Evolutionary Studies in Asterids
Emphasising Euasterids II

BY
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Abstract

This thesis deals with evolutionary relationships within the asterids, a group of plants comprising about one-third of all flowering plants.

Two new families are recognised: Pennantiaceae and Stemonuraceae. The woody Pennantia from New Zealand and Australia is the sole genus of Pennantiaceae. Stemonuraceae consist of a dozen woody genera with a pantropical distribution and a centre of diversity in South East Asia and the Malesian islands. They are characterised by long hairs on their stamens and/or fleshy appendages on their fruits. Both families were formerly included in Icacinaceae. While Pennantiaceae are unrelated to any of the former Icacinaceae and placed in the order Apiales, other former Icacinaceae genera are related to Cardiopteris, a twining herb from South East Asia and Malesia. The monogeneric family Cardiopteridaceae is enlarged as to include also these. Cardiopteridaceae and Stemonuraceae are sister groups and placed in Aquifoliales. The three other families of Aquifoliales are monogeneric and closely related. The Asian Helwingiaceae and the Central/South American Phyllonomaceae are suggested to be merged into Aquifoliales (hollies). The genera of Icacinaceae in the traditional sense not placed in any of the above families (all euasterids II) are members of early diverging lineages of the euasterids I and possibly included in the order Garryales.

The three woody Australasian families Alseuosmiaceae, Argophyllaceae, and Phelli-naceae are confirmed as members of Asterales, despite traditional placements not close to that order. They are, moreover, supported as each other’s closest relatives.

The results are based mainly on parsimony analysis of DNA sequence data, but morphological studies have revealed characters in support for the molecularly based conclusions. The gene that has provided most new information is the chloroplast ndhF gene. The results are, however, drawn from combined analyses of sequences from one or several additional genes (atpB, matK, rbcL, 18S rDNA). The data have also been explored with Bayesian analysis, a statistical, model-based method that most recently has been developed for phylogeny reconstruction.

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PAPERS INCLUDED IN THE THESIS

This thesis is based on the following papers, which are referred to in the text by their Roman numerals:


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1 In Paper I the first author is responsible for the morphological work, the analyses, and the writing of the paper. JL contributed with molecular work (DNA sequencing) in the laboratory facilities provided by BB. The project was initiated, financed, and supervised by KB.
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Introduction

Reading this thesis you will encounter well-known plants such as bluebell, holly, and celery. You will also meet very rare ones, some only known from a single locality or even as a single naturally occurring individual. They are all members of the group known under the name asterids. The asterids comprise one-third of the flowering plants and are named after the genus *Aster* in the sunflower family, Asteraceae.

Among the flowering plants there are a number of taxa (sing. taxon; group at any rank in the classification) with uncertain relationships. Botanists have since ancient times tried to classify the impressing plant diversity, but with the means at hand up to the last decades of the 20th century, the relationships of some groups could not be settled. In many cases it became a matter of opinion – various authors would not agree on the importance of certain characters and competing views on the affinities of some taxa were accordingly common. In this thesis several little known (at least in the northern hemisphere) plant families that have been difficult to place are studied and for many of these new relationships are proposed. To encompass the new information, two new families are described and the circumscriptions of others are re-defined. As several of these families are shown to have quite different affinities than once thought, the evolution of the groups to which they do belong must be re-evaluated in order to understand, for example, when and where they originated and how their ancestors have evolved into their present day morphological and taxonomic diversity.

When Linnaeus (e.g., Linnaeus, 1753) classified the about 10,000 plant species known at his days, he studied the number of stamens and pistils. This resulted in an artificial classification where species with separate histories grouped together. Since the publication of Darwin’s (1859) work, a modern classification is supposed to take evolution into account. Systematists want to study natural groups, i.e., groups with a common ancestor. The methods I have used to investigate ‘naturalness’ of the groups under study (parsimony analysis and Bayesian inference) are described below. The Angiosperm Phylogeny Group (APG II, 2002) recognised 458 natural families grouped in 45 orders for the more than 250,000 plant species known today. Within the asterids there are two major natural groups, euasterids I and II, each
comprising four orders and a few families unplaced to order. Most of the plant groups I have studied are members of the euasterids II, viz. taxa of the orders Asterales (Papers I-III), Aquifoliales (Papers IV-V), and Apiales (Paper VI). In Paper IV the circumscription of the euasterid I order Garryales with Aucuba, a quite common ornamental, is also discussed.

Several of the plants included in the thesis have a taxonomic history involving Swedish botanists. Linnaeus, of course, described many of the better-known genera, such as Ilex (hollies) and Apium (e.g., celery), but most of them were not known to him. Two of his disciples both sailed with Captain James Cook on his voyages around the world; Daniel Solander on the first and Anders Sparrman on the second. They collected the first specimens of some New Zealand (Alseuosmia, Pennantia) and New Caledonian genera (Argophyllum) described by Forster & Forster (1776). New Caledonia itself was “discovered” on the second voyage. One of the two new families I proposed in Paper IV (Pennantiaceae) was in fact described by another Swedish botanist, Jacob Georg Agardh, in the mid 19th century (Agardh, 1858), but the family name was, until now, never adopted.

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2 Euasterids I and II are by Bremer et al. (2002) referred to as lamiids and campanulids, respectively, in order to avoid confusion of the two. In the thesis, I will, however, keep to the older names to be consistent with the names used in the included papers.
Materials and methods

Sources of data
The morphology of the groups under study was investigated mainly on herbarium specimens, but for some taxa also live material was seen. Extensive literature studies provided additional morphological data, especially on wood anatomy and pollen morphology. As indicated, morphological studies alone are often not enough to reveal the relationships of certain taxa. The source of data providing most of the information yielding the hypothesis of the presented relationships is DNA sequences. From small pieces of leaves it is possible to extract DNA and by the Polymerase Chain Reaction (PCR) specific genes can be amplified. The nucleotide sequences of the amplified genes can be determined by sequencing reactions. The procedure is described more in detail in Paper I and V.

When choosing a gene to study relationships of a group of organisms, one has to consider the mutation rate of the gene. If the gene is evolving too fast the phylogenetic signal will be lost due to ‘multiple hits’, i.e., taxa will have the same nucleotide in a certain position of the gene by chance and not by common ancestry. On the other hand, if a gene is too conserved it will not be informative enough. The chloroplast genes rbcL and ndhF are the ones I have used the most (Papers I, IV-VI), but atpB, matK, and the nuclear 18S rDNA gene are also included in some instances (Papers IV, VI). All these genes have proven successful when inferring relationships at family or higher level; this is due to the fact that they have fundamentally important functions and therefore are relatively conserved. The proteins/enzymes that are encoded by these genes and their (presumed) function are as follows:

rbcL encodes for the large subunit of ribulose 1,5-biphosphate carboxylase/oxygenase (RUBISCO), which is vital in the photosynthesis and is present in large amounts in the chloroplasts of all green plants.

atpB encodes for the β subunit of ATP synthetase, the enzyme that couples translocation of protons across the chloroplast membranes with the synthesis
of ATP, the molecule that acts as the number one source of chemical energy in the metabolism of the cells. It evolves at about the same rate as \textit{rbcL} (Hoot, Culham & Crane, 1995).

