same time that the stigma can pick up pollen from other flowers.

ledges, centric petiolar bundles, and the leaf veinlets surrounded by pitted sclerenchymatous cells.

A recent addition to Asterales is *Platyspermation crassifolium* (R. Schmid and J. Lundberg, in prep.), which is the sole member of its genus. It is a shrub or small tree endemic to New Caledonia, from where it was described as late as 1950 (Guillaumin, 1950). It was at that time placed in Myrtaceae where it soon turned out to be highly anomalous, and was by some included in Rutaceae before it was suggested to be included in Escalloniaceae (Schmid, 1980; van Steenis, 1982). Since then it has been thoroughly neglected (as an example, it is not even mentioned once in Takhtajan, 1997), and since its original description in 1950 almost nothing has been published on its morphology, anatomy, embryology or chemistry. It thus came as a great surprise when the first preliminary analyses, based on maximum parsimony (**Paper I**) and Bayesian inference (R. Schmid and J. Lundberg, in prep.) gave very high support for a sister group relationship between *Platyspermation* and Alseuosmiaceae. Apparently *Platyspermation* shares no morphological synapomorphies with Alseuosmiaceae, but it is not quite out of place in Asterales, as it shares the valvate petal bud aestivation with most other members.

## ASTERALES, AN OUTSIDE VIEW

### What, if Anything, is Escalloniaceae?

Although many of the late nineteenth and early twentieth century angiosperm families are still circumscribed in more or less the same way today as then, a few have been known as notorious taxonomic dustbins. One of the worst family conceptions is that of the Englerian Saxifragaceae (Engler, 1928). The Saxifragaceae Adolf Engler apprehended comprised 80 genera distributed among 15 subfamilies. The naturalness of this assemblage has been questioned (e.g. Eyde, 1966), and recently aided by molecular data, it has now been shown that Engler's Saxifragaceae was a highly polyphyletic taxon (beginning with Soltis et al., 1990; see also e.g. Soltis and Soltis, 1997). It has also been shown that many of the subfamilies that Engler subdivided his Saxifragaceae into also were highly polyphyletic. Just to mention a few examples: Brexioideae sensu Engler, containing the three genera *Brexia*, *Ixerba* and *Roussea*, are now divided into three widely dispersed parts (e.g. Koontz and Soltis, 1999; also see **Paper II**); and Escallonioideae, containing 16 genera in Engler (1928), have been the subject of extensive and necessary splitting ever since. In the APG-system (APG, 1998), Engler's escallonioid genera *Cuttsia*, *Abrophyllum*, *Argophyllum*, *Corokia*, *Carpodetus*, *Berenice*, and *Colmeiroa* (today included in *Corokia*) are now included in various families in Asterales; *Choristylis* is considered a member of the Euasterids I; *Pottingeria* is one of the few remaining *incertae sedis* among the angiosperms (APG, 1998); and *Anopterus*, *Tribeles*, *Forgesia*, *Quintinia*, *Valdivia*, *Escallonia* and *Polyosma* are in various constellations treated as *incertae sedis* among the Euasterids II. It is these last seven genera, together with a few other poorly known taxa, and their relationships that have been the focus of the remaining part of this thesis.

In the APG-system (APG, 1998) *Polyosma* (Fig. 4) is the sole member of Polyosmaceae, and with an uncertain position in the Euasterids II. **Paper IV**<sup>2</sup> provides a detailed description of this monogeneric family. Due to editorial planning, being based on old classification, a rather traditional but unnatural Escalloniaceae was described in **Paper III**<sup>3</sup>. In this circumscription, constrained by the family classification in Kubitzki's Families and Genera of Flowering Plants, the family consisted of the six genera *Anopterus*, *Escallonia*, *Forgesia*, *Platyspermatum*, *Quintinia* and *Valdivia*. In **Paper V** (Fig. 5) a somewhat differently circumscribed, but monophyletic and highly supported (PP 100%) Escalloniaceae are presented for the first time. In this circumscription they include, apart from the closely related genera *Escallonia* (Fig. 6), *Forgesia* and *Valdivia*, also *Anopterus*, *Eremosyne* (Fig. 7), *Tribeles* and *Polyosma*. The family includes about 135 species widely distributed in the Southern Hemisphere: South America (*Escallonia*, *Tribeles* and *Valdivia*), Australasia and South-East Asia (*Polyosma*), Australia and Tasmania (*Anopterus*, *Eremosyne*, and *Polyosma*), and the Isle de Réunion east of Madagascar (*Forgesia*). All these genera have from time to time been included in a more widely circumscribed Escalloniaceae, but only *Anopterus*, *Escallonia*, *Forgesia* and *Valdivia* consistently so. The remaining three genera have often been treated as monogeneric families (Eremosynaceae, Polyosmaceae and Tribelaceae; e.g. APG, 1998), while Escalloniaceae in the APG-system (APG, 1998) apart from *Anopterus*, *Escallonia*, *Forgesia* and *Valdivia* also included *Quintinia* and apparently also *Platyspermatum*. The latter genus is, as discussed above, now with certainty placed in Asterales close to Alseuosmiaceae (R. Schmid and J. Lundberg, in prep.; supported by **Paper I**), while the exact position of *Quintinia* is somewhat less well known. However, it now seems certain that *Quintinia* is closely related to *Paracryphia* (Paracryphiaceae) and *Sphenostemon* (Sphenostemonaceae) and that this clade is only distantly related to Escalloniaceae (**Paper V**). The position of the *Paracryphia-Quintinia-Sphenostemon* clade (which I consider would be best treated as a single family, Paracryphiaceae s.l.; **Paper V**) seems to be as the sister group to a clade with Dipsacales and Apiales.

<sup>2</sup> **Material and Methods:** The literature on *Polyosma* was reviewed. The information thus gathered was as far as possible checked against herbarium material, and some new information was also obtained. For several species flowers were rehydrated, dissected and examined under dissection microscope before being mounted in Hoyer's solution. **Material examined:** *Polyosma alangiacea*: Clemens s.n. (S); *P. cambodiana*: Tsang 30103 (UPS); *P. dolichocarpa*: Poilano 7159 (K); *P. integrifolia*: Poilane s.n. (S); *P. mutabilis*: San 90519 (K).

<sup>3</sup> **Material and Methods:** The literature on Escalloniaceae, including several unpublished theses (i.e. Dravitzky, 1967; Jay, 1969; Gardner, 1976; Ramamonjariosa, 1980; Hils, 1985; Al-Shammary, 1990), was reviewed. The information thus gathered was as far as possible checked against herbarium material, and some new information was thus obtained. For several species flowers were rehydrated, dissected and examined under dissection microscope before being mounted in Hoyer's solution. **Material examined:** *Anopterus glandulosa*: Milligan s.n. (K, herb. Hook.), Vitt 29180 (UPS); *Escallonia illinita*: Frödin 334 (UPS); *E. myrtoidea*: Frödin 638 (UPS); *E. pendula*: Woytkowski 34334 (UPS); *E. pulverulenta*: Günther & Buchtien s.n. (UPS); *E. resinosa*: Hawkes et al. 5125 (UPS); *Forgesia racemosa*: Barclay 497 (K), Bernardi 14924 (K), Coode & Cadet 4921 (K), Lorence & Rolland 2435 (K), StJohn 26496 (K); *Platyspermatum crassifolium*: Bernardi (9454), McKee 4516 (K), McPherson 3463 (K), Stauffer & Blanchon 5710 (K); *Quintinia fawkeni*: White 1275 (S); *Q. ledermannii*: Brass 28473 (S), Kerenga & Cruttwell LEA 56658 (K); *Q. minor*: McKee 5322 (K); *Q. serrata*: Sussex s.n. (S), Travers s.n. (S); *Q. sieberi*: Hagman s.n. (S); *Q. verdonii*: Vitt 27650 (UPS); *Valdivia gayana*: Bredges 769 (K), Buchtien s.n. (S), Corral s.n. (K), Gunckel s.n. (S), Reed s.n. (K).



**Figure 4.** ESCALLONIACEAE. **A-C.** *Polyosma ilicifolium*. **A.** Flowering branch. **B.** Flower. **C.** Stamen with anther. **D-E.** *Polyosma mutabilis*. **D.** Fruit. **E.** Fruit, longitudinal section. Modified from Engler (1928).

**Figure 5** (next pages). The phylogenetic tree derived from the Bayesian analysis of the DNA nucleotide sequence matrix of the Euasterids. The posterior probability for the monophyly of the clades are given in %. Node numbers are given for each node. **A.** The relationships among the major clades of Euasterids. **B.** The relationships among the sampled taxa from Euasterids II. **C.** The relationships among the sampled taxa from Euasterids I.



