Morphology and phylogeny of the order Dipsacales

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Abstract

A phylogenetic analysis using cladistic methods was undertaken on the order Dipsacales and a number of putatively related taxa. The data matrix consists of 58 taxa and 109 morphological characters ranging from gross morphology, palynology, anatomy, and embryology to chemistry and structural rearrangements of the chloroplast genome. The morphological information has been analysed together with sequences of the chloroplast gene *rbc*L, when available. The results from this study indicate clearly that the family Caprifoliaceae sensu Takhtajan is paraphyletic, the different entities below referred to as caprifolioids. Data also support the delimitation of the family Adoxaceae including the genera *Adoxa*, *Tetradoxa*, *Sinadoxa*, *Sambucus*, and *Viburnum* as earlier suggested by Donoghue and others. Furthermore, these taxa are clearly separated from the family Caprifoliaceae sensu Takhtajan. The South American genera *Desfontainia* and *Columellia*, by analysis of molecular data connected to the Dipsacales, occupy a position basal to the caprifolioids. The families Valerianaceae, Dipsacaceae sensu Takhtajan, and Morinaceae as defined by Cannon are strongly supported as monophyletic entities. The long debated position of the genus *Triplostegia* is in this study reconfirmed with high support to be within the Valerianaceae, basal to the genera *Patrinia* and *Nardostachys*.

Key words

Dipsacales, Apiales, phylogeny, cladistics, Adoxaceae, Apiaceae, Aralidiaceae, Bruniaceae, Caprifoliaceae, Dipsacaceae, Eremosynaceae, Escalloniaceae, Griseliniaceae, Polyosmataceae, Toricelliaceae, Valerianaceae, Melanophyllaceae, *Viburnum*, *Sambucus*, *Adoxa*, *Triplostegia*

The phylogeny, circumscription, and affinities of the order Dipsacales Lindl. (Lindley 1836) have been discussed and reevaluated repeatedly. Considerable confusion has arisen concerning the systematic position of the members of Dipsacales, and their suggested connections to the Rubiaceae (Hallier 1905; Hallier 1912), Cornaceae (Dahlgren 1975a; Dahlgren 1980), Apiales (Takhtajan 1987), or even the Asterales (Cronquist 1981). Recent molecular evidence, i.e., chloroplast deoxyribo-nucleic-acid (cpDNA) restriction site mappings (Downie and Palmer 1992) and analyses of the ribulose-1,5-biphosphate carboxylase (*rbc*L) and other cpDNA gene sequences (e.g. Olmstead et al. 1992; Chase et al. 1993; Gustafsson et al. 1996), all point towards a position of the Dipsacales as a putative sister taxon to the Apiales. This Dipsacales-Apiales complex, including also former members of the Saxifragaceae sensu Engler (1930) and the Cornaceae sensu Wangerin (1910), has subsequently been placed as sister group to the order Asterales, the latter including also the families Calyceraceae and Goodeniaceae (Downie and Palmer 1992; Donoghue et al. 1992; Olmstead et al. 1992; Chase et al. 1993; Bremer et al. 1994; Gustafsson et al. 1996; Backlund et al. 1997).

Systematic problems in the Dipsacales include the question of monophyly of the Caprifoliaceae sensu Takhtajan and the uncertain proximity of the Adoxaceae s.lat. (including the genera *Sambucus* and *Viburnum*) to the Caprifoliaceae, which has been questioned repeatedly (e.g. Donoghue et al. 1992; Benko-Iseppon 1992; Judd et al. 1994). The relations and delimitations between Valerianaceae, Morinaceae and Dipsacaceae, and of these three families to Caprifoliaceae sensu Takhtajan, also include unresolved questions (e.g. Vijayaraghavan and Sarveshwari 1968; Verlaque 1977; Kamelina 1980; 1983; Caputo and Cozzolino 1994). The results from most the above mentioned cladistic studies are, largely due to a low or uneven degree of sampling, more or less congruent and compatible, as indicated in fig. 1. The aim of this study is sixfold, **1** - to investigate the influence of and possible additional support from morphological data on the phylogenies suggested by molecular data, **2** - to clarify the position of the *Adoxa-Sambucus-Viburnum* clade (Adoxaceae s.lat.) in relation to the rest of the order, **3** - to investigate the question of monophyly of Caprifoliaceae sensu Takhtajan and to resolve the relations between Caprifoliaceae and the other core families of the order, **4** - to further study the positions of Morinaceae and *Triplostegia* in relation to Valerianaceae and Dipsacaceae, **5** - to check the positions of *Desfontainia* and *Columellia*, as indicated by molecular studies (Bremer et al. 1994; Backlund et al. 1997) and finally **6** - to attempt a circumscription of the Dipsacales supported by both molecular and morphological data.

MATERIALS and METHODS

Taxon Sampling. Taxon sampling has been made to reflect the different suggested evolutionary lineages in the Dipsacales; all studied taxa are listed in Table 1. All recognized genera within Caprifoliaceae sensu Takhtajan (1987) have been included, as well as the genera *Sambucus*, *Viburnum*, and *Adoxa*. In the Dipsacaceae, taxa have been selected to represent the main groups retrieved by Caputo and Cozzolino (1994), included are also the three genera of Morinaceae (Cannon and Cannon 1984). In the Valerianaceae, taxon selection has been made to represent the main groups suggested on palynological grounds by Clarke (1978), and also to illuminate the presumed affinities between Caprifoliaceae and Valerianaceae (Judd et al. 1994). Included is, also, the genus *Triplostegia*, sometimes recognized as the monotypic family Triplostegiaceae (e.g. Takhtajan 1987).

Furthermore, based on results from analyses of *rbc*L sequences, *Escallonia*, *Eremosyne*, and *Anopterus* (all members of Saxifragaceae sensu Engler 1930), *Berzelia*, *Brunia*, and *Audouinia* of the Bruniaceae, and the South American *Desfontainia* and *Columellia*, are included. According to molecular data all these genera may occupy basal positions in the order Dipsacales or in the Apiales-Dipsacales complex (Olmstead et al. 1992; Chase et al. 1993; Bremer et al. 1994; Gustafsson et al. 1996; Backlund et al. 1997). In addition to the above mentioned, earlier sequenced taxa, an additional two genera earlier placed in the Saxifragaceae sensu Engler (1930), but of more uncertain affinities, *Forgesia* and *Tribeles*, were included.

As placeholders for large groups of the Apiales the genera *Pittosporum*, *Aralia*, *Apium*, and *Steganotaenia* are used in accordance with earlier studies (e.g. Olmstead et al. 1992; Chase et al. 1993; Backlund et al. 1997). Also a number of segregate taxa, formerly placed in the Cornaceae sensu Wangerin (1910), but by molecular data assigned positions in the Dipsacales-Apiales complex (Xiang and Soltis 1995; Backlund et al. 1997) are added. In this group of taxa belong the genera *Aralidium*, *Toricellia*, *Melanophylla* and *Griselinia*, all occasionally recognized at the familial level.

The genus *Alseuosmia*, formerly included in Caprifoliaceae (Fritsch 1897) but more recently excluded (Gardner 1978) have not been included as very strong molecular and morphological evidence for its placement in the Asterales have been demonstrated (Gustafsson 1995; Gustafsson et al. 1996; Jesper Kårehed, unpublished data).

TABLE 1. Taxa included in the analysis organized alphabetically in families according to Takhtajan's system (Takhtajan 1987), with the approximate number of recognized species listed.