\textit{matK} is embedded within an intron, which interrupts the two exons of the \textit{trnK} gene (one of the genes coding for transfer RNAs), and encodes for a maturase active in splicing the intron from the RNA transcript (Neuhaus & Link, 1987; Wolfe, Morden & Palmer, 1992). Of the protein-coding chloroplast genes, \textit{matK} is one of the fastest evolving (Wolfe, 1991).

\textit{ndhF} probably encodes for a subunit of chloroplast NADH dehydrogenase (Kim & Jansen, 1995; Olmstead & Reeves, 1995) because the amino acid sequence resembles the one of mitochondrial NADH dehydrogenase. The dehydrogenase is oxidising NADH to NAD\(^+\), a redox couple acting as coenzymes and as such catalysing a number of reactions in the cells. As a whole \textit{ndhF}, is evolving about twice as fast as \textit{rbcL}, but with the first part (5\textquoteleft end of the gene) rather conservative and the second part (3\textquoteleft end) more variable (Kim & Jansen, 1995; Olmstead & Reeves, 1995).

\textit{18S} rDNA encodes for the rRNA of the small subunit of the ribosomes and is highly conserved, it typically has one-third to one-half of the mutation rate of \textit{rbcL} (Nickrent & Soltis, 1995).

\textbf{Parsimony analysis vs. Bayesian inference}

To reconstruct phylogenetic trees, i.e., trees reflecting the evolutionary history of organisms/taxa and relationships between these, the majority of systematists have for the latest decades used the methods of cladistics (for more detailed descriptions of cladistics see, e.g., Kitching \textit{et al.}, 1998). Cladistics is based on the ideas of Hennig (1950, 1966). In a cladistic framework, a natural group include all descendants of a common ancestor. Such a group is referred to as monophyletic and is identified by shared derived characters, synapomorphies. Shared ancestral characters, synapomorphies, do not mirror evolutionary innovations and groups circumscribed by synapomorphies are not necessarily monophyletic.

Closely connected with cladistics is the use of parsimony thinking (e.g., Farris, 1983). The law of economy or parsimony (Ockham’s razor) was originally formulated by the medieval philosopher William of Ockham (1285-1349). In a phylogenetic context it can be applied when a choice has to be made between competing evolutionary hypotheses, the hypothesis requiring the least number of assumptions is favoured. In the absence of any
other evidence, two taxa with a unique character (character state) in common (i.e., the same kind of leaf hairs, the same kind of structures on the pollen surface, a specific nucleotide at the same position in the DNA sequence of a certain gene, etc.) have most likely inherited the character from their most recent common ancestor. When constructing phylogenies by parsimony analysis the number of times characters have to change, in order to explain the character distribution among the investigated taxa, are minimised, thus aiming at maximum parsimony. The phylogeny with the fewest character state changes is the preferred hypothesis explaining the evolutionary history of the studied taxa.

In a parsimony analysis an explicit model of evolution need not be specified. When studying the evolution of DNA sequences some consider this to be a draw-back, since one cannot take into account what actually is known about substitution processes, etc. Others would argue that it is an advantage not to have to define a specific model, thereby making the results dependent on the model as well as the data or observations. Furthermore, it can be argued that the more assumptions (e.g., specific models of evolution) that are made before making an analysis, the less confidence can be put into the conclusions (e.g., Kluge, 1997). Nevertheless, model-based approaches can handle different kinds of events more precisely than parsimony, and do not suffer from statistical inconsistency (long-branch attraction; Felsenstein, 1978). Thus, a model-based analysis possibly better takes into account the information embedded within sequence data and hopefully resolve or give better support for certain relationships where parsimony analysis has proven insufficient. I, therefore, wanted to explore how model-based analyses would affect parsimony-based conclusions on relationships of the studied groups (Paper V; I have also rerun analyses of Paper I and IV, see below).

One statistical method that can specify models of molecular evolution is maximum likelihood (ML), first used to infer phylogenies by Felsenstein (1981). The tree that gives the highest likelihood of observing the data given the model is favoured. Despite the possibility of employing a model-based approach, ML is not feasible to use on larger data sets (with many taxa and/or characters) because calculating the likelihood for all trees that have to be evaluated is very time consuming. To overcome this problem, a statistical approach to model-based analyses based on ideas by the 18th century Reverend Thomas Bayes has recently come into focus in phylogenetics (Rannala & Yang, 1996; Yang & Rannala, 1997; Huelsenbeck et al., 2001; Huelsenbeck & Ronquist, 2001a).

Where classical statistical inference uses models of probabilistic distributions based on what would have been observed if a process had been repeated an infinite number of times, Bayesian inference is based on the data actually observed and the prior probability distribution of parameters of a
model (tree topology, branch lengths, substitution models, etc.). Using prior assumptions about model parameters makes the method suffering from subjectivity, but a vague or flat prior distribution diminishes that risk. For larger data sets (as in most phylogeny reconstruction) the prior distribution will hardly affect the results (Huelsenbeck et al., 2002).

Bayes’ theorem defines how the posterior distribution of the model parameters (where the topology of the tree is of most interest in phylogeny reconstruction) is calculated from the probability of the prior distribution of the model parameters and the likelihood of the (sequence) data given the model parameters. In contrast to ML, which aims at finding the best tree explaining the observed data, Bayesian analysis is supposed to examine the entire distribution to be able to make inferences about the probability of each. Calculating the posterior distribution of all possible trees is in practice an impossible task. The computer program MRBAYES (Huelsenbeck & Ronquist, 2001a, b) uses a way of sampling the posterior distribution called Metropolis-coupled Markov Chain Monte Carlo (MC³). The theory is that the frequency by which a tree is sampled by the Markov Chain equals the probability that that tree is the true tree. If the chain is run for a large enough number of generations (samples), the trees sampled should give a proper approximation of the posterior distribution of trees. Several parallel chains are run (Metropolis-coupling) to minimise the risk of getting stuck on a local optimum and, thus, not finding all peaks in the “space of parameters” visited by the chain (a problem common to other methods of phylogenetic inference). By running such additional “heated” chains that explore a “melted” landscape with lower peaks and less deep valleys and letting the first, “cold” chain be able to switch to one of the other chains if stuck on a local optimum, the parameter space will be better sampled and the inference made more accurate.

The Bayesian analyses run specifically for this thesis (see the sections Families with a taxonomically complicated past and From one family to four) used the setting corresponding to the General Time Reversible Model with a proportion of invariant sites and a Gamma shaped distribution of among site variation (GTR+I+G), as suggested by the program MrModeltest (Nylander, 2002). The base frequencies were estimated from the data and MRBAYES was used for the analyses. Both data sets were run for 2,000,000 generations. For the first, the number of chains and the burn-in period were four and 10,000, respectively, and for the latter one and 200,000.
Measures of support

Often there is not a single phylogenetic tree depicting the hypothesis of the evolutionary history of a group. There may be several most parsimonious or equally probable trees and in addition even more trees almost as likely as those. How can you be certain of the proposed relationships?