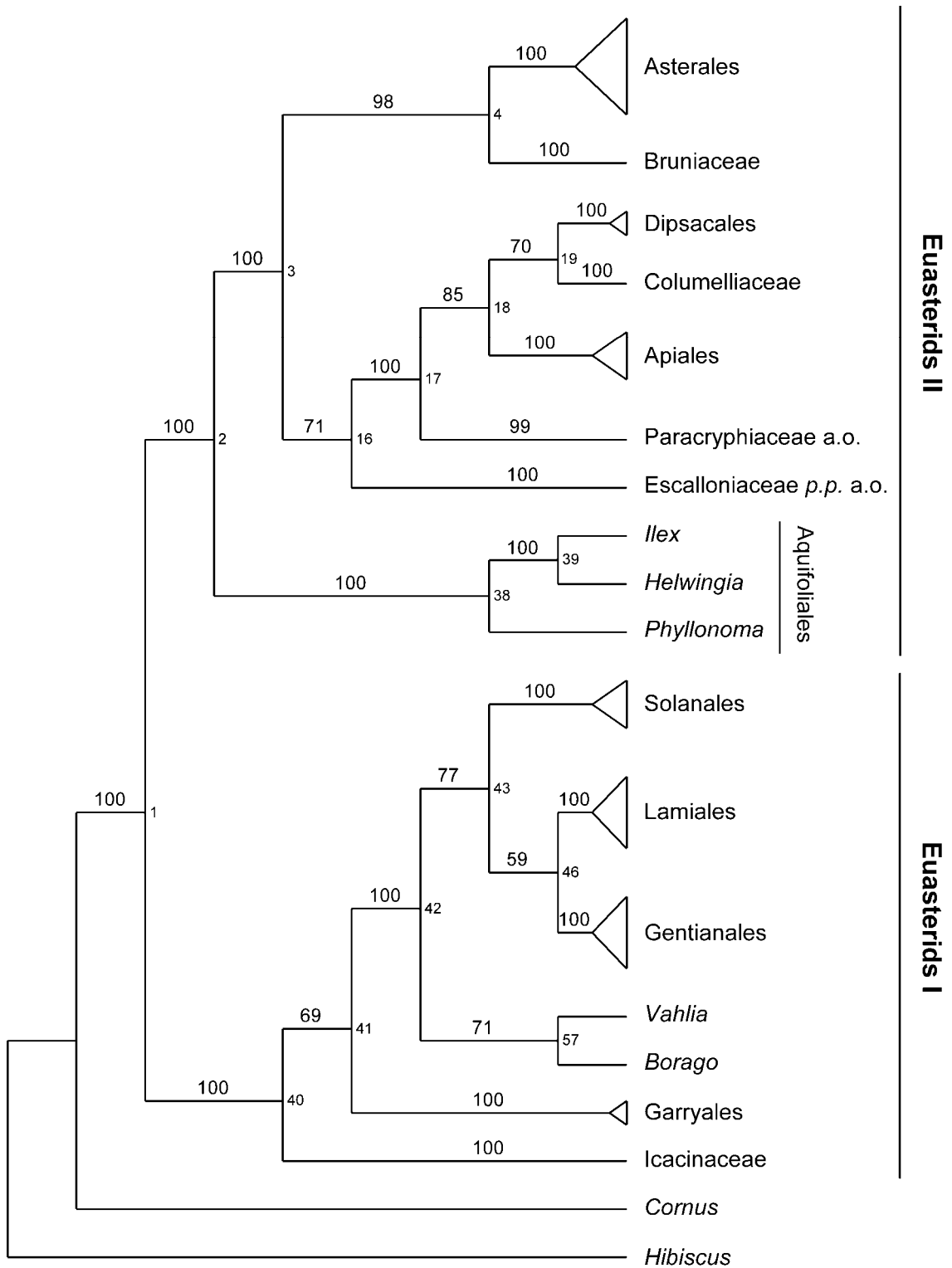


Figure 5A. The relationships among the major clades of Euasterids.

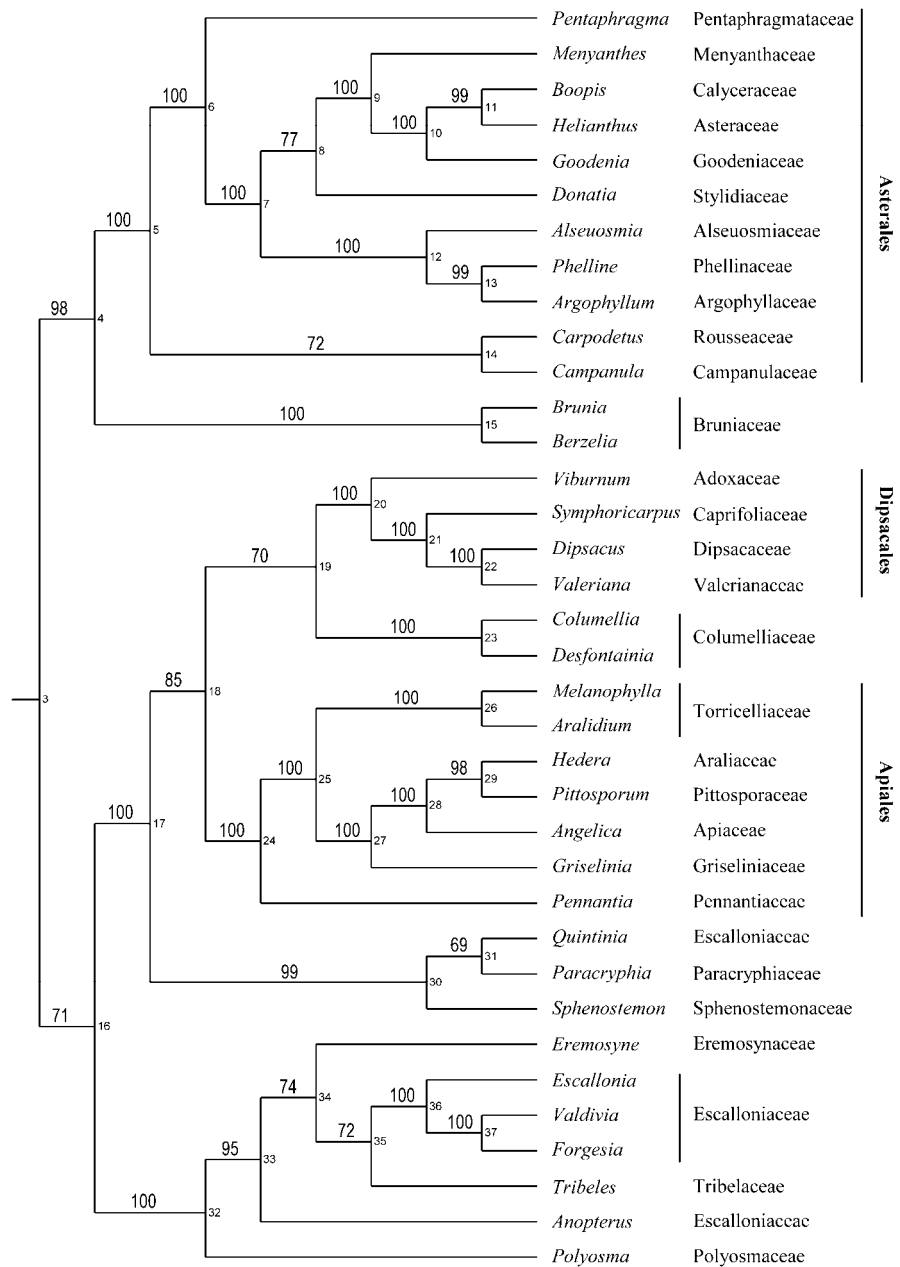


Figure 5B. The relationships among the sampled taxa from Euasterids II.

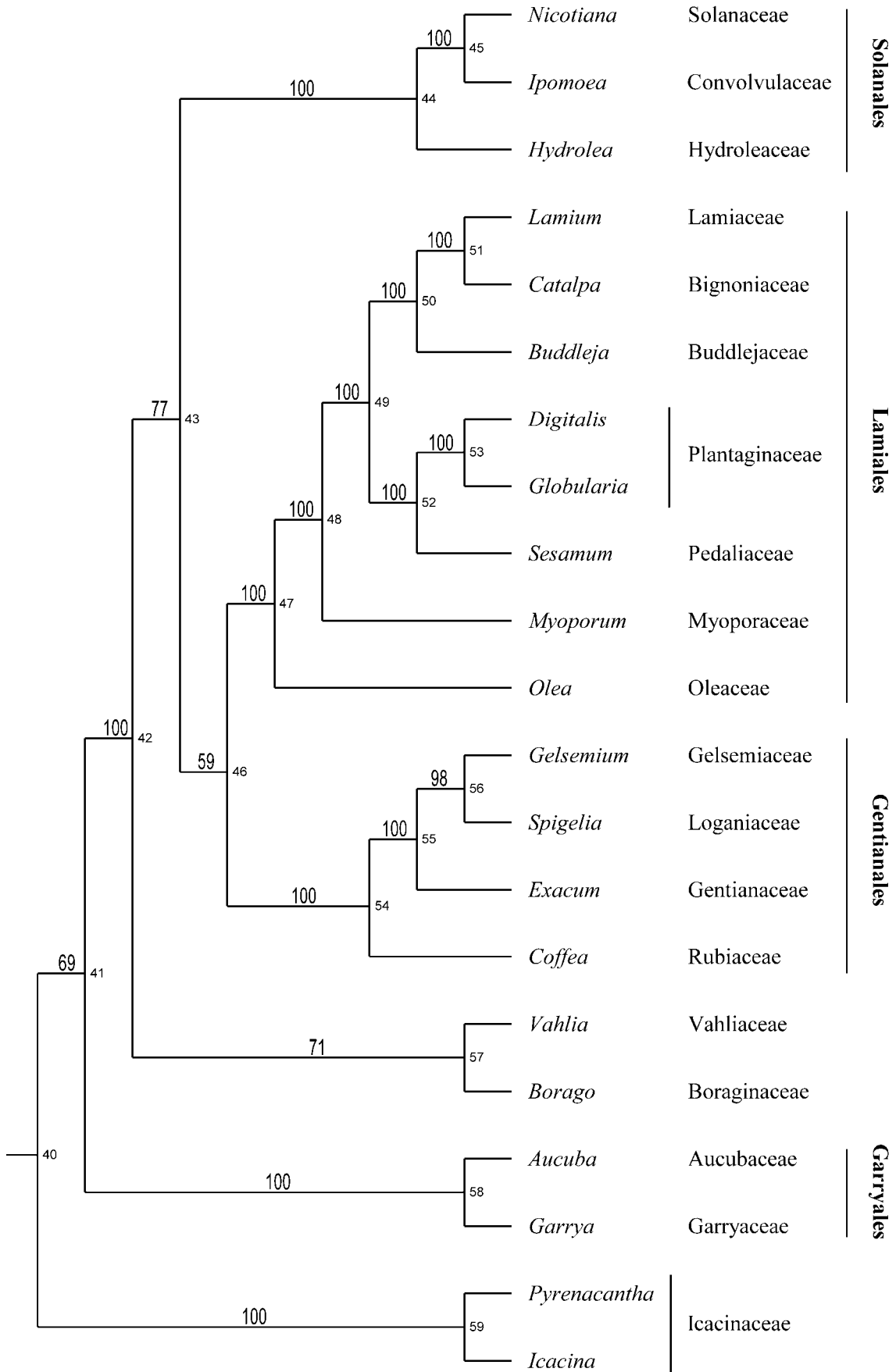
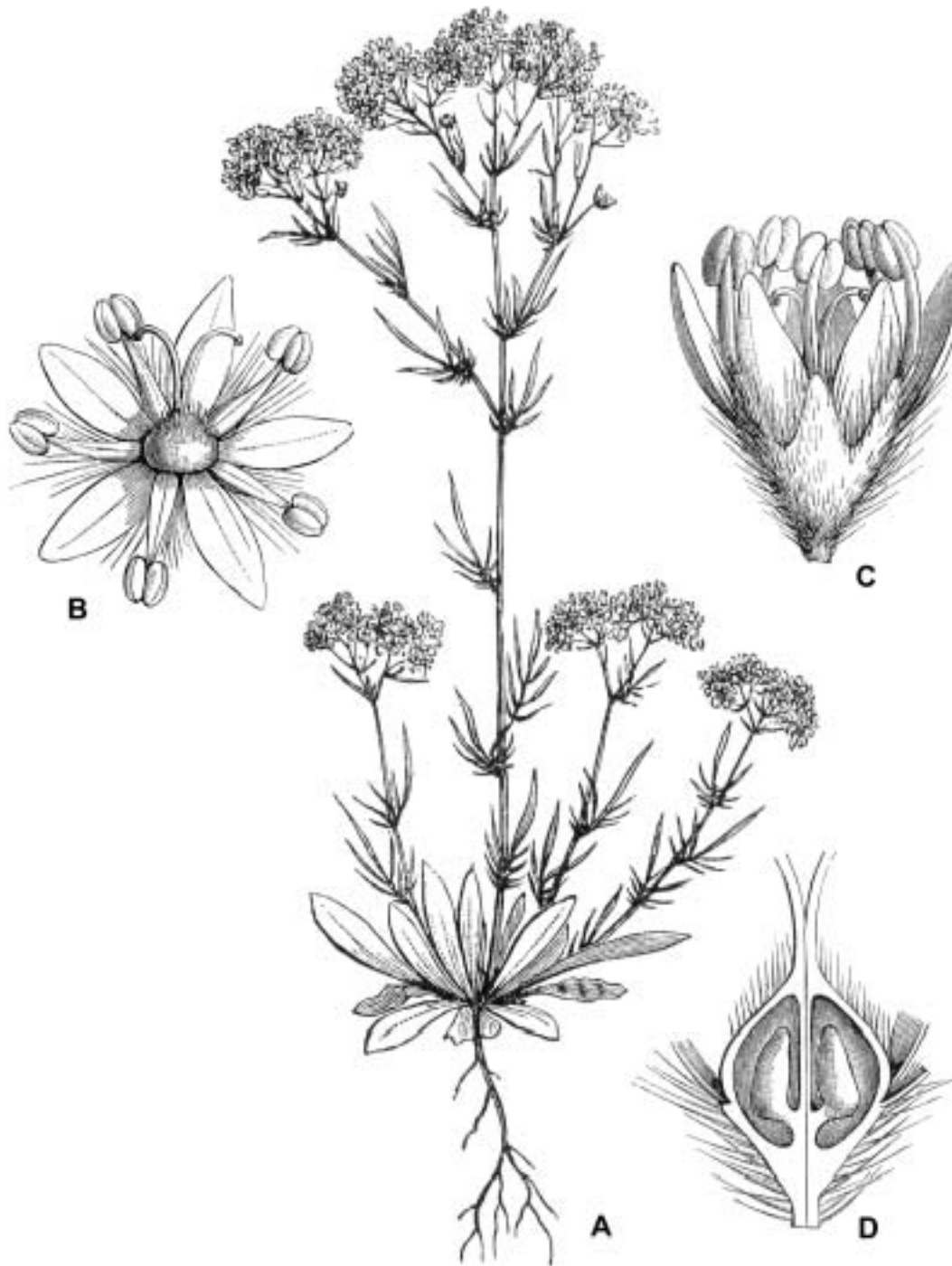