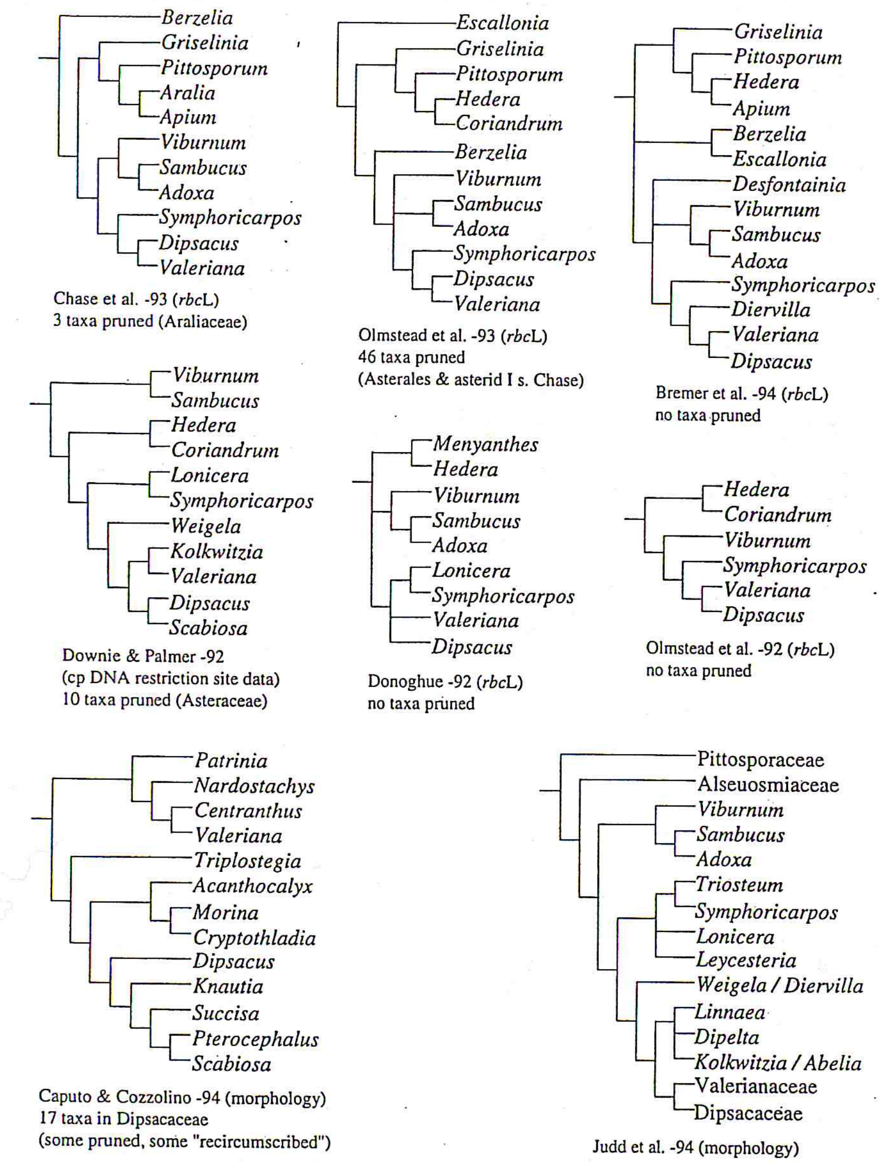
ADOXACEAE	*Adoxa* L.	4 spp.
	Sinadoxa C. Y. Wu, Z. L. Wu and R. F. Huang	1 sp.
	Tetradoxa C. Y. Wu	1 sp.
APIACEAE	*Apium* L.	20 spp.
	Steganotaenia Hochst.	2 spp.
ARALIACEAE	*Aralia* L.	40 spp.
ARALIDIACEAE	*Aralidium* Miq.	3 spp.
BRUNIACEAE	*Audouinia* Brongn.	1 sp.
	Berzelia Brongn.	12 spp.
	Brunia Lam.	7 spp.
CAPRIFOLIACEAE	*Abelia* R. Br.	30 spp.
	Diervilla Miller	2-3 spp.
	Dipelta Maxim.	4 spp.
	Heptacodium Rehder	2 spp.
	Kolkwitzia Graebner	1 sp.
	Leycesteria Wallich	6 spp.
	Linnaea L.	1 sp.
	Lonicera L.	180 spp.
	Symphoricarpos Duhamel	17 spp.
	Triosteum L.	5-6 spp.
	Weigela Thunb.	10 spp.
	Zabelia (Redher.) Makino	15 spp.
COLUMELLIACEAE	*Columellia* Ruíz and Pavón	2 spp.
DESFONTAINIACEAE	*Desfontainia* Ruíz and Pavón	1 sp.
DIPSACACEAE	*Dipsacus* s.lat. L.	15 spp.
	Knautia L.	60 spp.
	Pterocephalus Adans.	25 spp.
	Scabiosa s.lat L.	80 spp.
	Succisa s.lat. Haller	3 spp.

Matrices. All characters used and the states recognized in this analysis are listed below with comments. In Appendix B a complete list of references used for scoring of each character, additional to original observations made by the authors, is given. The entire morphological part of the data matrix used is shown in fig. 2. Sequences of the gene *rbc*L available for studied taxa were combined with the morphological characters. All taxa for which *rbc*L-sequences were available, and their respective sequences EMBL or NCGI/Genbank accession numbers, are listed in Table 2.

TABLE 1. CONTINUED. Taxa included in the analysis organized alphabetically in families according to Takhtajan's system (Takhtajan 1987), with the approximate number of recognized species listed.

EREMOSYNACEAE	*Eremosyne* Endl.	1 sp.
ESCALLONIACEAE	*Anopterus* Labill.	2 spp.
	Escallonia Mutis ex L. f.	40 spp.
	Forgesia Comm. ex Juss.	1 sp.
	Quintinia A. DC.	15 spp.
GRISELINIACEAE	*Griselinia* Forster f.	6 spp.
MELANOPHYLLACEAE	*Melanophylla* Baker	8 spp.
MORINACEAE	*Acanthocalyx* (DC.) M. Cannon	3 spp.
	Cryptothladia (Bunge) M. Cannon	6 spp.
	Morina L. pro parte	6 spp.
PITTOSPORACEAE	*Pittosporum* Banks ex Gaertner	200 spp.
POLYOSMATACEAE	*Polyosma* Blume	60 spp.
TORICELLIACEAE	*Toricellia* DC.	3 sp.
SAMBUCACEAE	*Sambucus* L.	23 spp.
TRIBELACEAE	*Tribeles* Phil.	1 sp.
TRIPLOSTEGIACEAE	*Triplostegia* Wall. ex DC.	2 spp.
VALERIANACEAE	*Belonanthus* Graebner	5 spp.
	Centranthus DC.	9 spp.
	Nardostachys DC.	1-2 sp.
	Patrinia Juss.	15 spp.
	Phyllactis Pers.	25 spp.
	Plectritis (Lindley) DC.	5 spp.
	Stangea Graebner	7 spp.
	Valeriana L. (s. str.)	250 spp.
	Valeriana clematitis H. B. and K.	
	Valeriana dioica L.	
	Valeriana hirtella H. B. and K.	
	Valeriana officinalis L.	
	Valerianella Miller	50 spp.
VIBURNACEAE	*Viburnum* L.	150 spp.

Characters. The morphological characters used in the study comprise features of vegetative and reproductional morphology, embryology, karyology, chemistry, and molecular information as chloroplast inversions and deletions. Some of these characters and their codings, however, require additional comments.



Chase et al. -93 (*rbc*L)
3 taxa pruned (Araliaceae)

Olmstead et al. -93 (*rbc*L)
46 taxa pruned
(Asterales & asterid I s. Chase)

Bremer et al. -94 (*rbc*L)
no taxa pruned

Downie & Palmer -92
(cp DNA restriction site data)
10 taxa pruned (Asteraceae)

Donoghue -92 (*rbc*L)
no taxa pruned

Olmstead et al. -92 (*rbc*L)
no taxa pruned

Caputo & Cozzolino -94 (morphology)
17 taxa in Dipsacaceae
(some pruned, some "recircumscribed")

Judd et al. -94 (morphology)

Figure.1. Results obtained from earlier cladistic studies of Dipsacales. Taxa not included in this paper are pruned from the trees.

TABLE 2. Enumeration of 34 co-analysed *rbc*L sequences. Species are listed alphabetically according to genus and species, with family classification following the system of Takhtajan (1987).

Accession number in the NCBI/Genbank or EMBL databases is indicated for submitted sequences. Unsubmitted sequences relate to: * = Backlund et al. 1997 (In Press, Plant Systematics and Evolution, 1997), ** = Xiang and Soltis 1995.