Considering uncertainties in the data and possibly also in the method of analysis you probably only want to talk of groups that have some kind of support. A number of measures are used to indicate which groups in a phylogeny are more strongly supported than others. Here I will briefly describe those I have used in the thesis. First, if looking on all most parsimonious trees there are conflicts between the separate trees. A strict consensus tree shows only those groups that are present in all of the most parsimonious trees (see Page, 1989). Other measures of support are the consistency (CI; Kluge & Farris, 1969) and retention indices (RI; Farris, 1989). They can be thought of as measurements on how much data are consistent with the tree or retained in the tree. In other words, they give some indications of how many homoplasies (parallelisms and reversals) there are in the data set, since if there were no homoplasies all data would be consistent with/retained in the tree (CI=1; RI=1). The Bremer support (Bremer, 1988, 1994; Källersjö et al., 1992) for a group is the number of extra steps (character changes) needed before alternative groupings appear such that the group collapses in the strict consensus tree, and is thus a straightforward measure of group support.

How sensitive is the phylogeny to the data analysed? Would the result be markedly different if other or less data had been collected? One approach to address such questions is jackknifing (Farris et al., 1996). Jackknifing is a resampling procedure where a large number of new matrices are created by sampling about two-thirds of the characters of the original data set (consisting of the taxon x character matrix). The new matrices are analysed and groups of taxa that are retrieved in about 70% of the jackknife trees are considered well supported. Groups with a jackknife value of over 95% are very strongly supported. As with CI, RI, and Bremer support, comparing these values between different analyses is difficult.

A Bayesian analysis gives in addition to the posterior probabilities (PP) of entire tree topologies posterior probabilities also for groups present in the trees. A group present in all sampled tree topologies have a posterior probability of 100%. The posterior probabilities should be interpreted as the probability that the group actually exists in nature (given the data and the model).
Families with a taxonomically complicated past become firmly placed in Asterales

About one-tenth of all flowering plant species are classified in the order Asterales, dominated by the sunflower family, Asteraceae. With 23,000 species the Asteraceae are the largest family of all, possibly sharing the number one position with the orchids, Orchidaceae. Many Asteraceae are herbs from the northern hemisphere as are many of the species of the second largest family of the order, the bluebell family (Campanulaceae). Considering this, an herbaceous and northern hemisphere origin of the order seems likely. In Asterales there are, however, a number of additional families, some only recently recognised as members of the order. These new members are mainly woody plants from the southern hemisphere, in particular Australasia, and they constitute the more basal lineages of the order (Gustafsson, Backlund & Bremer, 1996; Gustafsson & Bremer, 1997; Lundberg, 2001a). Apparently, the species-rich Asteraceae and Campanulaceae are derived from woody ancestors and have relatively recently spread to the north. The Asterales probably originated in east Gondwanaland in the Cretaceous (Bremer & Gustafsson, 1997).

In Paper I-III I deal with three of the recently added families, Alseuosmiaceae, Argophyllaceae, and Phellinaceae, all of them woody and with an Australasian distribution (east Australia, New Guinea, New Caledonia, and New Zealand). The genera included in these families have in the past been placed in a number of quite different, often distantly related, families (Table 1). They have, however, never been associated with Asterales, not until the dawn of DNA sequence analysis. Once sequenced, it was indicated that the three families do belong in Asterales and, in addition, form a monophyletic group (see Gustafsson et al., 1996, Backlund & Bremer, 1997, Gustafsson & Bremer, 1997, and Källersjö et al., 1998, who analysed DNA sequences from the chloroplast rbcL gene). By combining rbcL data with data from another chloroplast gene, ndhF, I confirm these results and discuss the evolution of the group (Paper I). Since Paper I was published, the group has repeatedly been retrieved in studies with varying sampling and with the inclusion of additional genes (e.g., Savolainen et al., 2000b; Soltis et al., 2000; Savolainen et al., 2000b; Albach et al., 2001a; Bremer et al., 2002; Paper IV), albeit often with rather weak support. But in the recent
study by Bremer et al. (2002) the group received a jackknife value of 94%. It has, however, also been noticed that the \textit{rbcL} sequence of \textit{Cyphia} (Cosner, Jansen & Lammers, 1994) used in the analyses of \textbf{Paper I} is from a probable \textit{rbcL}-pseudogene (Lundberg, 2001b). Here I have rerun the molecular analysis of \textbf{Paper I} with the erroneous \textit{Cyphia} sequence replaced. The new analysis yields two most parsimonious trees (Figure 1 shows the strict consensus of these), 2,327 steps long vs. 2,365 in the published tree. With the correct \textit{Cyphia} sequence, the CI is slightly lower while the RI is somewhat higher. The basal relationships are unresolved but the Alseuosmiaceae-Argophyllaceae-Phellinaceae group is still retrieved and the jackknife support for the group is increased (JK 73 vs. 58) as is the support for the sister group relationship of Argophyllaceae and Phellinaceae (JK 87 vs. 78) as well as for \textit{Alseuosmia} and \textit{Wittsteinia} (JK 81 vs. 75). The Bremer support is in essence the same, and is markedly different between the two analyses only for Alseuosmiaceae that are even more strongly supported (BS 83 vs. 72). A Bayesian inference of the same data set retrieves the same topology for the group under study and the posterior probabilities are very high for the three families together (PP 99 %), the sister group relationship between Argophyllaceae and Phellinaceae (PP 98 %), as well as for each of the families (100 %). Figure 1 shows the relationships within Asterales according to these analyses.

A well-supported phylogeny, used to reconstruct character states for the hypothetical ancestors for each of the families and of the Alseuosmiaceae-Argophyllaceae-Phellinaceae group as a whole, was obtained by combining the molecular data with morphological data. The group is probably of Australasian origin and its ancestor was likely a small tree or a shrub with simple, alternate, and serrate leaves, with paniculate inflorescences and regular, epigynous flowers with free petals. The diploid chromosome number seems to have been 18 as in Alseuosmiaceae (Gardner, 1976) and Argophyllaceae (Wanscher, 1933; Hamel, 1953; Hair & Beuzenberg, 1959). Phellinaceae have a haploid chromosome number of 17 (Carr & McPherson, 1986; two species investigated), compatible with the proposed number and suggestive of a tetraploid origin of the family. Wikström, Savolainen & Chase (2001) estimated the Alseuosmiaceae-Argophyllaceae-Phellinaceae lineage to be from the late Cretaceous, 70-77 mya, a date coinciding with a period of active seafloor spreading (80-60 mya) resulting in the opening of the Tasmanian basin separating New Zealand and New Caledonia from Australia (McLoughlin, 2001), presumably an opportunity for diversification. The subsequent separation of New Zealand from New Caledonia with the opening of the New Caledonian basin is estimated to about the same time (70-60 mya) or to 30 mya (McLoughlin, 2001; Sanmartin, 2002, and references therein).
Figure 1. A phylogenetic tree representing relationships within Asterales based on rbcL and ndhF sequence data. Posterior probabilities in percent are given above the branches and jackknife values below. The nodes without jackknife values are not present in the strict consensus tree of the two most parsimonious trees. The family classification follows APG II (2002).
Table 1. List of the genera studied in Paper 1, families associated with each genus by past studies, and authors who first suggested a new family placement.