Figure 5C. The relationships among the sampled taxa from Euasterids I.



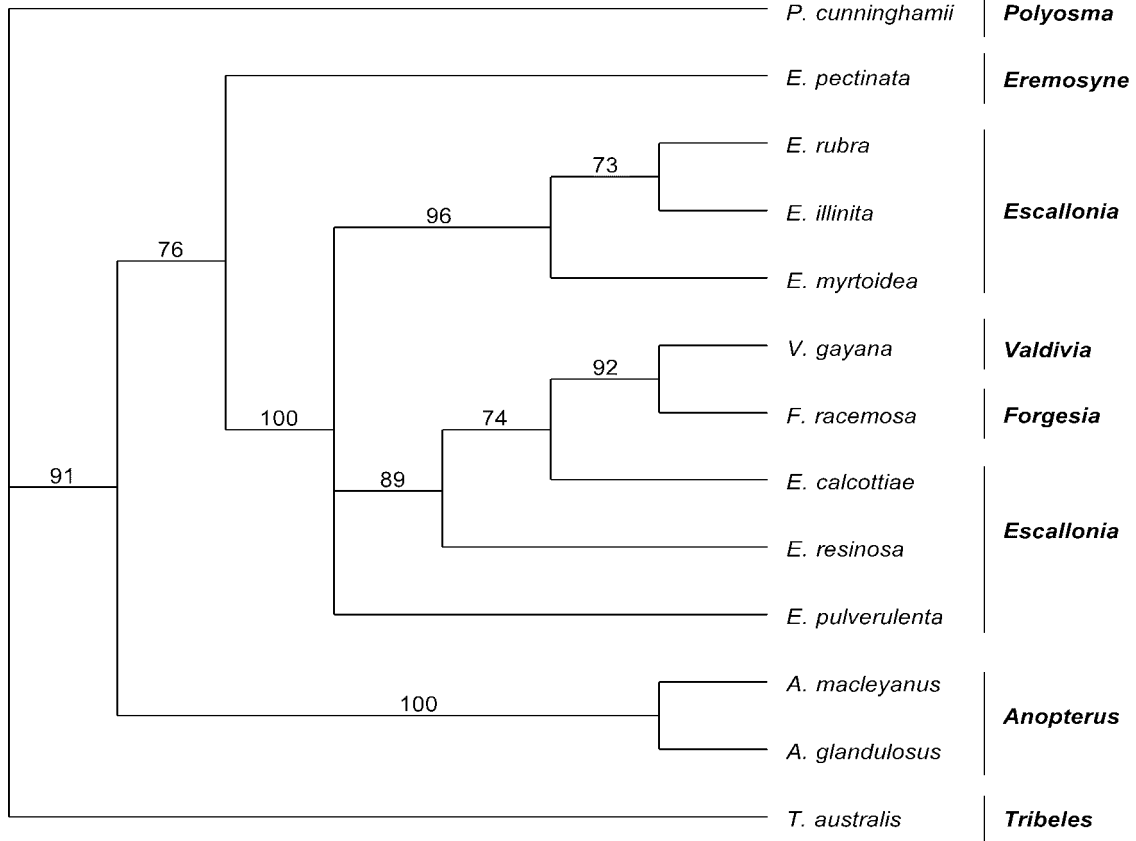
**Figure 6.** ESCALLONIACEAE. *Escallonia rubra*. **A.** Flowering branch. **B.** Flower. **C.** Flower, longitudinal section. Modified from Baillon (1872).



**Figure 7.** ESCALLONIACEAE. *Eremosyne pectinata*. **A.** Flowering branch. **B, C.** Flower. **D.** Gynoecium, longitudinal section. Modified from Engler (1928).

## The paraphyly of *Escallonia*

In a small pilot study<sup>1</sup>, which was restricted to the phylogeny of the family Escalloniaceae sensu **Paper V**, both species of *Anopterus* and six species from the genus *Escallonia* were included. The analysis resulted in two most parsimonious trees (Fig. 8), where a paraphyletic *Escallonia* which also includes *Forgesia* and *Valdivia* received very high support. This result was unexpected but not surprising. The gross



**Figure 8.** Strict consensus cladogram summarising the two most parsimonious cladograms resulting from the combined analysis (*atpB*, *ndhF*, and *rbcL* nucleotide sequence data) of a small data set representing all genera of Escalloniaceae. The trees are 904 steps long, with a consistency index (excluding uninformative characters) of 0.80, and a retention index of 0.87. The jackknife support (in %) are given for each branch.

<sup>1</sup> For this study, 6 new *ndhF* sequences, 5 new *rbcL* sequences and 6 new *atpB* sequences were obtained using the same procedure as described in **Paper V**. The new sequences were obtained from *Anopterus glandulosus* (Swenson & Martinsson 353, UPS; *atpB* AJ419683, *ndhF* AJ419704), *Escallonia calcottiae* (Stuessy & Crawford 15138, UPS; *atpB* AJ419684, *ndhF* AJ419705, *rbcL* AJ419693), *E. illinita* (Frödin 334, UPS; *atpB* AJ419685, *ndhF* AJ419706, *rbcL* AJ419694), *E. myrtoidea* (Frödin 712, UPS; *atpB* AJ419686, *ndhF* AJ419707, *rbcL* AJ419695), *E. pulverulenta* (Frödin 337, UPS; *atpB* AJ419687, *ndhF* AJ419708, *rbcL* AJ419696), and *E. resinosa* (Hawkins, Cribb & Huaman 5125, UPS; *atpB* AJ419688, *ndhF* AJ419709, *rbcL* AJ419697). They were combined with previously published sequences for *Anopterus macleyanus*, *Eremosyne pectinata*, *Escallonia rubra*, *Forgesia racemosa*, *Polyosma cunninghamii*, *Tribeles australis*, and *Valdivia gayana* (for accession numbers, see **Paper V**), and analysed in PAUP\* under the parsimony criterion using a branch and bound search. Following the results from **Paper V**, the root was placed between *Polyosma* and the rest of the family. The clade support was estimated by jackknife values obtained using the same procedure as outlined in **Paper I**.

morphology (including flowers and fruits) is strikingly different between *Forgesia*, *Valdivia* and *Escallonia* (summarised in **Paper III**): *Escallonia* are shrubs or small trees with flowers where the styles are fused and with capsules opening from the base; *Forgesia* is a climbing shrub or small tree, sometimes a strangler, where the flowers have two free styles and with capsules only opening at the top between the styles; and *Valdivia* is a small subshrub with indehiscent dry fruits and fused styles. When it comes to the placenta and seed morphology they are virtually identical (see photos 1-9 of Escalloniaceae seeds in Nemirovich-Danchenko, 2000; **Paper III**): the numerous seeds are small and have long, almost unbranched ridges, and are borne on deeply intruding, bilobed and pitted placentas.