Species and author	Family	NCBI/EMBL #
Adoxa moschatellina L.	Adoxaceae	L01883
Anopterus macleayanus F. Muell.	Escalloniaceae	*
Apium graveolens L.	Apiaceae	L01885
Aralia spinosa L.	Araliaceae	L11166
Aralidium pinnatifidum Miq.	Aralidiaceae	**
Berzelia lanuginosa Brongn.	Bruniaceae	L14391
Brunia albiflora Phillips	Bruniaceae	*
Columellia oblonga Ruiz & Pav.	Columelliaceae	*
Desfontainia spinosa Ruiz & Pav.	Desfontainiaceae	Z29670
Diervilla sessilifolia Buckl.	Caprifoliaceae	Z29672
Dipsacus sativus Garsault	Dipsacaceae	L13864
Eremosyne pectinata Endl.	Eremosynaceae	L47969
Escallonia coquimbensis Remy	Escalloniaceae	L11183
Griselinia lucida Forst. f.	Griseliniaceae	L11225
Knautia intermedia Pernh. & Wettst.	Dipsacaceae	*
Lonicera orientalis Lam.	Caprifoliaceae	X87389
Melanophylla pachypoda Airy Shaw	Melanophyllaceae	**
Morina coulteriana Royle	Morinaceae	*
Nardostachys jatamansi DC.	Valerianaceae	*
Patrinia rupestris (Pall.) Dufr.	Valerianaceae	*
Phyllactis bracteata Wedd.	Valerianaceae	*
Pittosporum japonicum Hort. ex Presl.	Pittosporaceae	L11202
Polyosma cunninghamii Benn.	Polyosmataceae	**
Pterocephalus lasiospermus Link	Dipsacaceae	*
Quintinia verdonii F. Muell.	Escalloniaceae	X87394
Sambucus racemosa L.	Sambucaceae	L14066
Steganotaenia araliaceae Hocst.	Apiaceae	*
Symphoricarpos albus C. Koch	Caprifoliaceae	L11682
Toricellia tiliaefolia DC.	Toricelliaceae	**
Triplostegia glandulifera Wall. ex DC.	Triplostegiaceae	*
Valeriana hirtella H. B. & K.	Valerianaceae	*
Valeriana officinalis L.	Valerianaceae	L13934
Valerianella locusta Betcke	Valerianaceae	*
Viburnum rhytidophyllum Hemsl. ex Forb. & Hemsl.	Viburnaceae	X87398

Vegetative Morphology: Chars. 1 — 15.

CHARACTER001. *Habit: 0 - woody, 1 - herbaceous*
The majority of the plants studied are small trees, shrubs or suffrutescent herbs. A smaller number of the taxa included are entirely herbaceous.

CHARACTER002. *Duration: 0 - annual, 1 - perennial*
Most of the plants studied are perennial, often long-lived. A couple, though, are obligately annual (or sometimes biennial).

CHARACTER003. *Rhizome: 0 - no specialized rhizomatous structure, 1 - rhizomatous, horisontal stolons, 2 - with vertical tap root*
There are many of the perennial taxa that have well developed vertical tap roots, and also some with horisontal stolons.

CHARACTER004. *Leaf persistence: 0 - deciduous, 1 - leaves withering but leaving persistent leafbases, 2 - evergreen, 3 - entire stems withering*
The majority of the taxa included in the groups under study are found in temperate areas, where a deciduous habit is common. A number of the presumably more plesiomorphic taxa are entirely tropical in distribution, and several of these are evergreen. The perennial herbs pose a special problem, as many of these are not deciduous but technically "evergreen" (e.g. *Morina*), although during the winter period the leaves wither away, leaving only remains of leafbases as a fibrous sheathing around the neck of their taproot. A specific state has been assigned for this syndrome, and also for the perennial plants where the entire stem wither away (e.g. *Triosteum*), while keeping subterranean parts living and already budding. In this case it is not a matter of leaves being deciduous, no abscission layer is developed in the petiole.

CHARACTER005. *Phyllotaxis of cauline leaves: 0 - alternate, 1 - opposite, 2 - whorled*
Many of the perennial herbs are rosette plants with dense whorls of leaves difficult to assign either to alternate or opposite phyllotaxis. Regarding the cauline leaves, however, the distinction is often clear.

CHARACTER006. *Leaf arrangement: 0 - basal rosette, 1 - basal rosette and cauline leaves, 2 - no rosette, only cauline leaves*
Extending character 005, it becomes evident that a separation between the plants with only cauline leaves (opposite or alternate), those that have only a rosette (where 005 becomes inapplicable) and finally the taxa with a combination of rosetted and cauline leaves. One could argue that characters 005 and 006 are dependent on each other. The distinction intended, however, is to separate phyllotaxis in 005 from leaf distribution on the whole plant in 006.

CHARACTER007. *Leaf insertion: 0 - lacking petiole, 1 - with petiole, 2 - with sheathing petiole, 3 - with sheathing petiole and ligulate process*
The leaf insertion has been extensively studied in the group. In members of the Apiaceae sheathing leafbases are very common, especially in the Apioideae.

Among several of the presumably plesiomorphic taxa, tendencies towards a sheathing leafbase have been observed (e.g. in *Toricellia*, *Melanophylla* and *Tribeles*). Among the Dipsacaceae, it is frequently common that the petioles join, forming a cup-like structure around the stem. This has not been interpreted as a sheathing petiole, which is defined as a structure formed by one single petiole.

CHARACTER008. *Stipules: 0 - not stipulate, 1 - with stipular line, 2 - stipulate, stipules filiform*
Stipules are not found in the Dipsacales, but stipule-like organs are prominent in some taxa. These, however, are not homologous to the stipules commonly found in, e.g., the Rubiaceae and therefore should be defined as "pseudostipules" (Weberling 1957). In some of the more plesiomorphic taxa remnants of stipules are still found.

CHARACTER009. *Bud scales: 0 - absent, 1 - present and prominent*
Prominent bud scales are found in several of the Adoxaceae s.lat. and Caprifoliaceae sensu Takhtajan.

CHARACTER010. *Leaf type: 0 - simple, 1 - pinnatisect, 2 - pinnately compound*
Simple and compound leaves are commonly distinguished, here also the state pinnatisect has been introduced to describe the deeply lobed and seemingly pinnate leaves found in many Dipsacaceae.

CHARACTER011. *Leaf outline: 0 - entire, 1 - minutely serrate/dentate, 2 - deeply lobed*

CHARACTER012. *Leaf margins: 0 - lacking spines or teeth, 1 - with prominent spines, 2 - with sinuate fringe and glandular teeth*
Some of the studied taxa (viz. Morinaceae) are vicously armed with needlelike spines along the leaf margins. In some of the escallonioid taxa another specialization of the leaf margin is found (see e.g. fig 8B), a sinuate fringe composed of separate elements between the glandular teeth.

CHARACTER013. *Leaf primary venation: 0 - pinnately veined, 1 - palmately veined/with few prominent parallel veins, 2 - reticulate venation*
The primary (main) veins of a leaf are usually either pinnately or palmately arranged. In some taxa, especially in some Valerianaceae, there are leaves with few prominent and more or less parallel veins. This state is here regarded as homologous to the palmate venation, because in neither case is there a repeated branching of the central vein. In a few very specialized taxa there is a type of reticulate venation, not easily attributed to any of the previous models and therefore assigned to a separate state.

CHARACTER014. *Stomata type: 0 - anomocytic, 1 - anisocytic, 2 - paracytic*

CHARACTER015. *Leaf vernation in bud: 0 - involute, 1 - conduplicate, 2 - supervolute*
The vernation (folding pattern) of the leaf in the bud has been studied, and found to follow three main types according to Cullen (1978), as coded in the matrix.

Anatomy: Chars. 16 — 28.