<table>
<thead>
<tr>
<th>Genus</th>
<th>Family</th>
<th>Author</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>ALSEUOSMIACEAE</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Alseuosmia</em></td>
<td>Cornaceae</td>
<td>Cunningham, 1839a</td>
</tr>
<tr>
<td></td>
<td>Caprifoliaceae</td>
<td>Hooker, 1853-55</td>
</tr>
<tr>
<td></td>
<td>Alseuosmiaceae</td>
<td>Airy Shaw, 1965</td>
</tr>
<tr>
<td><em>Crispiloba</em></td>
<td>Rubiaceae</td>
<td>Moore, 1917 (as <em>Randia</em>)</td>
</tr>
<tr>
<td></td>
<td>Alseuosmiaceae</td>
<td>van Steenis, 1984</td>
</tr>
<tr>
<td><em>Periomphe</em></td>
<td>Gesneriaceae</td>
<td>Baillon, 1888</td>
</tr>
<tr>
<td>(incl. <em>Memecylanthus</em> and <em>Pachydiscus</em>)</td>
<td>Caprifoliaceae</td>
<td>Schlechter, 1906</td>
</tr>
<tr>
<td><em>Wittsteinia</em></td>
<td>Ericaceae</td>
<td>von Mueller, 1861</td>
</tr>
<tr>
<td></td>
<td>Epacridaceae</td>
<td>Burtt, 1949</td>
</tr>
<tr>
<td></td>
<td>Alseuosmiaceae</td>
<td>Airy Shaw, 1965</td>
</tr>
<tr>
<td><strong>ARGOPHYLLACEAE</strong></td>
<td></td>
<td></td>
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<tr>
<td><em>Argophyllum</em></td>
<td>Brexiaceae</td>
<td>Lindley, 1830</td>
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<tr>
<td></td>
<td>Saxifragaceae</td>
<td>Endlicher, 1839</td>
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<td></td>
<td>Escalloniaceae</td>
<td>Willis, 1966</td>
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<td></td>
<td>Argophyllaceae</td>
<td>Takhtajan, 1987</td>
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<tr>
<td><em>Corokia</em></td>
<td>Rhamnaceae</td>
<td>Cunningham, 1839b</td>
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<tr>
<td></td>
<td>Cornaceae</td>
<td>Raoul, 1844</td>
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<tr>
<td></td>
<td>Saxifragaceae</td>
<td>Engler, 1928</td>
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<tr>
<td></td>
<td>Escalloniaceae</td>
<td>Willis, 1966</td>
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<tr>
<td></td>
<td>Corokiaeae</td>
<td>Dahlgren, 1980</td>
</tr>
<tr>
<td></td>
<td>Argophyllaceae</td>
<td>Takhtajan, 1987</td>
</tr>
<tr>
<td><strong>PHELLINACEAE</strong></td>
<td></td>
<td></td>
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<tr>
<td><em>Phelline</em></td>
<td>close to Pouteria (Sapotaceae)</td>
<td>Labillardière, 1824</td>
</tr>
<tr>
<td></td>
<td>Rutaceae</td>
<td>Hooker, 1862</td>
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<tr>
<td></td>
<td>Aquifoliaceae</td>
<td>Baillon, 1891</td>
</tr>
<tr>
<td></td>
<td>Phellinaceae</td>
<td>Takhtajan, 1966</td>
</tr>
</tbody>
</table>

The ancestor of the Alseuosmiaceae-lineage, which probably dates back to the end of the Cretaceous (66-69 mya; Wikström *et al.*, 2001), evolved into a well-characterised family with four extant genera. The flowers have become sympetalous with the stamens inserted in the corolla tube and the corolla lobes have developed more or less conspicuously lobed petal wings (Figure 2). Another distinctive character is the rusty brown, multi-cellular hairs in the leaf axils. See Paper II for a detailed description of the family.

The type genus *Alseuosmia* from New Zealand comprises five species (Merrett & Clarkson, 2000; Figure 2) mostly included in Caprifoliaceae before Airy Shaw (1965) described the family Alseuosmiaceae. That *Alseuosmia* was misplaced in Caprifoliaceae with its alternate leaves, valvate corolla, pollen morphology, and distribution had already been suggested by
several authors (e.g., Erdtman, 1952). Already Cunningham (1839a), the author of the genus, had suggested that it deserved family status. Also included in Airy Shaw’s family circumscription were two New Caledonian genera, *Periomphale* and *Memecylanthus*. The latter was by van Steenis (1978) regarded as congeneric with the former and he added to *Periomphale*...
a new species from Papua New Guinea, to my knowledge collected only once, but probably located for a second time recently (Michael Heads, pers. comm.). Realising that *Wittsteinia vacciniacea*, a subshrub from Victoria, Australia, with suggested affinities to Ericaceae or Epacridaceae (von Mueller, 1861; Bentham, 1869; Drude, 1889; Burtt, 1949; Stevens, 1971) also should be included in the family, he sunk *Periomphale in Wittsteinia* (van Steenis, 1984). However, since the New Caledonian species, for example, has entire leaves, terminal inflorescences and entire petal wings instead of thicker dentate leaves, axile inflorescences and lobed petal wings as the other *Wittsteinia*, it is here still regarded as a separate genus, *Periomphale*, following the view of Tirel (1996) and Tirel & Jérémie (1996). Van Steenis (1984) also realised that the true position of a species from Queensland, Australia, earlier regarded as a member of *Randia* (Rubiaceae), is in Alseuosmiaceae. He named the species *Crispiloba disperma*, emphasising its conspicuously fringed corolla lobes. All four genera do form a well-supported group and their position in Asterales is also strongly confirmed (Figure 2; Paper I). The presence of *Wittsteinia* on New Guinea is probably due to a rather recent dispersal from Australia, where the genus at present is restricted to the Victorian alps, since the New Guinean highlands were not formed until Late Miocene-Pliocene about 5 mya. Several taxa show a pattern with temperate taxa from east Australia dispersing to the New Guinean highlands in Late Pliocene (Sanmartín, 2002). The distribution of the other genera probably reflects a diversification after the separation of Australia, New Caledonia, and New Zealand (see above). In New Zealand, *Alseuosmia* fossils are only found from the Pleistocene (1.8 mya – 10,000 years ago), indicating that the genus is a rather recent member of the New Zealand flora (Lee, Lee & Mortimer, 2001).