*Valdivia* is today present on only three known localities in the province of Valdivia, south-central Chile (Ramírez and Sempe, 1981), where it grows in sheltered and calcareous habitats (caves) close to the coast. Its striking morphology might be explained as an adaptation to a confined habitat without many possibilities for fruit dispersal (despite that its seeds have a high germination frequency, its natural populations are on the verge of extinction; Ramírez and Sempe, 1981). More difficult to explain is the distribution of *Forgesia*. This genus is native to mountain mist forests of Isle de Réunion east of Madagascar, while the other members of the *Escallonia* clade are all confined to South America. All but one of the *Escallonia* species are growing in continental South America, particularly in the Andes (reaching down to sea level in the subantarctic South America). The exception is *E. calcottiae* which is endemic to the Juan Fernández Islands almost 500 km west of the Chilean coast. Interestingly this is also a species closely related to the *Forgesia-Valdivia* clade (in this sparsely sampled pilot study it showed up as the sister taxon to this clade). The dispersals to both Réunion and Juan Fernandez must have taken place comparatively recently as both islands are of volcanic origin and have a rather young subaerial age.

## Apiales and Dipsacales

If Asterales is dominated by Asteraceae, then Apiales is dominated by Apiaceae (Umbelliferae). Unlike Asteraceae, this family are closely related to another rather large family, Araliaceae. For some decades the exact relationship between these two families has been controversial, and there have been proposals to expand Araliaceae to also include the entire Apiaceae, or subdividing them into several minor families. A third family, Pittosporaceae, are clearly a member of the same clade as Araliaceae and Apiaceae, or at least their closest sister group, but have only rather recently been more regularly and confidently associated with Araliaceae and Apiaceae; earlier they were sometimes regarded as closely related to Saxifragaceae. More recent, molecular investigations (summarised in Plunkett, 2001) have indicated that the Core Araliaceae and the Core Apiaceae still can be maintained as distinct, monophyletic families, but a few aberrant groups may form new families (e.g. the Araliacean tribes Mackinlayeae and Myodocarpeae; Plunkett, 2001). The place of Pittosporaceae in this alliance is, however, still uncertain, although it can on morphological grounds be assumed that they form the sister group to the Araliaceae-Apiaceae alliance.

Basal to Araliaceae-Apiaceae-Pittosporaceae is a grade with *Aralidium*, *Griselinia*, *Melanophylla* and *Torricellia*. All four genera have from time to time been included in Cornaceae, or classified as monogeneric families. *Aralidium* is a monotypic west

Malaysian genus. *Griselinia* consists of six species of dioecious trees and shrubs with a disjunct distribution in New Zealand and Chile. The eight species of *Melanophylla* are all endemic to Madagascar, while the three species of *Toricellia* are native to the east Himalaya and China. Molecular studies have shown that *Aralidium*, *Melanophylla* and *Toricellia* form a monophyletic group (see Plunkett, 2001), and this clade has recently been treated as a family, Torricelliaceae. Torricelliaceae might be the sister taxon to the Core Apiales (i.e. Apiaceae, Araliaceae and Pittosporaceae), while *Griselinia* (the sole member of Griselinaceae) is the sister group to the Torricelliaceae-Core Apiales clade (**Paper V**).

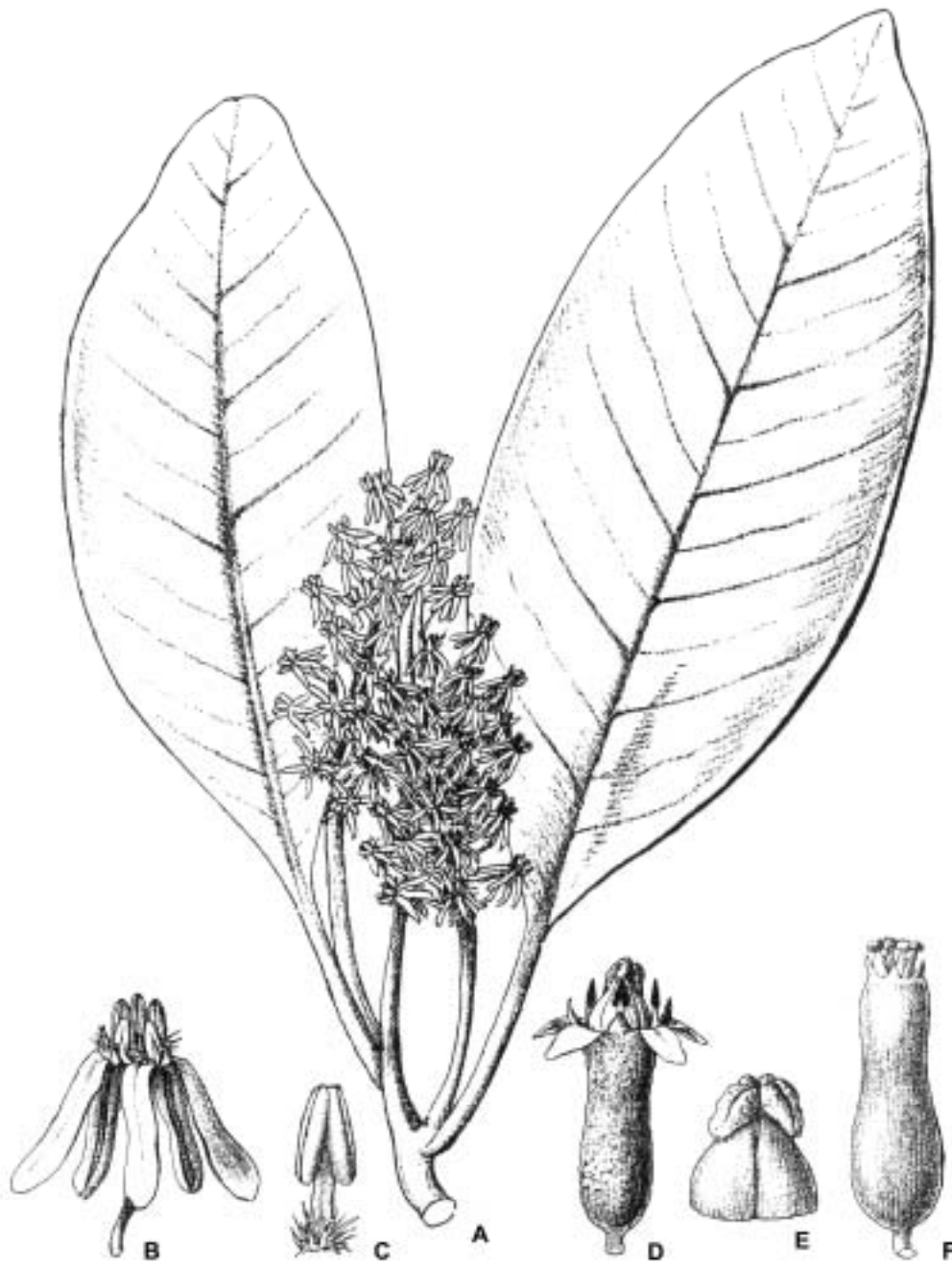
Recently, it has been shown that another small monogeneric family, Pennantiaceae, would probably also best be accommodated within Apiales, as the sister taxon to the rest of the order (Kårehed, 2001; J. Kårehed, in prep.; supported also in **Paper V**). Pennantiaceae with the sole genus *Pennantia* and four species are restricted to Australia, New Zealand and the Norfolk Islands, and have previously been included in a heterogeneous Icacinaceae.

The sister group to this Apiales s.l. is the Dipsacales s.l. The monophyly of the Core Dipsacales is well supported not only by the present analysis (**Paper V**), but also by morphological data and other analyses. In some systems (e.g. Judd et al., 1999) its members are all lumped into one single family, Caprifoliaceae s.l., while the alternative approach is to split Caprifoliaceae s.l. into Caprifoliaceae s.s., Dipsacaceae, Morinaceae, Valerianaceae and the newly erected Diervilleaceae and Linnaeaceae (Backlund and Pyck, 1998; the latter two were not included in **Paper V**). Both approaches to the Core Dipsacales taxonomy have their merits, but I will refrain from further discussion on this topic. The sister taxon to the Core Dipsacales is Adoxaceae. Despite their small size, they are a fairly heterogeneous assemblage consisting of *Adoxa* (and its closest relatives *Sinadoxa* and *Tetradoxa*) as well as the former Caprifoliaceous genera *Sambucus* and *Viburnum*. The latter two genera have also sometimes been treated as monogeneric families (Sambucaceae and Viburnaceae). The position of Adoxaceae among the Euasterids II has been difficult to determine, but in phylogenetic analyses they have usually occupied a position more or less close to the Core Dipsacales and they have sometimes (e.g. Backlund, 1996) been included in Dipsacales. This Dipsacales (including Adoxaceae) receives a very high posterior probability in **Paper V**. The sister group to Dipsacales s.l. (i.e. including Adoxaceae) appears, although with only low support in **Paper V** (PP 70%), to be the small South American family Columelliaceae (two genera, *Columellia* and *Desfontainia*; Backlund and Bremer, 1997), and it has earlier been suggested that they should be included in Dipsacales (Backlund and Donoghue, 1996).

### **Paracryphiaceae, Sphenostemonaceae, and Quintinia**

The exclusion of *Quintinia* (Fig. 9) from the Escalloniaceae has been suspected for some time now (e.g. Gustafsson et al., 1996), but it has never been possible to place the genus with any certainty among the Euasterids II. The same is true for the small family Sphenostemonaceae (one genus, *Sphenostemon*) and the new addition to the Euasterids II, Paracryphiaceae (Savolainen et al., 2000b). Paracryphiaceae with the single species *Paracryphia alticola* have earlier on morphological and anatomical grounds been suggested to be related to, among others, *Sphenostemon*, and this relationship is strongly supported by **Paper V** (the same relationship was also suggested by Savolainen et al.,





**Figure 9.** PARACRYPHIACEAE. *Quintinia resinosa*. **A.** Flowering branch with male flowers. **B.** Male flower. **C.** Stamen. **D.** Female flower. **E.** Top of ovary with stigma. **F.** Fruit. Modified from Schlechter (1907).

2000b, but with lower support). Somewhat surprising (but not entirely out of place morphologically and anatomically) was the inclusion of *Quintinia* in the same clade as *Sphenostemon* and *Paracryphia*. As this clade is very well supported, and as there are several similarities between the three genera especially when it comes to wood anatomy and certain floral traits, I suggest (**Paper V**) that they are merged into one single family, Paracryphiaceae s.l.