CHARACTER 016. *Leaf hypodermis: 0 - absent, 1 - hypodermis clearly developed and prominent*

CHARACTER 017. *Nodes: 0 - unilacunar, 1 - trilacunar, 2 - pentalacunar, 3 - multilacunar*

CHARACTER 018. *Ca-oxalate crystals in wood: 0 - absent, 1 - single large crystals, 2 - crystal druses/sand*
Traditional anatomical characters like stomata type, nodal structures and presence of calcium-oxalate crystals exhibit an interesting variation in the taxa studied.

CHARACTER 019. *Secretory channels: 0 - absent, 1 - present*
Secretory channels are a derived feature in most of the Apiales, the distribution among the phylogenetically more plesiomorphic members, however, is poorly studied. In the Dipsacales secretory channels are missing.

CHARACTER 020. *Endodermis in stem: 0 - absent, 1 - present*

CHARACTER 021. *Vessel-cylinder formation: 0 - not forming a continuous cylinder, 1 - forming a continuous cylinder*
Several related characters for wood and stem anatomy have been used.
In young stems of plants there are usually a number of distinct vascular bundles, eventually merging with age thus forming a vascular cylinder or stele which is normally interrupted by medullar rays. In some members of e.g. the Dipsacaceae the forming of a completely continuous cylinder may appear also in herbaceous plants (Metcalfe and Chalk 1950).

CHARACTER 022. *Vascular flankbridge in petiole: 0 - absent, 1 - with vertical branch, 2 - without vertical branch, 3 - with vertical branch subdivided*
At the nodes vascular traces leave the central cylinder to supply the leaves. In some members of Dipsacales these traces join laterally before entering the petiole. This feature, termed a "vascular flankbridge" (Howard 1970; Neubauer 1978), has been detected (though with minor modifications) in the families Valerianaceae, Dipsacaceae, Morinaceae, and Adoxaceae (in *Sambucus*).

CHARACTER 023. *Vessel-supporting thickenings: 0 - none, 1 - helical, 2 - scalariform*

CHARACTER 024. *Perforation plates in the primary xylem: 0 - simple, 1 - with 2-10 bars, 2 - with 12-20 bars, 3 - with >22 bars*
Another character connected to the vascular system is the type of perforation plates between the elements of the primary xylem. These are either simple or scalariform, and thus furnished with a number of horisontal bars, the number falling distinctly into either of three groups (DeVos 1951; Fukuoka 1972; 1975; Ogata 1988). This character was one of the four treated as ordered in the analysis, going from simple plates via 2-10, 12-20, up to exceeding 22 bars. Vascular characters have been studied from sectionings of young and mature stems of most taxa.

CHARACTER 025. *Imperforate tracheary elements: 0 - tracheids, 1 - libriform fibres*

CHARACTER 026. *Imperforate tracheary element pits: 0 - with simple pits, 1 - with bordered pits*

CHARACTER 027. *Phellogene/cork origin: 0 - pericyclic, 1 - superficial*
The origin of the phellogene is either in close association with the pericycle ("pericyclic"), or more superficially in the outermost cortical cells. This was extensively studied e.g. in the Caprifoliaceae by De Vos (1951).

CHARACTER 028. *Stem section: 0 - solid with no visual traces of pith, 1 - with "normal" spongy pith, 2 - with ultimately hollow center*
A prominent and spongy pith is encountered in members of e.g. *Sambucus*, in some of the Apioideae, on the contrary, the stems are hollow and occasionally with solid internodes.

Inflorescence: Chars. 29 — 31.

CHARACTER 029. *Inflorescence: 0 - monotelic, 1 - truncated monotelic, 2 - polytelic, 3 - polytelic, capitulum*
Concerning characteristics of the inflorescences in the Dipsacalean taxa, numerous theories have been presented (e.g. Rickett 1944; Philipson 1947; Weberling 1957; Vieth 1958; Weberling 1961; Vieth 1965; Weberling 1965; Fukuoka 1969; Weberling 1983; 1992). Summarizing, the inflorescences can be roughly divided into one of four groups. Either the inflorescence is polytelic, i.e., with several simultaneously active growth meristems, or monotelic with only one meristem. If the inflorescence is monotelic it may have a terminal flower, in which case the inflorescence is considered truncated. In the case of polytelic inflorescences, e.g. the family Dipsacaceae exhibits a special case with the polytelic inflorescence contracted to a capitula.

CHARACTER 030. *Supernumerary inflorescence bracts: 0 - absent, 1 - ±free or forming fruit wing, 2 - forming single epicalyx, 3 - forming double epicalyx*
Due to reduction of flowers in the inflorescence, supernumerary bracts (without supported flowers) may be retained in the inflorescences. Recent studies (Hofmann and Göttmann 1990; Roels and Smets 1996) have indicated that such supernumerary bracts may fuse to form the conspicous epicalyx found in Dipsacaceae and Morinaceae. Being photosynthesizing these epicalices have proved to be important for the development of the fruits in Dipsacaceae, providing a major part of the nutritional influx (Veronika Mayer, personal communication). Fruit wings present in some Valerianaceae have also been interpreted as originating from such supernumerary bracts, and might possibly also perform a similar role in fruit development.

CHARACTER 031. *Prophylls: 0 - aborted, 1 - present*
Prophylls as specified by Hofmann and Göttmann (1990) relate to sterile bracts in the lower parts of the inflorescence, as opposed to the supernumerary bracts resulting from reduction in flowers.

Flower Morphology: Chars. 32 — 46.

CHARACTER 032. *Sexual distribution: 0 - bisexual, 1 - dioecious, 2 - gynodioecious, 3- trioecious*
The majority of taxa are bisexual, with a few dioecious species. In a small group of South American taxa a trioecious type with female, male, and bisexual flowers on the same plant is frequently found. Also gynodioecious taxa with bisexual and female flowers on the same plant occur.

CHARACTER 033. *Perianth position: 0 - hypogynous, 1 - semi-epigynous, 2 - epigynous*

CHARACTER 034. *Flower / corolla orientation: 0 - one petal adaxial, 1 - one petal abaxial*

CHARACTER 035. *Sepal size: 0 - absent or not visible, 1 - very reduced, inrolled plumes or minute teeth, 2 - well developed prominent*
especially in the Valerianaceae and Dipsacaceae a wide variation in sepal type is found. In the Valerianaceae the sepals are often plumes, aimed for wind dispersal, whilst in the Dipsacaceae the epicalyx has often taken over parts of the calyx functions, and the sepals are reduced to awns or bristels.

CHARACTER 036. *Sepals, number of: 0 - two, 1 - three, 2 - four, 3 - five, 4 - six or more, indefinite*

CHARACTER 037. *Sepal vascularization: 0 - one trace, 1 - three, 2 - four traces, 3 - five traces*

CHARACTER 038. *Sepal modification for fruit dispersal: 0 - none, 1 - developing into a plumose seed/fruit, 2 - developing to seeds/fruits with awns/bristles,*
3 - enlarged and leaflike aiming for wind dispersal
In the Dipsacales the sepals are often modified to aid in fruit dispersal, sometimes in combination with the epicalyx. This is achieved either by forming a plume or a membranaceous or leaflike structure in seeds dispersed by wind, or by developing awns and bristles in animal-dispersed taxa.

CHARACTER 039. *Petal and sepal folding-pattern in buds: 0 - valvate, 1 - imbricate*

CHARACTER 040. *Petal fusion: 0 - fused, 1 - free*
The petals may be either more or less fused (sympetalous), or free from each other (choripetalous). Studies performed in the ingroup taxa show an early sympetaly with the formation of a ring-shaped primordium later developing the separate lobes (e.g. Erbar 1991; Roels 1993; Roels and Smets 1994; 1996). This syndrome of early sympetaly has also been verified in studied taxa of the Apiales, albeit not producing a traditional sympetalous corolla (Erbar and Leins 1988).

CHARACTER 041. *Petals, number of: 0 - three petals/lobes, 1 - four petals/lobes, 2 - five petals/lobes, 3 - six or more petals/lobes*

CHARACTER 042. *Corolla tube: 0 - petals weakly connate or no tube, 1 - tube rotate/small but distinct, 2 - tube well developed/long*

CHARACTER 043. *Corolla symmetry: 0 - actinomorphic, 1 - weakly zygomorphic, 2 - strongly zygomorphic/bilabiate*
The corolla is either actinomorphic or zygomorphic, the zygomorphic flowers considered to be weakly zygomorphic if the character only applies to minor traits such as the presence of a single nectary, and strongly so if the corolla limb is to a large extent modified, bilabiate, or furnished with a spur or other conspicuous adaptations.