Of the three families, Argophyllaceae seem to have retained most of the ancestral characters. The family has also developed a number of characteristic features. Most conspicuous are the fringed appendages (corolline ligules; Figure 3) on the adaxial side of the petals and the presence of so-called T-hairs, consisting of a multicellular stalk and a two-armed, T-shaped apical cell. Despite these and other similarities, the two genera of the family have not always been treated together – and never in a context as related to Asterales. *Argophyllum* was mostly placed in Saxifragaceae/Escalloniaceae (Engler, 1890, 1928; Willis, 1966; Takhtajan, 1983; Thorne, 1992) and *Corokia* in Cornaceae (Hooker, 1867; Harms, 1897; Wangerin, 1909; Melchior, 1964; Hutchinson, 1967; Cronquist, 1981). They were first suggested to be related by Hallier (1908) and based on increasing evidence from, for example, floral anatomy (Eyde, 1966) and pollen morphology (Hideux & Ferguson, 1976; Ferguson & Hideux, 1978) showing that the two genera are distinct enough to be regarded as a separate family, Takhtajan
(1987) erected the Argophyllaceae. Later, he (Takhtajan, 1997) also described Corokiaceae as a new family, emphasising ovule and fruit characters; *Corokia* has a single-seeded drupe (Figure 3) while *Argophyllum* has a loculicidal capsule with many seeds. That family is not recognised here. The two genera are closely related and accepting Corokiaceae would lead to loss of the phylogenetic information contained in the family name Argophyllaceae, a negative effect of accepting monogeneric families. In Paper III a thorough description of the family is given.

*Argophyllum* is restricted to New Caledonia and eastern Australia and comprises about twenty species. The New Caledonian species seem to favour rather open, sunny places (Schlechter, 1906; Guillaum and Virot, 1953). At least two of them are able to hyperaccumulate nickel (Jaffré, Brooks & Trow, 1979). Nickel is normally toxic to plants, but on New Caledonia there is a remarkably high concentration of plant species tolerating the element. Quite recently several new species have been found in Queensland (Forster, 1990; Paul Forster, pers. comm.). These new species are often only known from their type localities, i.e., isolated remnants of the once much larger Australian rain forest.

The single Australian *Corokia* is also a rare rain forest species. *Corokia whiteana*, discovered in the 1940s, is only known from the Nightcap range in northern New South Wales and even there only scattered individuals are found (Smith, 1958; Nicholson & Nicholson, 1994). The Nightcap range was threatened by deforestation in the late 1970s but fortunately saved after demonstrations by environmentalists. From this easternmost locality, *Corokia* is found on the Lord Howe Island 700 km northeast of Sydney (one species), on New Zealand, (one species on both islands, one restricted to the North Island, and one to the Chatham Islands) and on the isolated, volcanic Rapa Island, more than 6,000 km away from Australia. Considering that the fruits of *Corokia* are fleshy drupes, likely to be bird-dispersed, this distribution might reflect relatively recent dispersal events (Lord Howe Island is the remnants of a volcano, which erupted 7 million years ago; McDougall, Embleton & Stone, 1981). *Corokia* is one of comparatively few woody New Zealand genera without a fossil record (Lee et al., 2001) and a recent dispersal to the area thus seems plausible. The family, however, probably originated early in the Tertiary (Wikström et al., 2001).

The split between Argophyllaceae and Phellinaceae probably occurred at the very beginning of the Tertiary (62-63 mya; Wikström et al., 2001). Phellinaceae are a distinct family, rather aberrant in Asterales. They were consequently not associated with that order before the aforementioned *rbcL* studies, but mostly treated as a member of Aquifoliaceae (Table 1; Baillon, 1891; Loesener, 1901, 1908, 1942). The sole genus with a dozen species is endemic to New Caledonia and is distinct by, for example, unisexual flowers.
Figure 3. Argophyllaceae. Corokia cotoneaster, with its characteristic interlacing branches. Note the fringed appendages at the base of the petals, a distinctive feature of the family. The fruits of Corokia are one-seeded drupes in contrast to the many-seeded capsules of Argophyllum. Taken from Raoul (1846).
with sessile stigmas and superior ovaries developing into drupes with separate pyrenes (Figure 4). Baas (1975) considered Phellinaceae to have among the most ‘primitive’ wood of all dicotyledons with vessels. Notwithstanding the differences between Phellinaceae and the two other families, they are supported as sister to Argophyllaceae and their placement in Asterales seems correct. Although monogeneric, I choose not to merge them with Argophyllaceae, since I favour morphologically recognisable families.

A new relative – *Platyspermation*

New Caledonia houses members of all three families of the Alseuosmiaceae-Argophyllaceae-Phellinaceae group. Recent data suggest that the island in fact has yet another species that is related to the three families. *Platyspermation crassifolium*, the only member of its genus, is a small tree or shrub and was not described until 1950 (Guillaumin, 1950). This little known species has been suggested to belong in Myrtaceae, Rutaceae, or Escalloniaceae (Schmid, 1980; van Steenis, 1982). Molecular data now dismiss all these families as related to *Platyspermation* and instead support Alseuosmiaceae as the sister to *Platyspermation* (Lundberg, 2001b; Lundberg & Bremer, 2001; R. Schmid & J. Lundberg, in prep.).

*Figure 4. Phellinaceae. A-C. Phelline comosa. A. Flowering branch. B. Fruit. C. Transverse section of fruit. Drupes with separate pyrenes make Phellinaceae distinct from both Alseuosmiaceae and Argophyllaceae. D. P. erubescens. A female flower with reduced staminodes. Unisexual flowers with sessile stigma and superior ovary contrast Phellinaceae from their closest relatives. Modified after Labillardière (1824; A-C) and Loesener (1942; D).*
From one family to four (at least) – the case of Icacinaceae

In the history of plant systematics a number of highly unnatural families have been recognised. Two of these are Cornaceae and Escalloniaceae (Saxifragaceae-Escallonioideae). The genera included in these (e.g., by Wangerin, 1909; Engler, 1928) are now known to belong to a number of other families, often distantly related to each other. Corokia was, for example, assigned either to Cornaceae or Escalloniaceae before its true affinities were revealed and Alseuosmia, Argyrophyllum, and Platypermation have all been associated with Escalloniaceae (see above). As mentioned, these genera are in fact members of Asterales. Several other genera at times included in Cornaceae or Escalloniaceae are today treated as separate families of Aquifoliales (Helwingia and Phyllonoma) or Apiales (Aralidium, Griselinia, Melanophyllum, and Torricellia; see Papers V and VI). Another such unnatural family is Icacinaceae.

Icacinaceae were first described by Miers (1851) and by time more than 400 species grouped in about 54 genera were recognised in this predominately pantropical family of tall rainforest trees, shrubs, and lianas (Howard, 1940, 1942a, b, c, d, 1943a, b, c, 1992; Sleumer, 1942, 1969, 1971). Following Miers (1851, 1852) the family has mostly been placed near Celastraceae or Aquifoliaceae and was regarded as a rosid taxon (e.g., Baillon, 1862-63a, b, 1872, 1874; Sleumer, 1942; Cronquist, 1981; Takhtajan, 1997); Celastraceae do belong to the rosids but Aquifoliaceae as well as Icacinaceae are assigned to the asterids (APG, 1998; APG II, 2002). Not only were Icacinaceae misplaced in earlier classifications, moreover, they do not have a common origin. The one characteristic most often emphasised when diagnosing a supposed member of Icacinaceae was the presence of two pendulous ovules in each locule, one of which matures.