## A Synopsis of the Classification of Euasterids II

### Aquifoliales

- Aquifoliaceae
- Helwingiaceae
- Phyllonomaceae
- Cardiopteridaceae
- Stemonuraceae

### Core-Euasterids II

#### Asterales

- Rousseaceae (incl. Carpodetaceae)
- Campanulaceae *sensu lato*
- Pentaphragmataceae
- Menyanthaceae
- Goodeniaceae
- Calyceraceae
- Asteraceae
- Stylidiaceae (incl. *Donatia*)
- Alseuosmiaceae
- Phellinaceae
- Argophyllaceae
- Platyspermatia*

#### Dipsacales

- Columelliaceae? (incl. *Desfontainia*)
- Adoxaceae (incl. *Sambucus*, *Viburnum*)
- Caprifoliaceae *sensu stricto*
- Diervillaceae
- Linnaeaceae
- Dipsacaceae
- Valerianaceae
- Morinaceae

#### Apiales

- Pennantiaceae
- Griselinaceae
- Torriceiliaceae (incl. *Aralidium*, *Melanophylla*)
- Apiaceae
- Pittosporaceae
- Araliaceae
- Mackinlayeae
- Myodocarpeae
- Bruniaceae
- Escalloniaceae (incl. *Eremosyne*, *Polyosma*, *Tribeles*)
- Paracryphiaceae (incl. *Quintinia*, *Sphenostemon*)

## A NOTE REGARDING MODEL BASED INFERENCE OF PHYLOGENY

In the last paper I wanted to use a model based approach to the phylogenetic inference, mostly because I wanted to see if this approach could resolve the basal branches of the Euasterids II, which in all previous (parsimony based) analyses have been unresolved or only poorly supported. A model based approach, I hoped, would perhaps be more efficient in taking care of the information in the nucleotide sequences, and thus be able to at least give resolved relationships among the previously unplaced members of Euasterids II, and generate a hypothesis about sister relationships of the three large Euasterids II-orders. Whether the relationships thus obtained would be correct or wrong are something for the future to show, but at least there would be a hypothesis that could be falsified (or in the best case, corroborated by other data or analyses). However, model based approaches have until very recently been either very time consuming for large data sets (maximum likelihood) or very crude approximations using “corrected” distance data (e.g. neighbour joining). But the last years have seen several improvements, the most important for this task is the introduction of a bayesian framework for model based phylogenetic analyses (see, for example, the review by Lewis, 2001).

### Bayesian inference—a short introduction

Bayesian inference is based upon the posterior probability of a parameter, e.g. a phylogenetic tree (Lewis, 2001, and references therein), which is calculated using prior knowledge (or guesses) about the parameters used.

The theoretical basis of Bayesian inference is formed by the theorem by Reverend Thomas Bayes (1702-1761):

$$\Pr(\tau_i | D) = \frac{\Pr(\tau_i)L(D | \tau_i)}{\sum_{j=1}^{B(s)} \Pr(\tau_j)L(D | \tau_j)} \quad (1)$$

In a phylogenetic analysis using nucleotide sequence data the data  $D$  represents the observed matrix of aligned DNA sequences, and  $\tau$  the topology of the phylogenetic tree. The left term of equation (1),  $\Pr(\tau_i | D)$ , can be read as the (posterior) probability of the  $i$ :th phylogenetic tree, given the data  $D$  (i.e. the aligned nucleotide sequences), and it is exactly this probability that we are interested in if we want to estimate a phylogeny.

In the right part of the equation (1) we have some terms that need some explanation.  $\Pr(\tau_i)$  is the prior probability for the tree topology  $\tau_i$ , which must be specified before analysis (one way is to assign a prior probability of  $1/B(s)$  to each tree  $\tau_i$ , where  $B(s)$  is the number of possible trees for  $s$  terminal taxa), and  $L(D | \tau_i)$  is the likelihood, that is the probability of the data, given the phylogeny. The denominator, the unconditional probability of the data, can be calculated by summing the product  $\Pr(\tau_j)L(D | \tau_j)$  for all possible phylogenetic trees (i.e. for  $\tau_1, \tau_2, \dots, \tau_j, \dots, \tau_{B(s)}$ ). The likelihood  $L(D | \tau_i)$  can be expressed as

$$L(D | \tau_i) = \int \int_{\nu, \theta} L(D | \tau_i, \nu, \theta) L(\nu, \theta) d\nu d\theta \quad (2)$$

where  $\tau_i$  represents the  $i$ :th phylogenetic tree and  $L(\nu, \theta)$  is the prior given to the branch lengths ( $\nu$ ) and the model parameters ( $\theta$ ). The calculation of the likelihood function  $L(D | \tau_i, \nu, \theta)$  can be done using the same models of DNA substitution that are used in maximum likelihood analyses and corrected distance analyses (see, e.g., Swofford et al., 1996; Page and Holmes, 1998; Nei and Kumar, 2000).

A problem with Bayesian inference is that for calculating the posterior probability of a phylogenetic tree it means that we need to make a summation over all possible trees (i.e. B(s) trees) and also an integration over the parameter space. The value of B(s) rises very quickly when the number of terminal taxa increases, and the minimum of parameters are the branch lengths in the tree (that is, there are at least as many parameters as there are branches in the tree) and often several more depending on the substitution model selected (the extra parameters,  $\theta$ , can for example be a transition/transversion rate ratio). It is thus obvious that computation of the posterior probability will be impractical even for rather small numbers of terminals, if there is no shortcut that can be used to overcome this problem. Fortunately, there are such shortcuts, and one of the most suited for approximating the posterior probabilities of phylogenetic trees is Markov chain Monte Carlo (MCMC; for an introduction, see e.g. Lewis, 2001, or Huelsenbeck and Bollack, 2001). By drawing a large enough number of dependent but valid samples from the parameter space (including tree topologies) a good approximation of the posterior probability distribution will be made, and the approximation will be better the more samples are drawn.

The crucial question now is what constitutes a sufficiently large number of samples? As usual the answer will be: it depends (on the selected model, the data matrix, and the number of terminals), but in most cases it will be several hundreds of thousands or even more. In practice, when running MRBAYES (Huelsenbeck and Ronquist, 2001a, b), if the estimated negative log-likelihood values have reached apparent stationarity, then this can be taken at least as an indication that samples before this should be discarded and that samples after this represent a valid draw from the posterior distribution.

One way that is utilised by MRBAYES to reduce the necessary minimum number of samples, and to reduce the risk that the MCMC will be stuck on a local peak in the parameter space, is to run several simultaneous chains of which all but one are “heated“. The heated chains in this so called Metropolis-coupled Markov chain Monte Carlo, or (MC)<sup>3</sup>, can be viewed as visiting a melted parameter landscape, where the peaks are lowered and the valleys are filled in, and thus they can more easily explore this landscape (Huelsenbeck and Ronquist, 2001a). The phylogenetic inference is however only based on the cold, “unheated“ chain, but there are proposal mechanisms for swapping between the heated chains and the cold chain (these mechanisms are called proposal mechanisms because they do just that: propose a swich between the unheated and a heated chain). This means that the cold chain more easily can jump between peaks if a successful swap is made between a cold chain that might be stuck on a local peak and a heated chain that is exploring another peak (Huelsenbeck and Ronquist, 2001a).

No method for phylogenetic inference is foolproof, and this is of course also true for Bayesian inference (see, e.g., J. P. Huelsenbeck, in manuscript), ranging from programming bugs (which can be difficult to detect) to inappropriate model choices (a

problem that of course is common with all other model-dependent inferences) or a MCMC stuck on local optima (also common with most other tree exploring methods, but the problem can be reduced by using multiple chains). Another, more specific problem touched upon above involves determining when a sufficient number of samples has been drawn. A graphical examination of the negative log-likelihood values given by MRBAYES plotted against the sample generation number will give a good indication whether the chain has reached stationarity or not, and only the topologies visited during the stationary phase should be used to estimate the phylogeny (the sampling period before reaching the stationary phase is called the burn-in period).

Despite the problems, there appear to be many advantages with Bayesian inference over other methods for phylogenetic inference. In using a model it takes into account what we believe about the evolutionary process at a molecular level (or at least the processes we have useful models for), and even under fairly complicated models computations can be reasonably fast. The output is a phylogenetic tree which also includes nodal support in an easily interpretable way (i.e. as credibility values, which can be interpreted as the posterior probability that the clade in question is monophyletic).

## SVENSK SAMMANFATTNING

Om du går ut på en sommaräng i Uppland är chansen ganska stor att du kommer att hitta stor blåklocka (*Campanula persicifolia*), hundkäx (*Anthriscus sylvestris*) och prästkrage (*Leucanthemum vulgare*). Vid den lilla vägen som kanske passerar en bit bort växer förstås åkertistel (*Cirsium arvense*), och i närheten dessutom några kärrtistlar (*Cirsium palustre*) och en grupp ängsvädd (*Succisa pratensis*). Fortsätter du längs vägen, och om du är lite längre in i landet, kan du komma till en liten klar skogssjö, i vars grunda vatten det växer notblomster (*Lobelia dortmanna*). På den fuktiga stranden finner du dessutom flädervänderot (*Valeriana sambucifolia*). På väg ner till sjön har du dessutom, på ett litet stenblock i granskogen, sett några linneor (*Linnaea borealis*) med sina små vita klockformade blommor. Dessutom stod det några överblommade skogstry (*Lonicera xylosteum*) i närheten. Skulle du ta och traska in i skogen, bort till myren, kan det hända att du hittar vattenklöver (*Menyanthes trifoliata*) i myrgölarna.

Alla dessa växter du hittills har sett (det finns förstås många fler runt omkring dej, men dem har du inte lagt märke till än) är, i ett längre evolutionärt perspektiv sett i alla fall, rätt nära släkt med varandra. De brukar informellt alla föras till en grupp växter som kallas Euasterider II (alltså grupp två bland de äkta Asteriderna; från grupp ett kan vi hitta andra växter i vårt somriga Uppland: Uppländsk vallört (*Symphyticum x uplandicum*), vitmåra (*Galium boreale*), snårvinda (*Calystegia sepium*), vitplister (*Lamium album*), besksöta (*Solanum dulcamara*) och ängskovall (*Melampyrum arvense*), bland många andra), och några av dem är förstås närmare släkt med varandra än andra. De båda tistlarna tillhör, som deras vetenskapliga namn antyder, samma släkte (*Cirsium*) men två olika arter. I samma familj, korgblommiga eller asterväxter (Asteraceae) har vi också sett en tredje art, prästkragen. Trots att ängsvädden till det yttre kan vara lik en korgblommig växt tillhör den en annan ordning (ordningar är grupper som består av en eller oftare flera familjer; familjerna består av släkten, och släktena av arter).