CHARACTER 044. *Corolla nectary type: 0 - absent, 1 - nectar disk, 2 - multicellular hairs, 3 - unicellular hairs*
The nectaries are either intrafloral, organized as an ovary disk, or arranged basally on the corolla tube below or near the insertion of the stamens; alternatively, they may occur as extrafloral nectaries (e.g. Wagenitz and Laing 1984).

CHARACTER 045. *Corolla nectary number: 0 - one, or fewer than number of lobes, 1 - five, or equal to number of lobes*

CHARACTER 046. *Corolla vascularization: 0 - lacking lateral connections, 1 - with lateral connections*
The vascularization of the corolla has been extensively studied (see Appendix A). In a large part of the Dipsacalean taxa the main petal veins are prominently connected laterally with one or a number of vascular traces. These are furnished with helical thickenings, and easily studied at low magnification in light microscopy. In some taxa with very small corollas, notably *Valerianella* and *Stangea*, the vascularization is strongly reduced, making their interpretation somewhat obscure. Such lateral connections of the petal main veins have not been found in any of the outgroup taxa, or in any other putatively related taxa including Apiales, Campanulales, and Asterales (Gustafsson 1995).

Androecium: Chars. 47 — 54.

CHARACTER 047. *Stamen number: 1 - one, 2 - two, 3 - three, 4 - four, 5 - five, 6 - more, indefinite*
Most members of the studied taxa have basically pentamerous flowers, albeit often with reductions in floral parts especially in number of stamens.

CHARACTER 048. *Stamen relative length: 0 - ≈ equal in length, 1 - prominently unequal in length, 2 - didynamous*

CHARACTER049. *Staminal filament indumentum: 0 - glabrous, 1 - hairy*

CHARACTER050. *Filament attachment: 0 - free from corolla, 1 - weakly fused to corolla, 2 - prominently fused to corolla*
In most members of Dipsacaceae, Valerianaceae and Caprifoliaceae sensu Takhtajan, the staminal filaments are prominently fused to the corolla. This is however not the case in members of the Adoxaceae s.lat., nor in most Apian or escallonioid taxa.

CHARACTER051. *Staminal modifications: 0 - all stamens fertile, 1 - sterile staminodia present*
In the Dipsacales one of the prominent trends is that of reductions in the number of stamens. Only occasionally, however, do we find staminodia (e.g. in the family Morinaceae and some gynodioecious taxa), more often the entire stamen is reduced leaving only traces in the vasculatory system of the corolla.

CHARACTER052. *Anther attachment: 0 - dorsifixed, 1 - basifixed, 2 - sagittate*
The anthers are subject to some intriguing variation, in some members of e.g. the Caprifoliaceae the thecae are not joined by the connective in their full length giving a sagittate shape to the anther. In such cases it is not possible to determine whether the filament attachment to the anther is basal or dorsal, and a separate state "sagittate" has been defined as separate from basifixed and dorsifixed.

CHARACTER053. *Anther orientation at dehiscence: 0 - extrorse, 1 - introrse*

CHARACTER054. *Sporangium number in thecae: 0 - one, 1 - two*
In some South American Valerianacean taxa the number of thecae in each anther is reduced from two to one (e.g. Larsen 1986; Eriksen 1989), but then still retaining a connective. This situation is not to be confused with the situation in *Adoxa*, where the stamens are deeply split with each half carrying one theca, but the thecae having two sporangia (Sprague 1927; Fukuoka 1974).

Gynoecium: Chars. 55 — 59.

CHARACTER055. *Carpels, number: 1 - one, 2 - two, 3 - three, 4 - four, 5 - five*
Parallel to the trend in reduction of stamen number, a reduction in carpel number and in fertility of the remaining carpels has been suggested (Cronquist 1981). The total number of carpels in the ovary is deduced from studies of ontogeny and cross sections of ovaries and vascular traces. In coding this character, also very reduced carpels have been included, the reduction being accounted for in characters 056 and 057 respectively.

CHARACTER056. *Carpel abortion: 0 - all fertile, 1 - one aborted, 2 - two adjacent aborted, 3 - two adjacent aborted and ovule displaced, 4 - two opposite aborted*
A distinction has been made between different abortion schemes. Obviously state 4 is not even possible in the majority of taxa with initially three carpels, but in some of the taxa with four and five a difference in how the remaining fertile carpels develop is observed. Studies of the resulting ovary vascularization indicate that several mechanisms are involved, necessitating a distinction between the states where two adjacent carpels are aborted in contrast to when two adjacent carpels are aborted and the ovule displaced relative to the margin of the ovary (Wilkinson 1948a; 1948b; 1948c; 1949).

CHARACTER057. *Sterile loci: 0 - none, 1 - present but much reduced and visible only as minor openings, 2 - normal/prominent in cross sectioning of ovary*
The aborted carpels are in some taxa very reduced, only visible as very small cavities in the ovary; in other taxa the aborted carpels can be as large as, or larger than, the fertile ones (Nielsen 1949). This latter state, encountered in some Valerianacean taxa, is interpreted as a modification to wind dispersal.

CHARACTER058. *Carpel vascularization: 0 - free adaxial and abaxial, 1 - adaxial bundles only, 2 - only free abaxial, adaxial not recessed*
Carpel vascularization patterns have been extensively studied from anatomical sectionings, and also earlier by Wilkinson (1948a; 1948b; 1948c; 1949)

CHARACTER059. *Stigma shape: 0 - entire and slender, 1 - capitate, 2 - bilobate, 3 - trilobate, 4 - pentalobate*

Fruits: Char. 60.

CHARACTER060. *Fruit type: 0 - capsule, loculicidal, 1 - capsule, septicidal, 2 - berry, 3 - drupe, 4 - cypsela, with persistent remains of calyx, 5 - cypsela, lacking remains of calyx, 6 - schizocarp*
The variation in fruit type within the studied group is moderate; most commonly it is a many-seeded capsule or berry or a more or less dry drupe in the more basal taxa. In the higher taxa a small dry nut with or without persistent calyx remains. In the taxa with capsules, e.g. *Diervilla* and *Weigela*, a distinction is made between loculicidal and septicidal dehiscence types.

Embryology: Chars. 61 — 70, 83 — 86.

In this category major structural aspects of the organization of the ovary as well as anatomy of anther walls are also included.

CHARACTER061. *Ovule vascularization: 0 - single bundle, 1 - double or compound bundles*
The vascular supply to the ovule usually consists of one single bundle. In the taxa with reduced number of carpels, however, the vascular traces to the aborted carpels can be taken over by the remaining carpels, thus giving the (often single) fertile ovule a compound vascular supply consisting of several parallel traces (e.g. Wilkinson 1948a; 1948b; 1948c; 1949).

CHARACTER062. *Ovule position with respect to the central axis.: 0 - marginal, 1 - marginal above, median below, 2 - median*

CHARACTER063. *Ovule reduction: 0 - no traces of reductions, 1 - sterile ovules, 2 - vestigial archespore surrounded by nucellar tissue, 3 - vestigial archespore*
The reduction in number of ovules in the carpels varies in degree, in some taxa frequently resulting in sterile ovules, in others only in vestigial archespores.

CHARACTER064. *Integument number: 0 - unitegmic, 1 - -bitegmic*

CHARACTER065. *Nucellus thickness: 0 - tenuinucellate, 1 - crassinucellate*
The common co-variation between number of integuments and thickness of nucellus is well known (Philipson 1974). Arguments could then be raised as to unite these features into one single character. In the studied group, however, there are some taxa with comparably uncommon combinations of the available states (e.g. Lange et al. 1993a; 1993b), supporting the treatment of integument number and nucellus thickness as two distinct characters.