As is shown in Paper IV former Icacinaceae belong to both euasterids I and II, and are best treated as belonging to three different orders and (at least) four families (Table 2; Figure 5). The first indications of a non-monophyletic Icacinaceae came from the large molecular analyses by Savolainen et al., 2000a, b) and Soltis et al., 2000). They showed that some Icacinaceae genera probably belong in Garryales of euasterids I and that other genera are related to Cardioglossaceae, a monogeneric family only recently realised to
belong in Aquifoliales, euasterids II. In Paper IV I further examined the relationships of the former Icacinaceae by sequencing the ndhF gene for 25 ‘icacinaceous taxa’ and analysing these together with published sequences also from other genes (rbcL, atpB, 18S rDNA) from a wide array of taxa, covering all major groups of flowering plants but focusing on asterids. In addition, an analysis of morphology was conducted to explore morphological support for the resulting clades including icacinaceous taxa. A Bayesian inference on the ndhF data supports Icacinaceae s.s. as a monophyletic group, but fails to resolve the base of euasterids I, i.e., it leaves a trichotomy (that probably will be resolved with a more thorough Bayesian inference) consisting of Icacinaceae s.s., Garryales s.s., and the rest of the euasterids I. The result of the Bayesian analysis is shown in Figure 6.

Table 2. All genera formerly included in Icacinaceae sensu lato listed under the (informal) taxa where they belong according to the study of Paper IV. Taxa with uncertain relationships are indicated with a question mark.

<table>
<thead>
<tr>
<th>ICACINACEAE SENSU LATO</th>
<th>Euasterids I/Garryales</th>
<th>Euasterids II/Aquifoliales</th>
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<tr>
<td><strong>ICACINACEAE SENSU STRICTO</strong></td>
<td></td>
<td>CARDIOPTERIDACEAE</td>
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<tr>
<td>Icacina group</td>
<td>Alsodeiopsis, Casimirella,</td>
<td>(incl. Leptaulaceae, Metteniusaceae?):</td>
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<tr>
<td></td>
<td>Chlamydocarya, Desmostachys, Hosiea,</td>
<td>Cardiopteris, Citronella, Dendrobaanga,</td>
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<td></td>
<td>Icacina, Iodes, Lavigeria, Leretia,</td>
<td>Gonocaryum, Leptaulus, Metteniusa?,</td>
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<td></td>
<td>Mappia, Mappianthus, Merilliodendron,</td>
<td>Pseudobotrys?</td>
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<td>Miquelia, Natsiatopsis, Natsiatum,</td>
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<td></td>
<td>Nothapodytes, Phytocrene,</td>
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<td>Pittosporopsis?, Pleurisanthes,</td>
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<td>Cassinopsis</td>
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<td>STEMONURACEAE</td>
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<td>Cantleya, Codicarpus, Discophora,</td>
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<tr>
<td>Poraqueiba, Calatola?, Platea?</td>
<td>Gastroplepis, Gomphandra, Grisollea,</td>
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<td>Apodytes, Raphiostylis</td>
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<td><strong>EUASTERIDS II/APIALES</strong></td>
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<td></td>
<td>PENNANTIACEAE</td>
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<tr>
<td></td>
<td></td>
<td>Pennantia</td>
</tr>
</tbody>
</table>

A number of genera are shown to be related to Garryales of euasterids I and should possibly be included in that order (Table 2). Among these are Icacina itself (Figure 7), an African genus with sometimes very large, starch-rich tubers. I treat all the genera related to Icacina as Icacinaceae s.s., although the support for them as a unit is low (PP 65%). There are, however, four well supported groups within Icacinaceae s.s., but how these are related to each
other and to Garryales s.s. cannot be ascertained. Until their interrelationships are better known I include all of these in Garryales, but if they and Garryales s.s. instead are shown to form a grade basal to euasterids I, new families or even orders might have to be erected. Garryales are the first branching taxon of euasterids I and as such an old lineage with an estimated age (100-107 mya) almost as old as the split between euasterids I and II (102-112 mya; Wikström et al., 2001).

**Figure 5.** The relationships within the euasterids as deduced from the analyses in Papers IV-VI. Only taxa with sequence data are included. For simplicity, genera from groups that are not specifically discussed are lumped into higher taxonomic names and the number of genera in each group indicated within parentheses. The tree is mainly based on the total evidence analysis of Paper IV (ndhF, rbcL, atp8, 18S rDNA, and morphology), but for Stemonuraceae and Apiales results of Papers V and VI, respectively, are incorporated. Jackknife values are given above the branches. For Apiales the values are from Paper VI.

A. Euasterids I.  →  B. Euasterids II.

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A. Euasterids I.  →  B. Euasterids II.
The *Icacina* group (Figure 7) is the largest of the four icacinaceous groups of Garryales and comprises most of the traditional Icacinaceae and is, thus, almost as heterogeneous as the latter. The *Emmotum* group is predominately a Central and South American taxon recognised by flowers with fleshy petals, sometimes hairy on the inside, and stamens with latrorse anthers and broad, prolonged connectives. A close relationship of *Emmotum*, *Ottoschulzia*, and *Poraqueiba* is also supported by chemical data. The same kind of the iridoid (a group of chemical compounds present in most asterids) secologanin is found in *Ottoschulzia* and *Poraqueiba* (Søren Jensen, pers. comm.) and emmotins (a class of sesquiterpenes) are found in *Emmotum* and *Poraqueiba* (Kaplan, Ribeiro & Gottlieb, 1991). The genus *Cassinopsis* from southern Africa and Madagascar is not supported as closely related to any of the other groups. Neither are the pantropical *Apodytes* and the African *Raphioystylis* (Figure 7) which together receive high support from the molecular data and also have similar pollen (Lobreau-Callen, 1972, 1973).
Figure 6. The relationships of the euasterids according to a Bayesian analysis on ndhF data (see text), for Apiales information from the four-gene analysis of Paper V are included. Posterior probabilities are given above the branches.

A. Euasterids I.  B. Euasterids II.
Turning to those icacinaceous taxa belonging to euasterids II, it seems that they are best treated in three different families (Table 2; Papers IV-VI). One genus, Pennantia, is not closely related to any of the others and will be dealt with below. Some group with Cardiopteridaceae, a family of two Malesian and South East Asian species. They are here included in that family, although they are rather different from Cardiopteris. Cardiopteris is a twining herb with white latex and dry, winged fruits. These characters are unmatched by the new members, all of them shrubs or trees with drupes. Possible synapomorphies for Cardiopteridaceae might be free, imbricate sepals and sympetalous corollas with inserted stamens (Figure 8). Apart from Cardiopteris the family includes four to six genera (Table 2) and the
inclusion of these extends the distribution of Cardiopteridaceae to Africa and Madagascar (*Leptaulus*; Figure 8) and Central and South America (*Citronella, Dendrobangia, Metteniusa*).

![Figure 8. Cardiopteridaceae. Leptaulus daphnoides. The flowers are sympetalous with the stamens inserted in the corolla tube as in most members of the family. Taken from Oliver (1894).](image)

Additional former Icacinaceae genera are strongly supported as sister to Cardiopteridaceae (Table 2). Apart from having very high molecular sup-
port, they are a morphologically well-defined group, making them worthy of family status. I choose to name them Stemonuraceae, after the Malesian and South East Asian genus *Stemonurus* (Figure 9 and photo on front page). They share easily recognised characters such as filaments with club-shaped hairs and/or fleshy appendages on the ovaries. They also seem to contain similar kinds of iridoid constituents (Kaplan *et al.*, 1991; *Cantleya* and *Gastrolepis* investigated). Their present day distribution suggests a Gondwanan ancestry with a centre of diversification in Malesia. As *Stemonurus*, several genera have a mainly Malesian distribution (*Cantleya*, *Codiocarpus*, *Gomphandra*, *Hartleya*, *Medusanthera*, *Whitmorea*), two are endemic to New Caledonia and Queensland, respectively (*Gastrolepis*, *Irvingbaileya*), but the family is also found on Madagascar (*Grisollea*), in Africa (*Lasianthera*) and Central and South America (*Discophora*).