De korgblommiga växterna tillhör ordningen Asterales, den grupp av växter som mina första två bidrag (**I** och **II**) i avhandlingen behandlar. I Asterales finns också vattenklöver som en rätt nära släkting till de korgblommiga växterna, medan blåklockan och notblomstret sitter på en gren lite längre ner i släktskapsträdet. Det är alltså just detta evolutionära släktskapsträd som jag har försökt rekonstruera i **bidrag I**, både genom växternas morfologi, kemi och anatomi, men också genom att jämföra deras DNA-sekvenser. Med hjälp av kraftfulla datorer och sofistikerade datorprogram har jag så lyckats bygga hypoteser om dessa växters släktskap. Många detaljer har förstås varit kända sedan tidigare, men det har också funnits många konkurrerande idéer som inte alla samtidigt har kunnat varit riktiga. Genom att använda mej av en stor mängd information och många representanter från hela ordningen Asterales (som förutom blåklockor, korgblommiga och vattenklöver består av ett antal rätt små växtfamiljer från framför allt Australien, Nya Zeeland, Nya Kaledonien och områdena däromkring) har flera av dessa tveksamheter kunnat göras om inte helt säkra så i alla fall mycket mindre osäkra, och jag har också lyckats visa att en nästan helt oundersökt växt från Nya Kaledonien (*Platyspermatum*, som dess vetenskapliga namn är, saknar förstås svenskt namn, men samlades in för första gången av den svenske botanisten Carl Skottsberg i slutet av 1940-talet under en av hans många insamlingsresor) som ingen har vetat var den har hört hemma någonstans i blomväxternas klassificeringssystem, faktiskt är närmast släkt med växter i ordningen Asterales.

Men även om vi skulle veta alla detaljer om släktskapen inom en ordning som Asterales, så finns det ju också släktingar strax utanför (på långt håll är ju allt levande på jorden släkt med varandra, också du och jag är släkt inte bara med varandra och alla andra däggdjur, utan på lite längre håll också med de växter jag har arbetat med — förutom allt annat som är i liv eller någon gång har varit det...). För Asterales del hittar man dem bland de andra Euasteriderna II, men det har varit oklart vilka bland dessa som skulle passa bäst som systergrupp — närmast släkting — till Asterales. Så är det i och för sej fortfarande, men många av de grupper som tidigare har föreslagits har jag nu lyckats visa vara närmare släkt med andra ordningar i Euasteriderna II, och det återstår nu i stort sett bara två alternativ: endera är systergruppen till Asterales den lilla sydafrikanska familjen *Bruniaceae* (och i så fall borde Asterales utökas så att ordningen också inkluderade *Bruniaceae*), eller så består systergruppen av alla andra Euasterider II, det vill säga ordningarna *Apiales* (här hittar vi hundkäxet vi såg på vår sommaräng tidigare, men också tropiska och subtropiska släktingar som rumsaralia *Pseudopanax lessonii* och för all del också ginseng *Panax ginseng*) och *Dipsacales* (till exempel linnean, ängsvädden och skogstryt) tillsammans med ett par små familjer som i **bidrag V** för första gången har fått en avgränsning som i alla fall möjligen är naturlig (det vill säga familjerna — om mina hypoteser är korrekta — inkluderar alla avkomlingar till en gemensam förfader, men inga andra). Det första alternativet, det med *Bruniaceae*, är det som föreslås i **bidrag V**, men det har ännu inte gått att hitta några gemensamma karaktärer mellan Asterales och *Bruniaceae* som styrker släktskapet, och dessutom är det förvånande att ha en sydafrikansk grupp som närmast släkting till en ordning som verkar ha sitt ursprung i de delar av den forntida jättekontinenten Gondwana som senare blev till bland annat Australien. Men å andra sidan så rör vi oss nu bland släktskap som var samtida med dinosaurierna, och mycket kan ha hänt under alla dessa årmiljoner. Med andra ord: mer forskning behövs!

En av de två familjerna i närheten av *Apiales* och *Dipsacales* som nu fått en (i alla fall möjlig) naturlig avgränsning är *Escalloniaceae* (**bidrag III** och **IV** beskriver några av dess medlemmar). Inte heller denna har något svenskt namn, och de allra flesta av dess sydöasiatiska, australasiska och sydamerikanska representanter är helt okända för oss i Sverige, möjligen med undantag för *sommarescallonia* (*Escallonia virgata*) från de sydamerikanska Anderna (där man hittar de allra flesta medlemmarna i släktet *Escallonia*) som ibland odlas hos oss. Historiskt sett har *Escalloniaceae* behandlats som en riktig slasktratt för växter som man inte har kunnat placera någon annan stans (till exempel *Platyspermatum* som nämndes ovan). Numera är tidigare *Escalloniaceae*-medlemmar placerade inte bara på olika håll bland Euasteriderna II (flera har visat sej vara bäst placerade i Asterales) utan också bland grupper utanför Asteriderna. Trots att *Escalloniaceae* har skalats av mer och mer, och allt färre släkten har återstått, har man misstänkt att familjen fortfarande har varit en onaturlig grupp. I **bidrag V** har jag lyckats visa att några avvikande släkten som tidigare har uteslutits från *Escalloniaceae* faktiskt ska inkluderas i familjen, och att ett av de få återstående släktena ska uteslutas (och föras till *Paracryphiaceae* som är den andra nyavgränsade familjen). Med den avgränsningen som *Escalloniaceae* nu har fått verkar det som om det är en fullt naturlig grupp som nu förhoppningsvis ska kunna få en stabil klassificering som inte ändras varje gång någon skriver om den.

Men preliminära resultat (som summerats tidigare i detta **Comprehensive Summary**) har visat att även om *Escalloniaceae* nu är en naturlig grupp så är *Escallonia* kanske inte det. *Escalloniorna* är buskar eller små träd som framför allt växer i Anderna

i Sydamerika och har ganska stora, vackra blommor (flera arter odlas i lite varmare trakter och de är rätt populära som häckväxter i till exempel Storbritannien). I Sydamerika finns också en nära släkting till *escalloniorna*, *Valdivia gayana*, men denna är en liten rätt oansenlig halvbuske som växer i grottor och andra små skyddade håligheter nära kusten i provinsen Valdivia i södra Chile och är dessutom nu nästan helt utrotad från det vilda (bara tre små populationer är kända). På den knappt två miljoner år gamla vulkanön Réunion utanför Madagascars östkust i Indiska Oceanen växer *Forgesia racemosa*, en annan nära släkting till *escalloniorna*. Till skillnad från *Valdivia* är *Forgesia* en lian med rätt stora, vackra blommor som dessutom är ganska vanlig på sina håll i Réunions bergsregnskogar. Finge man gissa så skulle man vilja placera *Valdivia* som systergrupp till *escalloniorna* (bägge finns ju i Sydamerika) och *Forgesia* som systergrupp till grenen med *escalloniorna* och *Valdivia* (trots alla skillnader som finns så har alla tre släktena frön som är i stort sett identiska, vilket i alla fall ger en antydning om att de kan vara nära släkt). Men verkligheten verkar vara annorlunda. *Forgesia* och *Valdivia* verkar vara mycket närmare släkt med varandra än vad man skulle kunna tro (de bildar en egen liten gren), och vad som verkligen är förvånande är att grenen med *Forgesia* och *Valdivia* verkar sitta *inuti Escallonia*-grenen. Släktskapsundersökningarna av *escalloniorna* och dess närmaste släktingar har nu bara påbörjats, men om de första resultaten visar sej hålla så betyder det att också släktet *Escallonia* behöver omdefinieras, till exempel genom att inkludera både *Forgesia* och *Valdivia* i släktet. Men: mer forskning behövs!

Många frågor har fått sina svar under mitt arbete, kanske ännu fler frågor har väckts. Självklart har jag inte gjort mitt arbete helt ensam. En stabil grund har lagts under många år, inte minst av tidigare doktorander på dåvarande institutionen för systematisk botanik (Mats H. G. Gustafsson och Anders Backlund), av min handledare Kåre Bremer och andra kollegor på nuvarande avdelningen för systematisk botanik (Birgitta Bremer, Bengt Oxelman och Mats Thulin). Jag har också fått mycket hjälp av doktorandkollegan Jesper Kårehed, som delvis har jobbat med samma växter (eller i alla fall samma grupper) som jag. Dessutom har jag varit oändligt hjälpt av Nahid Heidari som har sekvenserat en stor del av de gensekvenser jag har använt i min forskning. Förhoppningsvis kommer mina bidrag kunna utgöra grunden för kommande framtida forskning, och jag ser fram emot att få se mina resultat bekräftade (och för den delen också vederlagda).