CHARACTER066. *Placenta outline: 0 - normal, 1 - with upcurving projection*
The upcurving projection of the placenta presumably acts as guiding tissue for pollen tubes (e.g. Apiaceae, Philipson 1974).

CHARACTER067. *Endothelium: 0 - absent, 1 - present, feebly differentiated, 2 - prominent, with crystal layer*
The presence of a well developed endothelium is distinctive of e.g. Dipsacaceae and Morinaceae, and have been studied by Kapil and Tiwari (1978), and Kapil and Bhatnagar (1991).

CHARACTER068. *Endothecium with fibrous thickenings: 0 - absent, 1 - present*
The fibrous thickenings of the endothecial cells are readily observed in sectionings of anthers.

CHARACTER069. *Tapetum type: 0 - glandular, 1 - amoeboid, 2 - cellular*
The type and development of the anther tapetum have been studied to some extent (e.g. Kamelina 1980; Johri 1992).

CHARACTER070. *Tapetum cells: 0 - uninucleate, 1 - binucleate, 2 - multinucleate*

CHARACTER083. *Embryo sac development: 0 - Polygonum type, 1 - Adoxa type, 2 - Allium type*
The rare *Adoxa*-type embryo sac is one of the morphological features that unite *Adoxa* and *Sambucus* (which normally develops this type) and also *Viburnum*, where some observations have been made of a very similar pattern. The *Adoxa*-type embryo sac is not encountered elsewhere in the Dipsacales-Apiales association.

CHARACTER084. *Embryogeny type: 0 - Solanad, 1 - Asterad, 2 - Piperad, 3 - Onagrad*

CHARACTER085. *Endosperm in seed: 0 - absent, 1 - scanty, 2 - copious*

CHARACTER086. *Embryo development: 0 - leucoembryote, 1 - chlorophyllous*
Observations from a number of taxa show that in some families embryos develop chlorophyll already at the embryo-stage, and that chlorophyll therefore is present in the seed (e.g. Dipsacaceae and Valerianaceae, Yakovlev and Zhukova 1980). The opposite situation with an embryo lacking chlorophyll, leucoembryote, is encountered in Morinaceae, Caprifoliaceae, Adoxaceae s.lat. and in all outgroup taxa.

Palynology: Chars 71 — 82.

Much of the nomenclature used in describing the pollen grains comes from the works by Erdtman (1952; 1966).

CHARACTER071. *Male gametophyte at shedding: 0 - bicellular, 1 - tricellular*

CHARACTER072. *Pollen outline: 0 - spheroidal, 1 - prolate, 2 - cylindric*
The shape of the pollen grain outline can in the studied taxa roughly be described as spheroidal or prolate. A grain is here considered prolate when the ratio between polar and equatorial measures is 1.5 or more.

CHARACTER073. *Aperture operculum: 0 - lacking, 1 - from simple echinae, 2 - from branched echinae*
The pollen apertures may be covered by operculae forming a grid-like lid; these operculae are made up by echinae-like structures which may be either branched or simple. Observations by Clarke (1978) shows that the operculae often come off during acetolysis, and can therefore be difficult to observe. The operculae formed by branched echinae though, leave a rough, spiny margin around the apertures and can thus be detected. On the other hand, the operculae formed by simple echinae on the contrary detach clean from the margins, and often remain intact and can then be detected among the "debris" on the prepared slide.

CHARACTER074. *Aperture margin modifications: 0 - non, 1 - halo, 2 - costae, 3 - domed protrusions, 4 - equatorial bridge, 5 - periendoapertural thickenings*
The aperture margins show a wide variety of different modifications. In the Valerianaceae a "halo" around the apertures has been reported repeatedly (Erdtman 1952; 1966; Clarke 1978); this results from a rupture in the inner layers of the pollen wall, making the area around the aperture thinner and in light microscopic studies appearing as a bright band. In some Dipsacaceae a "halo" has also been reported, but SEM studies here shows a different structure (Clarke 1981). In a wide portion around the margins the inner wall of the pollen grain is ruptured, but the very margin of the aperture is considerably thicker forming so called "costae". In parts of the Morinaceae domed protrusions around the porous apertures make up a very conspicuous feature; these are formed by the outer layers of the pollen wall (Blackmore and Cannon 1983). In some taxa an equatorial bridge over the center of the aperture is formed (Donoghue 1985), whilst in other "periendoapertural thickenings", apparently different from the costae of Dipsacaceae, frequently occur (Hideux and Ferguson 1976).

CHARACTER075. *Aperture type: 0 - colpate, 1 - pororate, 2 - colporate*

CHARACTER076. *Aperture width: 0 - very narrow, 1 - prominently wider at equator*
In the taxa with colpate or colporate apertures, the apertures differ considerably in shape, and two easily separated types are found, either with an aperture that is very narrow and with parallel sides of the colpus, or an elliptic aperture with a broad colpus in the range of 25% - 75% as wide as long.

CHARACTER077. *Colpi membrane modification: 0 - none/membranes smooth, 1 - membrane granulose*

CHARACTER078. *Exine structure: 0 - semitectate, 1 - tectate, 2 - sparsely perforate tectum, 3 - semitectate with interrupted muri*
The exine is either tectate, i.e., more or less entire and covering the larger part of the surface of the pollen grain, or semitectate. These states are easily distinguished as the semitectate exine remains in ridges (muri) forming patterns on the pollen grain surface (Agababian 1964; Hideux and Ferguson 1976; Donoghue 1985).

CHARACTER079. *Columella layer and columella type: 0 - reduced/absent, 1 - prominent unbranched, 2 - prominent branched columellae*
The columella layer between exine and sexine is normally present and consisting of either unbranched or branched columellae (Agababian 1964; Clarke 1978; 1981; Clarke and Jones 1981). In a few taxa though, the columella layer is reduced.

CHARACTER080. *Tegillum perforation: 0 - no, 1 - showing microperforations*
Occasionally the tectum or tegillum shows small round microperforations. This is a feature easily observed in SEM micrographs, and most often found in Caprifoliaceae.

CHARACTER081. *Echinae/verrucae/clavae: 0 - absent, 1 - echinae, 2 - verrucae, 3 - clavae*

CHARACTER082. *Microechinae: 0- absent, 1 - present*
Another characteristic of some pollen grains is the presence of large spines, so called echinae (1-4 µm). In some Valerianaceae these echinae are furnished with a wide, domed base supported by groups of columellae, and usually referred to as verrucae. Between the larger echinae, or sometimes in taxa devoid of "macroechinae", numerous very small microechinae (<1 µm) cover the surface.

Chemistry: Chars. 87 — 102.

Characters 83 to 86 are treated under the section on embryology, above. Frequently chemical information has been used in attempts to elucidate phylogenetic relationships between plants. A number of compounds studied are considered to be important precursors in various biochemical pathways.

The occurrence of compound classes such as tannins, polyacetylenes, and monoterpenoid iridoids are assumed to reflect certain levels of advancement in chemical defence systems of the plants (Cronquist 1981). Arguments have been made that the presence and/or absence of these substance classes should also be of phylogenetic importance, as markers of distinct changes in use of different pathways.

CHARACTER087. *Iridoids: 0 - none, 1 - normal, 2 - seco-iridoids, 3 - both*
The systematic importance of iridoids has been observed in a series of publications (e.g. Rosendal Jensen 1971; Dahlgren 1975b; Rosendal Jensen et al. 1975; Rosendal Jensen 1992).

CHARACTER088. *Iridoid triesters: 0 - absent, 1 - present*
A number of specific groups of iridoid compounds have been identified in several of the studied taxa. One of these, the so called valepotriates (valeriana-epoxy-triesters), are thus far only found in some of the Valerianacean taxa (e.g. Thies and Funke 1966a; Thies 1968; Stahl and Schild 1971; Popov et al. 1974; Hölzl and Jurcic 1975; Houghton 1988; Backlund and Moritz 1996, and references therein).

CHARACTER089. *Valeric acid: 0 - absent, 1 - present*

CHARACTER090. *Alkaloids: 0 - absent, 1 - present*
Alkaloids are a group of substances that since long have attracted attention due to the many interesting and valuable pharmaceutical compounds included (Willaman and Li 1970).