Figure 9. Stemonuraceae, *Stemonurus ammui*. The hairs on the filaments of the protruding stamens are a characteristic of several genera of Stemonuraceae. Photo: J. Kårehed.
Holly days – the expansion of Aquifoliales

Cardipteridaceae + Stemonuraceae are strongly supported as the sister group to the order Aquifoliales (Figures 5, 6). Aquifoliales are here proposed to be expanded as to include the two families. In Paper V the evolution of the expanded Aquifoliales is discussed. By analysing ndhF sequence data together with morphology I investigated the interrelationships of the families and possible synapomorphies for groups within the order. Apart from the addition of Cardipteridaceae and Stemonuraceae (see above), the concept of Aquifoliales s.s. themselves has also changed recently. *Ilex* (hollies), the sole genus of Aquifoliales after *Nemopanthus* was sunk into it (Baas, 1984; Cuénod et al., 2000; Powell et al., 2000), belong here per definition. *Phelline* was long thought to be closely related to *Ilex* (Loesener, 1942; Cronquist, 1981), but wood anatomical and molecular studies (see above) disapprove such a relationship. Molecular studies do, however, support the two genera *Helwingia* (Figure 10) and *Phyllonoma* as the closest relatives to Aquifoliales. As mentioned, they have both been placed in the heterogeneous families Cornaceae and Escalloniaceae (Grossulariaceae), *Helwingia* often also associated with Araliaceae (e.g., Thorne, 1992; Takhtajan, 1997), but lately treated as monogeneric families. Although the interrelationships between the two and Aquifoliaceae are uncertain, they clearly form a monophyletic group and I suggest merging the two smaller families into the large, well-known, and first described Aquifoliaceae, increasing the phylogenetic information content in the classification. The unfortunate side effect of this is a family where both imbricate and valvate corollas as well as both inferior and superior ovaries occur. These characters do, however, vary within other families. For example, inferior, semi-inferior, and superior ovaries are all found in the small family Carpodetaceae/Rousseaceae of the Asterales (Gustafsson & Bremer, 1997; Lundberg, 2001a).

*Ilex* is a genus with characteristic pollen grains with fossil records from Late Cretaceous strata (Martin, 1977; Galle, 1997; and references therein). The *Ilex*-lineage probably was cosmopolitan well before the end of the Cretaceous and the diversification into the present day genera possibly took place in the Tertiary (Cuénoud et al., 2000; Wikström et al., 2001). Cardipteridaceae + Stemonuraceae might also have had a Tertiary origin, but split from the Aquifoliales in the late Cretaceous (91-97 mya), and the
order as a whole might date back to the late Early Cretaceous (99-107 mya; Cuénoud et al., 2000; Wikström et al., 2001).

Figure 10. Aquifoliaceae sensu lato/Helwingiaceae. Helwingia japonica. Both Helwingia and Phyllonoma have their inflorescences on their leaves, a very rare condition among the asterids. Taken from Wangerin (1909).

Recognising the expansion of Aquifoliales and the position of the order as sister to all other euasterids II gives new ideas on the early evolution of the euasterids II and the split between them and the euasterids I. Synapomorphies proposed for the euasterids II (cf. Lundberg & Bremer, 2001) must be re-evaluated, since it seems that some of them evidently evolved after Aquifoliales diverged from the other euasterids II. Corollas with well-developed corolla tubes and inferior ovaries might be such apomorphies for the later diverging taxa.
The new family Pennantiaceae and the ancestry of Apiales

The one genus of the former Icacinaceae not closely related to any of the other is *Pennantia*, a small genus of four species from New Zealand and eastern Australia. One of the species is so rare that it outside cultivation only exists as a single individual. They are small trees or shrubs with hard wood, which was used by the Maoris on New Zealand to obtain fire by friction. A sharp stick was worked against a flat piece of softer wood. The flowers are small and whitish and the drupes blackish (Figure 11). Molecular analyses give strong support for a relationship of *Pennantia* to Apiales (Paper IV, VI; Figures 5, 6), the order including, for example, Apiaceae (the carrot family). This relationship has never been suggested before and since there is no support for including *Pennantia* in any of the other families of Apiales, the genus should be treated as a separate family, Pennantiaceae (Agardh, 1858).

As in the cases of Asterales and Aquifoliales, the APG (1998; APG II, 2002) circumscription of Apiales is quite different from the traditional. The close relationship of Apiaceae to Araliaceae have long been recognised (see Constance, 1971; Rodriguez, 1971), but, as with the other orders, also families once placed in Cornaceae or Saxifragaceae/Escalloniaceae are now known to belong in Apiales. Pittosporaceae are one of these families, morphologically distinct from Apiaceae and Araliaceae, but the exact relationship between the three has as yet not been resolved or rather support Pittosporaceae as closer to Apiaceae (Plunkett, Soltis & Soltis, 1997; Olmstead *et al.*, 2000; Soltis *et al.*, 2000; Savolainen *et al.*, 2000b; Plunkett & Lowry II, 2001; Bremer *et al.*, 2002). The Bayesian inference presented in Paper VI does, however, indicate very high posterior probabilities favouring the morphological-based view with Pittosporaceae as sister to the other two (Figure 6). Aralidiaceae, Melanophyllaceae, Torricelliaceae, and Griseliniaceae are other families recently included in Apiales, the first three probably constitute a well supported monophyletic group and could be treated as one family in order to reduce redundancy in the flowering plant classification (cf. Stevens, 2001).
With the inclusion of Pennantiaceae in Apiales, the ideas on the early evolution of the order must be re-evaluated. In Paper VI I use information from morphology and DNA sequences from four genes (ndhF, rbcL, atpB, and matK) to understand the origin of the order. The most recent common
ancestor of Apiales is suggested to have been a shrub or small tree with alternate, simple leaves, paniculate inflorescences, five-merous flowers with free petals, and drupes, i.e., most of the characters associated with the traditional, more narrow view of the order are later innovations. As the typical Asteraceae with condensed flower heads and specialised one-seeded indehiscent fruits, the Apiaceae with umbellate inflorescences and schizocarpous fruits are clearly derived from ancestors with a more general suite of asterid characters. Furthermore, including Pennantiaceae in Apiales probably puts the origin of the order back to the Late Cretaceous (cf. Wikström et al., 2001) and considering the present day distributions of the more ancestral lineages of the order, an East Gondwanan ancestry, as for Asterales (Bremer & Gustafsson, 1997), or a wider Gondwanan distribution seems likely.