## REFERENCES

- Agardh, J. G. 1858.** *Theoria systematis plantarum*. Gleerup, Lund, Sweden.
- Airy Shaw, H. K. 1942.** XIII.—Additions to the flora of Borneo and other Malay islands: XIX. The Pentaphragmataceae of the Oxford University Expedition to Sarawak, 1932. *Kew Bulletin* **1941**: 233-236.
- Al-Shammary, K. I. 1980.** Systematic studies of the Saxifragaceae s.l., chiefly from the southern hemisphere. Unpublished Ph.D. Thesis, University of Leicester, Leicester, U.K.
- Angiosperm Phylogeny Group (APG) 1998.** An ordinal classification for the families of flowering plants. *Annals of the Missouri Botanical Garden* **85**: 531-553.
- Backlund, A. 1996.** Phylogeny of the Dipsacales. Ph.D. Thesis, Uppsala University, Uppsala, Sweden.
- Backlund, A., and B. Bremer. 1997.** Phylogeny of the Asteridae s. str. based on *rbcL* sequences, with particular reference to the Dipsacales. *Plant Systematics and Evolution* **207**: 225-254.
- Backlund, A., and M. J. Donoghue. 1996.** Morphology and phylogeny of the order Dipsacales. Paper IV in A. Backlund: Phylogeny of the Dipsacales. Ph.D. Thesis, Uppsala University, Uppsala, Sweden.
- Backlund, A., and N. Pyck. 1998.** Diervillaceae and Linnaeaceae, two new families of caprifolioids. *Taxon* **47**: 657-661.
- Baillon, H. 1872.** *Histoire des Plantes*, vol. 3. Librairie Hacette et C<sup>ie</sup>, Paris, France.
- Bremer, K., and M. H. G. Gustafsson. 1997.** East Gondwana ancestry of the sunflower alliance of families. *Proceedings of the National Academy of Sciences, USA* **94**: 9188-9190.
- Carlquist, S. 1997.** *Pentaphragma*: a unique wood and its significance. *IAWA Journal* **18**: 3-12.
- , and M. L. DeVore. 1998. Wood anatomy of Calyceraceae with reference to ecology, habit, and systematic relationships. *Aliso* **17**: 63-76.
- Chandler, B. 1911.** Note on *Donatia novae-zelandiae*, Hook. f. *Notes from the Royal Botanic Garden of Edinburgh* **5**: 43-47.
- Cosner, M. E., R. K. Jansen, and T. G. Lammers. 1994.** Phylogenetic relationships in the Campanulaceae based on *rbcL* sequences. *Plant Systematics and Evolution* **190**: 79-95.
- Demker, O. 1998.** Phylogeny and origin of the bellflower family. Unpublished M.Sc. Thesis, Uppsala University, Uppsala, Sweden.
- Downie, S. R. and J. D. Palmer. 1992.** Restriction site mapping of the chloroplast DNA inverted repeat: a molecular phylogeny of the Asteridae. *Annals of the Missouri Botanical Garden* **79**: 266-283.
- Dravitzky, P. V. 1967.** A comparative study of the wood anatomy and floral vascular systems of the New Zealand genera of the Escalloniaceae, *Carpodetus*, *Ixerba* and *Quintinia*. Unpublished M.Sc. Thesis, University of Canterbury, Christchurch, New Zealand.
- Dunbar, A. 1978.** Pollen morphology and taxonomic position of the genus *Pentaphragma* Wall. (Pentaphragmataceae). The use of compound fixatives. *Grana* **17**: 141-147.
- Engler, A. 1890.** Saxifragaceae. Pages 41-93 in A. Engler and K. Prantl (eds.): *Die natürlichen Pflanzenfamilien*, vol. 3: 2a. Wilhelm Engelmann, Leipzig, Germany.

- **1928.** Saxifragaceae. Pages 74-226 in A. Engler (ed.): *Die natürlichen Pflanzenfamilien*, 2nd ed., vol. 18a. Wilhelm Engelmann, Leipzig, Germany.
- Eyde, R. H. 1966.** Systematic anatomy of the flower and fruit of *Corokia*. *American Journal of Botany* **53**: 833-847.
- Gardner, R. O. 1976.** Studies in Alseuosmiaceae. Unpublished Ph.D. Thesis, University of Auckland, Auckland, New Zealand.
- Guillaumin, A. 1950.** Plantae Neocaledonicae a C. Skottsberg a. 1949 lectae. *Acta Horti Gotoburgensis* **18**: 247-265.
- Gustafsson, M. H. G. 1996.** Phylogenetic hypotheses for Asteraceae relationships. Pages 9-19 in D. J. N. Hind, H. Beentje and G. V. Pope (eds.): Proceedings of the International Compositae Conference, Kew, 1994, vol. 1. Systematics. Royal Botanic Gardens, Kew, UK.
- Gustafsson, M. H. G., A. Backlund, and B. Bremer. 1996.** Phylogeny of the Asterales sensu lato based on *rbcL* sequences with particular reference to the Goodeniaceae. *Plant Systematics and Evolution* **199**: 217-242.
- Gustafsson, M. H. G., and K. Bremer. 1997.** The circumscription and systematic position of Carpodetaceae. *Australian Systematic Botany* **10**: 855-862.
- Hansen, H. V. 1991.** SEM-studies and general comments on pollen in tribe Mutisieae (Compositae) sensu Cabrera. *Nordic Journal of Botany* **10**: 607-623.
- Hansen, H. V. 1992.** Studies in the Calyceraceae with a discussion of its relationship to Compositae. *Nordic Journal of Botany* **12**: 63-75.
- Hils, M. H. 1985.** Comparative anatomy and systematics of twelve woody Australasian genera of Saxifragaceae. Unpublished Ph.D. Thesis, University of Florida, Gainesville, Florida, USA.
- Huelsenbeck, J. P. and J. P. Bollback. 2001.** Empirical and hierarchical Bayesian estimation of ancestral states. *Systematic Biology* **50**: 351-366.
- Huelsenbeck, J. P. and F. Ronquist. 2001a.** MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* **17**: 754-755.
- Huelsenbeck, J. P. and F. Ronquist. 2001b.** MRBAYES: Bayesian inference of phylogenetic trees. Computer software available at <http://morphbank.ebc.uu.se/mrbayes/>
- Inoue, N., and H. Tobe. 1999.** Integumentary studies in Menyanthaceae (Campanulales sensu lato). *Acta Phytotaxonomica et Geobotanica* **50**: 75-79.
- Jansen, R. K. and K.-J. Kim. 1996.** Implications of chloroplast DNA data for the classification and phylogeny of the Asteraceae. Pages 317-339 in D. J. N. Hind and H. Beentje (eds): *Compositae: Systematics*. Proceedings of the International Compositae Conference, Kew, 1994, vol. 1. Royal Botanic Gardens, Kew, UK.
- Jay, M. 1969.** Contribution biochimique a la connaissance taxonomique et phylogenetique des Saxifragacees et familles affines. Unpublished Ph.D. Thesis, L'Universite de Lyon, Lyon, France.
- Judd, W. S., C. S. Campbell, E. A. Kellogg, and P. F. Stevens. 1999.** *Plant systematics a phylogenetic approach*. Sinauer Associates, Sunderland, Massachusetts, U.S.A.
- Kårehed, J. 2001.** Multiple origin of the tropical forest tree family Icacinaceae. *American Journal of Botany* **88**: in press.
- Kårehed, J., J. Lundberg, B. Bremer, and K. Bremer. 1999 (2000).** Evolution of the Australasian families Alseuosmiaceae, Argophyllaceae, and Phellinaceae. *Systematic Botany* **24**: 660-682.

- Koontz, J. A., and D. E. Soltis. 1999.** DNA sequence data reveal polyphyly of Brexioidae (Brexioaceae; Saxifragaceae sensu lato). *Plant Systematics and Evolution* **219**: 199-208.
- Lammers, T. G. 1992.** Circumscription and phylogeny of the Campanulales. *Annals of the Missouri Botanical Garden* **79**: 388-413.
- Laurent, N., B. Bremer, and K. Bremer. 1999.** Phylogeny and generic interrelationships of the Stylidiaceae (Asterales), with a possible extreme case of floral pedomorphosis. *Systematic Botany* **23**: 289-304.
- Lewis, P. O. 2001.** Phylogenetic systematics turns over a new leaf. *Trends in Ecology and Evolution* **16**: 30-37.
- Lindley, J. 1853.** *The Vegetable Kingdom*, 3rd ed. Bradbury and Evans, London, UK.
- Merrett, M. F., and B. D. Clarkson. 2000.** Reinstatement of *Alseuosmia quercifolia* (Alseuosmiaceae) from New Zealand. *New Zealand Journal of Botany* **38**: 153-164.
- Mildbraed, J. 1908.** Stylidiaceae. Pages 1-98 in A. Engler (ed.): *Das Pflanzenreich*, vol. 4: 278. Wilhelm Engelmann, Leipzig, Germany.
- Morgan, D. R., and D. E. Soltis. 1993.** Phylogenetic relationships among members of Saxifragaceae sensu lato based on *rbcL* sequence data. *Annals of the Missouri Botanical Gardens* **80**: 631-660.
- Nei, M., and S. Kumar. 2000.** *Molecular Evolution and Phylogenetics*. Oxford University Press, Oxford, UK.
- Nemirovich-Danchenko, E. N. (Volume Editor). 2000.** *Sravnitel'naja anatomija semjan. Vol. 6. Dvudol'nye. Rosidae II*. NAUKA, S:t Petersburg, Russia.
- Olmstead, R. G., H. J. Michaels, K. M. Scott, and J. D. Palmer. 1992.** Monophyly of the Asteridae and identification of their major lineages inferred from DNA sequences of *rbcL*. *Annals of the Missouri Botanical Garden* **79**: 249-265.
- Page, R. D. M., and E. C. Holmes. 1998.** *Molecular Evolution A Phylogenetic Approach*. Blackwell Science, Oxford, U.K.
- Plunkett, G. M. 2001.** Relationship of the order Apiales to subclass Asteridae: a re-evaluation of morphological characters based on insights from molecular data. *Edinburgh Journal of Botany* **58**: 183-200.
- Ramamonjiarisoa, B. A. 1980.** Comparative anatomy and systematics of african and malagasy woody Saxifragaceae sensu lato. Unpublished Ph.D. Thesis, University of Massachusetts, Amherst, Massachusetts, U.S.A.
- Ramírez, C. and J. Sempe. 1981.** *Valdivia gayana* als Beispiel einer im suantarktischen Bereich von Südamerika endemischen Pflanzenart. *Oberheissische Naturwissenschaftliche Zeitschrift* **46**: 75-80.
- Savolainen, V., R. Spichiger, and J.-F. Manen. 1997.** Polyphyletism of Celastrales deduced from a chloroplast noncoding DNA region. *Molecular Phylogenetics and Evolution* **7**: 145-157.
- Savolainen, V., M. W. Chase, S. B. Hoot, C. M. Morton, D. E. Soltis, C. Bayer, M. F. Fay, A. Y. de Bruijn, S. Sullivan, and Y.-L. Qiu. 2000a.** Phylogenetics of flowering plants based on combined analysis of plastid *atpB* and *rbcL* gene sequences. *Systematic Biology* **49**: 306-362.
- Savolainen, V., M. F. Fay, D. C. Albach, A. Backlund, M. van der Bank, K. M. Cameron, S. A. Johnson, M. D. Lledó, J.-C. Pintaud, M. Powell, M. C. Sheahan, D. E. Soltis, P. S. Soltis, P. Weston, W. M. Whitten, K. J. Wurdack,**