CHARACTER091. *Myreticin: 0 - absent, 1 - present*

CHARACTER092. *Quercetin or Kaempferol: 0 - none, 1 - Quercetin, 2 - Kaempferol, 3 - both*

CHARACTER093. *Ellagic acid: 0 - absent, 1 - present*

CHARACTER094. *Proanthocyanidin precursors: 0 - none, 1 - Delphinidin, 2 - Cyanidin*

CHARACTER095. *Saponins: 0 - absent, 1 - present*

CHARACTER096. *Coumarines: 0 - absent, 1 - present*

CHARACTER097. *Sinapic or Ferulic acid: 0 - none, 1 - Sinapic, 2 - Ferulic, 3 - both*

CHARACTER098. *Cephalarosid = Dipsacan: 0 - absent, 1 - present*

CHARACTER099. *Cathecolic tannins: 0 - absent, 1 - present*

CHARACTER100. *Polyacetylenes: 0 - absent, 1 - present*
Polyacetylenes have been studied in the order Asterales, where they are comparably common, and also in some members of the Apiaceae. From the Dipsacales there is a very limited amount of data available, but a few indications have been found in the Valerianaceae.

CHARACTER 101. *Monoterpenoids: 0 - absent, 1 - present*

CHARACTER 102. *Griselinoside: 0 - absent, 1 - present*

Cytology And Molecular Information: Chars. 103 — 109.

CHARACTER 103. *Chromosome base number: 0 - x=6, 1 - x=7, 2 - x=8, 3 - x=9, 4 - x=10, 5 - x=11, 6 - x=12, 7 - x=17*
Variation of the base chromosome number is limited within the studied group, except for a small number of notable exceptions.

CHARACTER 104. *Chromosome size: 0 - small (≤1.5 µm), 1 - large (≥≈2 µm)*
The size of the chromosomes though has been studied especially within the Dipsacales (e.g. Hillebrand and Fairbrothers 1970; Verlaque 1977, Hara 1983), and they fall within two readily recognizable groups.

CHARACTER 105. *Deletion of ORF235: 0 - absent, 1 - present*
Among the molecular information of a non-sequenary type is the deletion of the Open Reading Frame (ORF) 235, a region in the chloroplast genome, that have been detected during amplification of the adjacent *ndh*F-gene. The ORF235 is deleted (or rearranged) in all members of Dipsacales s.str. studied, with the sole exception for *Viburnum* (K.-J. Kim, personal communication).

CHARACTER 106. *Structural rearrangements in the Inverted Repeat: 0 - not modified cf. Nicotiana, 1 - deletion of 400bp, 2 - deletion of 400 bp, and subsequent insertion of 500 bp.*
Based on information from tab. 2. in Downie and Palmer (1992).

CHARACTER 107. *Deletion of clpP - gene: 0 - absent, 1 - present*
A third notable feature is the deletion of the gene *clp*P, coding for a heat-shock protein, which is indicated as missing in a small group of taxa within the Caprifoliaceae (M. Donoghue, unpublished data).

CHARACTER 108. *Size of inverted repeat: 0 - no change cf. Nicotiana, 1 - expansion of IR at coordinate 84087, 2 - expansion of IR at coordinate 85632, 3 - contraction of IR at coordinate 88041.*
Also within the Inverted Repeat (IR) region structural rearrangements has been recorded during a chloroplast DNA restriction site mapping; resulting in a size variation of the IR and a shift of the border between the IR and the Large Single Copy region (LSC) near the rpl23 operon with respect to tobacco (S. Downie, personal communication).

CHARACTER 109. *Presence of CIRs: 0 - absent, 1 - present*
Recently Benko-Iseppon (1992), and Benko-Iseppon and Morawetz (1993) studying karyosystematics in the Dipsacales observed the presence of cold-induced undercontracted chromosome segments (CIRs) in a few Dipsacalean taxa.