För att få en översikt över växtvärldens släktsskapsförhållanden förs besläktade arter samman i släkten. En växtfamilj består av oftast flera släkten och ingår i sin tur i en ordning. För att direkt förstå var i denna hierarki en grupp befinner sig har alla ordningar ändelsen –ales medan alla familjer slutar på –aceae. Allt som allt räknar vi med 45 ordningar och över 450 familjer av blomväxter. Bland de resultat jag presenterar i min avhandling är nya rön om släktsskap för några tidigare oidentifierade släktta familjer. Jag har dessutom visat att en tropisk familj egentligen bestod av flera mer eller mindre obesläktade grupper och för att spegla den nya kunskapen har jag beskrivit två nya familjer.

Den grupp av växter jag studerat är asteriderna som omfattar ungefär en tredjedel av alla blomväxter. Bland välkända representanter som figurerar i avhandlingen kan nämnas blåklocka, aster och selleri. De växter jag framför allt studerat är inte lika välkända. En del är så ovanliga att de bara är kända i det vida från en enda växtplats och någon till och med som en enda individ. Här skall jag sammanfatta vad de sex bidragen i avhandlingen behandlar samt kort beskriva de metoder jag använt.


I Bidrag IV undersöker jag den företrädesvis tropiska familjen Icacinaceae. Tidigare studier har visat att de släkten som ingår i familjen inte har en gemensam förfader, dvs. familjen är inte naturlig. Genom att studera fler släkten än tidigare kunde jag visa att familjen måste delas upp i åtminstone fyra mer eller mindre närbesläktade familjer.

De flesta släktena hör till den grupp av asteriderna som kallas euasterider I (en av de två grupperna av de egentliga asteriderna, här ingår kaffe, potatis, timjan m.fl.). De hör till den kanske tidigaste grenen bland euasteriderna I och en bättre förståelse av hur de är besläktade med varandra och andra euasterider I kommer att ge en ökad inblick i var, hur och när skiljelinjen mellan euasteriderna I och II går. Easteriderna II innehåller ca 40 familjer, bland annat de jag beskrivit ovan och dessutom de som beskrivs i det följande. De icacinaceärer som hör till euasteriderna I räknar jag fortfarande till samma familj, men det är möjligt att inte heller Icacinaceae i sitt begränsade omfång är en naturlig grupp. Jag har visat att det finns fyra välstödda grupper inom familjen (Icacina-gruppen, Emmotum-gruppen, Apodytes-gruppen och släktet Cassinopsis) och det är alltså möjligt att dessa egentligen inte är varandras närmaste släktingar.

Några släkten är så nära släkt och dessutom så lika varandra att jag beskrev en ny familj för dem. Familjen kan känna igen på speciella hår på
ständarna eller ett köttigt bihang på frukten. Den fick namnet Stemonuraceae
efter släktet *Stemonurus* från sydöstra Asien och den malayiska övärlden. Ett
släkte visade sig inte vara nära släkt med några av de andra släktena som
ingick i Icacinaceae. *Pennantia* hör till ordningen Apiales där bland annat
dill och hundkäx ingår. Att *Pennantia* skulle höra dit har aldrig föreslagits
förut. Dessutom passar släktet inte in i någon av familjerna i Apiales, så
ytterligare en ny familj måste erkännas. Mer om det senare.

Andra släkten visade sig höra samman med ett släkte *Cardiopteris* från
sydöstra Asien, den malayiska övärlden och nordöstra Australien, tidigare
den enda medlemmen av sin familj. Det kan tyckas märkligt eftersom
*Cardiopteris* är en slingrande ört med vit mjölsaft och torra frukter. De
släkten som numera också hör till Cardiopteridaceae är nämligen alla buskar
eller träd utan mjölsaft och med stenfrukter. Dock verkar alla cardiopter-
eridaceaerna förutom ett släkte ha en samkronbladig blomma med ståndarna
fastvuxna i kronan. Liksom Stemonuraceae hör Cardiopteridaceae till
Aquifoliales, samma ordning som järnek. I och med att de två familjerna
tillkommit till Aquifoliales fås en något annorlunda bild av den allra
tidigaste utvecklingen av euasteriderna II. Jag konstaterar i Bidrag V att
karakterer som ofta förknippas med euasteriderna II, såsom välutvecklade
samkronbladiga blommor med lång kronstub och undersittande fruktämne,
snarare är avancerade karaktärer som utvecklats efter det att Aquifoliales
grenade sig från de övriga euasteriderna II. I Aquifoliales ingår förutom
Stemonuraceae och Cardiopteridaceae ytterligare tre familjerna som var och en
består av ett enda släkte. Dessa är järnek och dess släktingar (*Ilex*) samt de
två släktena *Helwingia* och *Phyllonoma* som är ovanliga bland blomväxterna
genom att ha sina blomställningar på bladen. Hur deras förhållande är
sinsemellan är oklart. Det är först på senare tid som man har insett att de tre
släktena är närstående och för att visa den kunskapen i klassifikationen
föreslår jag att de slås ihop i familjen Aquifoliales.

Åter till *Pennantia*. Släktet består av fyra arter från Nya Zeeland och
östra Australien. En av dessa finns i det vilda bara som ett enda honträd på
en ö utanför Nordöns kust. Maorierna använde *Pennantia* hårda ved för att
få eld genom att gnida vässade kvistar mot ett mjukare trädslag. Bidrag VI ger
en tydligare bild av hur *Pennantia* hör hemma i Apiales. I den traditionella
tolkningen av Apiales ingår bara de flockblomstriga växterna, fa-
miljen Apiaceae, och araliaväxter, Araliaceae. Förutom *Pennantia* förs
numera även flera andra familjer till ordningen. Det finns inga goda skäl att
låta *Pennantia* ingå i någon av dessa, så släktet får utgöra en egen familj,
Pennantiacae. Familjen var egentligen redan föreslagen av Jacob Georg
Agardh i mitten av 1800-talet, men namnet kom aldrig i bruk. Pennantiacae
visar sig vara den första familjen som grenar av sig i Apiales och därmed får
vi omvärdera ordningens ursprung. Den gemensamma anfaden till Apiales

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växte på södra halvklotet och var troligen en buske eller ett litet träd med strödda, enkla blad och femtaliga blommor med fria kronblad och stenfrukter. De karaktärer som brukar förknippas med Apiaceae, örtartade växter med blommor i dubbel flock och torra klyvfrukter, uppkom långt senare.


Målet med släktspasanalysen är att kunna definiera naturliga grupper. Idéer från Willi Hennig, en tysk insektsforskare verksam i mitten av förra seklet, är basen för hur grenarna i ett släktträd delas in i naturliga grupper. Enligt så kallad kladistisk teori (gr. klados = gren) identifieras naturliga eller monofyletiska grupper av karaktärer som är unika för gruppen, synapomorfier, och en naturlig grupp består av alla avkomlingarna till en gemensam förfader.

Förutom parsimonianalys har jag också använt Bayesiansk analys för att rekonstruera växternas släktskap. Tack vare Bayesianska analyser har det först på sistone blivit möjligt att analysera en större mängd data med

Tack också till min familj, och särskilt då Karin och Sofia, förstås. Vad skulle jag göra utan att komma hem till?
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