- and M. W. Chase. 2000b. Phylogeny of the eudicots: a nearly complete familial analysis based on *rbcL* gene sequences. *Kew Bulletin* **55**: 257-309.
- Schlechter, R. 1907. Beiträge zur Kenntnis der Flora von Neu-Kaldeenien. *Botanische Jahrbücher* **39**: 1-274.
- Schmid, R. 1980. Comparative anatomy and morphology of *Psiloxylon* and *Heteropyxis*, and the subfamilial and tribal classification of Myrtaceae. *Taxon* **29**: 559-595.
- Schönland, S. 1889. Campanulaceae. Pages 40-70 in A. Engler and K. Prantl (eds): *Die natürlichen Pflanzenfamilien*, vol.4: 5 (1-3). Wilhelm Engelmann, Leipzig, Germany.
- Skottsberg, C. 1915. Notes on the relations between the floras of Subantarctic America and New Zealand. *Plant World* **18**: 129-142.
- Skvarla, J. J., B. L. Turner, V. C. Patel, and A. S. Tomb. 1977. Pollen morphology in the Compositae and in morphologically related families. Pages 141-265 in V. H. Heywood, J. B. Harborne, and B. L. Turner (eds): *The biology and chemistry of the Compositae*, vol. 1. Academic Press, London, UK.
- Soltis, D. E., and P. S. Soltis. 1997. Phylogenetic relationships in Saxifragaceae sensu lato: A comparison of topologies based on 18S rDNA and *rbcL* sequences. *American Journal of Botany* **84**: 504-522.
- Soltis, D. E., P. S. Soltis, M. T. Clegg, and M. Durbin. 1990. *rbcL* sequence divergence and phylogenetic relationships in Saxifragaceae sensu lato. *Proceedings of the National Academy of Sciences, USA* **87**: 4640-4644.
- Soltis, D. E., P. S. Soltis, D. L. Nickrent, L. A. Johnson, W. J. Hahn, S. B. Hoot, J. A. Sweere, R. K. Kuzoff, K. A. Kron, M. W. Chase, S. M. Swensen, E. A. Zimmer, S.-M. Chaw, L. J. Gillespie, W. J. Kress, and K. J. Sytsma. 1997. Angiosperm phylogeny inferred from 18S ribosomal DNA sequences. *Annals of the Missouri Botanical Garden* **84**: 1-49.
- Soltis, D. E., P. S. Soltis, M. W. Chase, M. E. Mort, D. C. Albach, M. Zanis, V. Savolainen, W. H. Hahn, S. B. Hoot, M. F. Fay, M. Axtell, S. M. Swensen, L. M. Prince, W. J. Kress, K. C. Nixon, and J. S. Farris. 2000. Angiosperm phylogeny inferred from 18S rDNA, *rbcL*, and *atpB* sequences. *Botanical Journal of the Linnean Society* **133**: 381-461.
- van Steenis, C. G. G. J. 1982. 157. Preliminary note on the taxonomic disposition of Platyspermatium Guillaumin (Myrtaceae) from New Caledonia. Pages 24-25 in C. G. G. J. van Steenis and J. F. Veldkamp: Miscellaneous botanical notes XXVI. *Reinwardtia* **10**: 21-26.
- Swofford, D., G. Olsen, P. Waddell, and D. M. Hillis. 1996. Phylogenetic inference. Pages 407-511 in D. M. Hillis, C. Moritz, and B. K. Mable (eds.): *Molecular Systematics*, 2nd ed. Sinauer, Sunderland, Massachusetts, USA.
- Takhtajan, A. 1987. *Systema Magnoliophytorum*. NAUK, S:t Petersburg, Russia.
- Takhtajan, A. 1997. *Diversity and Classification of Flowering Plants*. Columbia University Press, New York, USA.
- Vogel, S. 1998. Remarkable nectaries: structure, ecology, organophyletic perspectives IV. Miscellaneous cases. *Flora* **193**: 225-248.
- Zhao, Z., J. J. Skvarla, R. K. Jansen, and M. L. DeVore. 2000. Phylogenetic implications of pollen morphology and ultrastructure in the Barnadesioideae (Asteraceae). *Lundellia* **3**: 26-40.

## TACK!

Mitt största tack går till min handledare **Kåre Bremer**, som inte bara gav mej en intressant frågeställning, utan också har litat på att den skulle gå att lösa, och som har låtit mej arbeta ganska fritt och som jag själv har valt (även om alla val kanske inte har varit de bästa så har jag lärt mej oändligt mycket på det), förutom att ha ekonomiskt stöttat forskningen (bland annat genom bidrag från Naturvetenskapliga forskningsrådet och Vetenskapsrådet). Kåre har också varit en stor inspiratör ända sedan första gången vi träffades på hösten 1987. En annan inspiratör har **Birgitta Bremer** varit, som dessutom har låtit mej utnyttja det molekylärsystematiska laboratoriet hon har byggt upp och all hennes kunskap om sekvensering och sekvensanalyser. Hon har dessutom läst igenom alla manuskript och kommit med många förslag till förbättringar. Tack Birgitta!

Här kan det också vara på plats att tacka personalen på lab: **Nahid Heidari** har varit ovärderlig med sitt tålamod när jag har gjort mina taffliga försök med att sekvensera gener, och hon har visat att det faktiskt går att ta fram sekvenser på otroligt kort tid. Det är förresten Nahid som har gjort många av de sekvenser som tagits fram för min forskning. **Jessica Rönnholm** visade en stor pedagogisk talang när hon introducerade mej till manuell sekvensering för fem år sedan. **Ulla-Britt Sahlström** ska också ha stort tack för hjälp med att snitta växtdelar i otroligt tunna snitt så de har gått att undersöka under mikroskop. Avdelningens sekreterare **Ulla Hedenqvist** ska också ha ett stort tack för hjälp med många praktiska ting.

Också övriga lektorer och professorer på Avdelningen för Systematisk botanik har bidragit till många förbättringar av avhandlingen, inte minst på slutet: **Bengt Oxelman**, **Mats Thulin** och **Leif Tibell** har läst igenom alla manuskript och kommit med många förslag till förbättringar, varav jag har följt i alla fall några (ett särskilt tack till Mats som pekade ut att en tidigare publicerad *Cyphia*-sekvens borde bytas ut, vilket ledde till att Paper I till stora delar måste skrivas om i sista stunden...). **Jesper Kårehed**, **Hanne Grundt** och **Fredrik Ronquist** har också läst igenom delar av manuskripten och kommit med många värdefulla kommentarer. Professor emeritus **Olof Hedberg** och tidigare docenten på avdelningen **Inga Hedberg** har alltid funnits i bakgrunden och många gånger haft en alternativ syn på hur botanisk forskning kan bedrivas, vilket verkligen har uppskattats.

I must also give my very sincere thanks to **Stéphane Baret** (Isle de Réunion) and **Peter Seemann** (Valdivia, Chile) for invaluable help with collecting good material of *Forgesia racemosa* and *Valdivia gayana*. Your help saved me much trouble, and saved a few valuable old herbarium specimens from partial destruction! **Rudi Schmid** sent me herbarium material of *Platyspermation crassifolium* that we could use for sequencing this interesting plant, and did not oppose the use of the *Platyspermation* sequences for Paper I despite ongoing research on the genus. Many thanks Rudi! Thanks also to **Mark W. Chase**, **Douglas S. Soltis**, **Robert K. Jansen** and **Ki-Joong Kim** for sharing DNA samples and (at that time) unpublished gene sequences with us. The curators at K, P, S and UPS are thanked for loan of herbarium material. The librarians at Uppsala University Library and many foreign libraries also deserve a thank for helping me in locating sometimes very obsolete literature. Stort tack också till **Ilya Zelikman** för hjälp med att översätta ryska texter.

**Sahara Hotnights** har underlättat skrivandet och gjort många långa nätter med korrektur och analyser uthärdliga.

Självklart hade tiden som doktorand varit mycket tråkigare och kanske omöjlig att härda ut utan mina doktorandkollegor (och övriga) på Avdelningarna för Systematisk Botanik och Systematisk Zoologi. Ett särskilt tack måste gå till **Dick, Jesper, Annika, Magnus, Per K, Per E, Elisabeth, Johanne, Kristina, Henrik, Björn-Axel** och **Maria**. De forna lunchvännerna (och biokompisarna) på fysiologisk botanik måste förstås också få sitt tack: **Katarina, Annelie, Johannes, Ingela** och många fler. Jag har haft många doktorandföregångare på avdelningen som har varit till stor hjälp och inspiration. Om jag ska nämna några får det bli **Lars-Gunnar Reinhammar, Ulf Swenson, Anders Backlund, Mats Gustafsson** och **Nadina Laurent**. Mina många vänner från tiden innan doktorandstudierna är inte glömda, även om det var länge sedan jag sist träffade några av er: **Åsa, Malin, Sara, David, Johan, Anna** (tack för att du fick mej att pröva jujutsu!), **Lina, Janne, Jenny, Sylwia, Stefan** och många, många fler.

Jag har också hunnit med ett liv utanför växtsystematiken. Under somrarna har jag nästan årligen ägnat ett par veckor åt att bila runt i Nordland tillsammans med **Torbjörn Doj** (tack för skjutsen!) för att leta grottor, vilket sommaren 1993 ledde till upptäckten av **Tjoarvekråjgge** som numera är längst i Norden... Stort tack alltså till alla som har hjälp till med utforskandet av denna jättegrotta och som har varit sällskap under många, långa, kalla och mörka (och leriga!) timmar under jord. Tack också till alla andra grottisar som ännu inte har varit till Tjorve (här måste jag särskilt tacka **Alf Sidén, Rabbe Sjöberg** och **Lars-Erik Åström** för uppmuntran och hjälp, särskilt under mina tidigare grottår). Förutom grottor har mycket tid stulits från forskningen genom jujutsun. Stort tack till alla vänner vid **Uppsala Ju-jutsuklubb** (det är omöjligt att nämna alla, men jag måste tacka **Matti Nikkola** som stod ut med mej vid graderingarna till blått och brunt och dessutom gjorde mej sällskap under några härliga grottveckor i Nordnorge för några somrar sedan, och **Ingrid Eklund** utan vars hjälp jag aldrig hade kunnat gradera till svart), **Kraftverket ju-jutsuakademin** och **Uppsala Budoklubb!**

Mina många vänner i Norge förtjänar också ett tack för att ha fått mej att tänka på andra saker än fylogener: I Oslo særlig **Elin, Hanne, Sissel, Kristine, Katinka, Gunvor, Liv Borgen, Reidar Elven, Inger Nordal** og mange, mange flere. Til tross for at jeg ikke har truffet mange av dere på lang tid, så er jeg med dere ofte i mine tanker! Siskelii davás: **Trine Kalstad**.

Ett självklart tack för praktiskt taget allt till mina föräldrar **Bosse** och **Eva**, dessutom till mina bägge bröder, **Anton** och **Eskil** – jag hoppas ni får lika skoj som jag har haft!

Sist men absolut inte minst: **Mia, tack!**