TAXA	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000001	111
	0000000001	1111111112	2222222223	3333333334	4444444445	5555555556	6666666667	7777777778	8888888889	9999999990	000
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	123
Adoxa	11d1111002	2000000000	0300201100	00102d0010	d1a21ai001	0001i00013	02300011a0	1100200010	0011203001	0000?100??	003
Sinadoxa	1121111002	2000?0?00?	0?002?1??0	00102k0010	a11210h001	0001400?0?	?230001100	1100200010	001120300?	?00?0?00??	?03
Tetradoxa	1121111002	2000?0?00?	0?002?1??0	00a0220010	11021a4001	0001400?1?	?230001100	1100200010	001120300?	?00?0?00??	?03
Abelia	010b121010	a000201201	1012010011	1021231310	22d3014212	0211320214	1210000110	1000210110	1001203000	0110112000	00
Diervilla	011012a010	1000001201	1003010110	102123a010	22d3015012	0211200211	0010000110	1000111100	1001203000	0110112000	003
Dipelta	0100121010	0000201201	10020?0111	1021231010	22d3014212	0b11420214	1210000110	1000200110	1001203000	0312113000	002
Heptacodium	0100121010	a010001200	1021010021	1021231010	22d3015002	0011322213	??10000110	1000111111	1001203000	0??0110000	00?
Kolkwitzia	0100121010	0000201d00	1002010111	1021231010	2223014212	021132d214	1210000110	1000200111	1001203000	0112110000	002
Leycesteria	0100121010	a000001201	1011010d20	1021231010	22a31150a2	0211i002r2	0010000110	1000200110	1001203000	0010110000	003
Linnaea	0112121010	1000200201	1002010011	1021231010	2213014202	0211320214	1210000110	1000200110	1001203000	01?0110000	002
Lonicera	010b121010	0000201200	101q010a20	1021231010	22k3115aa2	0211f00212	0010000110	1000200110	10b1203000	031011d000	003
Symphoricarpos	01a0121010	0000200200	101a0?00d0	1021231010	d2a301i002	0211440213	1210000110	1000210111	0001203000	00?0110000	003
Triosteum	1113120010	b000200d00	0011000120	1021231010	2223015012	0211410213	1210000110	1000210111	0001203000	00?0110000	003
Weigela	0100121010	1000001d00	1013010110	1021231010	22d30150a2	0211200211	0010000110	1000111100	1001203000	0312110000	003
Zabelia	0100121010	a000201201	101a010111	10212fa310	d2d301i212	0211320214	1210000110	1000210100	0001203000	0??0110000	003
Dipsacus s.lat.	1121111000	da00102201	1110010d32	0021142210	1223014002	001132a2a6	1210002100	1022110111	1102212001	000010011?	1031
Knautia	1ab11d100a	d000101201	11da010d32	0a211g1210	1223014012	001132a2f5	1210002100	1010110121	1102212001	00001?011?	1041
Pterocephalus	aaba1d100a	a000101201	1111010132	0021dg2110	d2d3014002	001132a214	1210002100	1112000121	1102212001	00001?011?	1031
Scabiosa s.lat	aab11d100a	a000101201	1111010132	0021131210	2223014002	001132a224	1210002100	10d2a00121	1102212001	000011011?	10f1
Succisa s.lat.	1113111000	a000101201	1110010132	00211fd210	1213014002	001132a2d4	1210002100	1020010121	1102212001	000011011?	1021
Acanthocalyx	1121112000	111a001200	1012210202	0021221010	2223014202	0011321214	1210002120	1000210101	0000200001	0100??001?	1070
Cryptothladia	1121212000	111a002201	1212210202	0021221010	22230142a2	1011321214	1210002120	1203110101	0000200001	01000?001?	1070
Morina	1121212000	111a002201	1212210202	0021222010	22230142a2	1011321214	121000212a	1203110101	2000200001	0100?1201?	1070
Sambucus	a1a0121b12	1000002201	0300201100	10d11m00a0	k10101n001	0101n000h3	1230000100	1100200010	0011203011	0300?02010	0031
Triplostegia	1121111000	1000101201	1310200113	1021120010	2213014002	0011321214	1210002110	1001001121	1101113111	030?10001?	1031
Belonanthus	1121001000	0010102001	1310b00010	1f21111010	0213013002	011032a1f4	1210002110	1001011110	1101012111	030000001?	1021
Centranthus	a12a1d100b	a000101001	1310200110	1021130110	2223011002	001132a2e4	1210002110	102101a120	1101012111	030200001?	1021
Nardostachys	1121112000	a010101101	1310200d10	1021231310	221301p002	0011322214	1210002110	1021011110	2101013111	030010001?	1031
Patrinia	11b111d000	d000101101	1310200d11	1021a30c10	221301p002	0011322214	1210002110	1021011110	2a01013111	030010001?	1021
Phyllactis	112100d000	a0d0100001	0320200110	1q21000010	k2d0013002	001032a235	1210002110	1021011110	1101012111	030000001?	1021
Plectritis	10031d1000	0000101001	1310200d10	1021130010	2223013102	001132d2f5	1210002110	1021011120	1a01012111	030000001?	1021
Stangea	1121001000	0020100001	1310200111	1021140110	22130a3002	0a1032a224	1210002110	1021011110	3?01012111	030000001?	1021
Valeriana clematitis	0121121000	0000101001	131m200d10	1221140110	2213013002	0111321234	1210002110	100101a110	1101013111	0300000011	1021
Valeriana dioica	112111100b	0000101001	131mb0a110	1121140110	2213013002	0011321224	1210002110	1001011110	1101013111	0300000011	1021
Valeriana hirtella	0102021000	0000101001	131m200010	1021140110	2213013002	0111321234	1210002110	100101a110	d101013111	0300000011	1021
Valeriana officinalis	1111121002	1000101001	131m200110	1021130110	2213013002	0011320234	1210002110	1001011110	1101013111	0300000011	1011
Valerianella	100e1d1000	0000101001	131020021a	1021230010	22d3003002	0011322235	1210002110	102101a120	0101012111	030000001?	1031
Viburnum	010b121ba0	k0a0a01201	00a3211a00	1a11130010	2d01005b0d	0111331033	1220a00100	1104200010	00b1201010	030210b010	0031
Apium	1121012002	k002113210	0000201d21	1020k30001	20a1005000	0111200026	1200110100	1100200110	0000200001	0300a1?0?1	?05?
Steganotaenia	0102022002	1002113210	0001201120	1020230001	2001005000	0111200026	1200011100	1100200110	0000200001	0300a1?0?1	?05??
Aralia	a102022m1b	a00211ed10	001k201110	1a2a1f001a	d001005000	0111t0200f	0210111100	010000011a	100320000a	0300110001	00j?
Aralidium	0102022002	2001203201	0003201100	1121130010	2001005000	0011320033	1210101100	1000210111	0001201000	0b000000??	?111?
Audouinia	0122020000	0010200101	0013011021	1011230011	2001005000	0211322030	12101001??	?0000111?0	000120000?	100???01?	?05??
Berzelia	0122021b10	0000200201	0023011010	1011230011	2000005000	0201100205	12001001??	?004210100	20012010??	1?000??010	?01??
Brunia	012202ab10	0000?00201	0023011010	1011230011	2000005100	0201dab20i	12k01001??	?000210100	20012010??	1?000??010	?01??
Columellia	0102121000	a000100201	1012010100	1011230010	2211005002	0101200021	120000111?	1000210110	00??20000?	???0???00?	?0???
Desfontainia	0102121100	1100100201	1003011010	0001231010	2211015002	01115000d2	0200001100	0000211111	0000203000	???????00?	?01??
Eremosyne	1003021000	d0102??001	?01001?100	0b10230001	2001005000	0011200?10	120000??0?	1105200020	00??20?00?	???????0??	?0???
Anopterus	0102021000	1200211201	001d010100	1000241011	4000?05000	0211200201	1000001???	1105210210	000?20?00?	0301??01?	?0???
Escallonia	0102a22000	a000210201	a01d010100	001023e00a	2k01005000	001120abs1	0100001???	1000210110	000?20100?	0301?1301?	?060?
Forgesia	0102021000	120011a20?	001m010120	1010230001	2001005010	0211200011	0200001???	1???2??2?0	0?0?20100?	?301???0??	?0???
Quintinia	0102021000	0000211201	0013010100	1010230011	2001005000	0011n00001	0201001???	10002112?a	000?20?00?	???????0??	?0???
Griselinia	0102022010	aa0011d200	0013211000	112?a3?011	2001005000	001132a233	1200101100	00??2??1??	??01201000	?30001?000	?13??
Melanophylla	0102022?0	a000???2??	0010211100	1021230011	2001005000	0211fa0203	1200101100	0005200110	000120000?	???0???000	?0???
Pittosporum	0102021010	a002101d11	00aa20a110	1a0123001a	2k00005002	01112000b0	1200000100	1100010110	000120000?	0301113011	100?
Polyosma	0102a21000	a00??1?20?	0??3011101	102?22e001	1201004010	0111100012	1100101???	100511?2?0	00??20100?	???????0??	?0???
Toricellia	0102022000	10102???2??	0010211120	1121230001	2001005000	0111322?33	?010101100	0000210110	0001201000	?2??00?0??	?16??
Tribeles	01?1022000	000?1??20?	00??01?1b0	100?230011	2001005000	0111300231	0200101???	???????3?0	0???20?00?	???????0??	?0???

Equative codings follows: a = (01) 116st, b = (02) 28st, c = (03) 1st, d = (12) 76st, e = (13) 5st, f = (23) 12st, g = (24) 2st, h = (34) 2st, i = (45) 6st, j = (56) 1st, k = (012) 11s
m = (123) 7st, n = (345) 11st, p = (145) 2st, q = (0123) 2st, r = (14) 1st, s = (1234) 1st, t = (2345) 1st.

Figure. 2. Data matrix used containing all 109 characters, including uninformative characters later omitted during search. Missing data are indicated with ?, inapplicable characters with -. For polymorphic characters the translation table below the matrix has been used.

ANALYSIS

Analysis of the data matrices was performed using the computer program "Phylogenetic Analysis Using Parsimony" (PAUP), version 4.0d49_noFPU (Swofford 1996) on an Apple Macintosh LC630 with 20 MB of physical RAM. The same scheme of analysis was followed for both the primary ALLMATRIX (combined morphological and molecular) and the secondary MORPHMATRIX (only morphology) matrices. First a heuristic search was performed with 100 replicates of random taxon addition sequences followed by the tree bisection reconnection (TBR) branch swapping algorithm, defining multistate taxa as uncertainties due to the problem in PAUP estimating consistency indexes (CI) for polymorphic characters. Initially all characters were given equal weight, and treated as unordered, except for characters 024, 029, 042, and 079, which were treated as ordered. All uninformative characters, as well as positions 1-26, 172, 173, 1132, and 1133 in the nucleotide sequences (corresponding to characters 110-135, 281, 282, 1241, and 1242) were excluded from the analysis. The rational for excluding positions 1-26 is that these correspond to the 5'-end PCR primer, and positions 172, 173, 1132 and 1133 are so called "C/G-positions" known to yield ambiguous results depending on sequencing direction (from 5'-end or 3'-end). During analysis of the MORPHMATRIX all molecular characters, viz. characters 110 to 1537, were excluded.

Following the first analysis, a bootstrap analysis (Felsenstein 1985), and a parsimony jackknifing analysis (Farris 1996) as implemented in PAUP were performed. To further evaluate the relative stabilities of the obtained groupings, a Bremer support analysis (Bremer 1988; 1994) calculating the support for each node using enforced topological constraints and the same settings as in the primary run was performed.

RESULTS

The result of the ALLMATRIX analysis consists of 12 equally parsimonious trees with a length of 1413 steps. The trees were rooted by defining *Escallonia* and *Eremosyne* as outgroups in accordance with previous molecular studies (Backlund et al. 1997). The retention index (RI, Farris 1989) and consistency index (CI, Kluge and Farris 1969) were calculated to 0.685 (RI) and 0.378 (CI), respectively. The strict consensus tree from the ALLMATRIX analysis is shown in fig. 3.

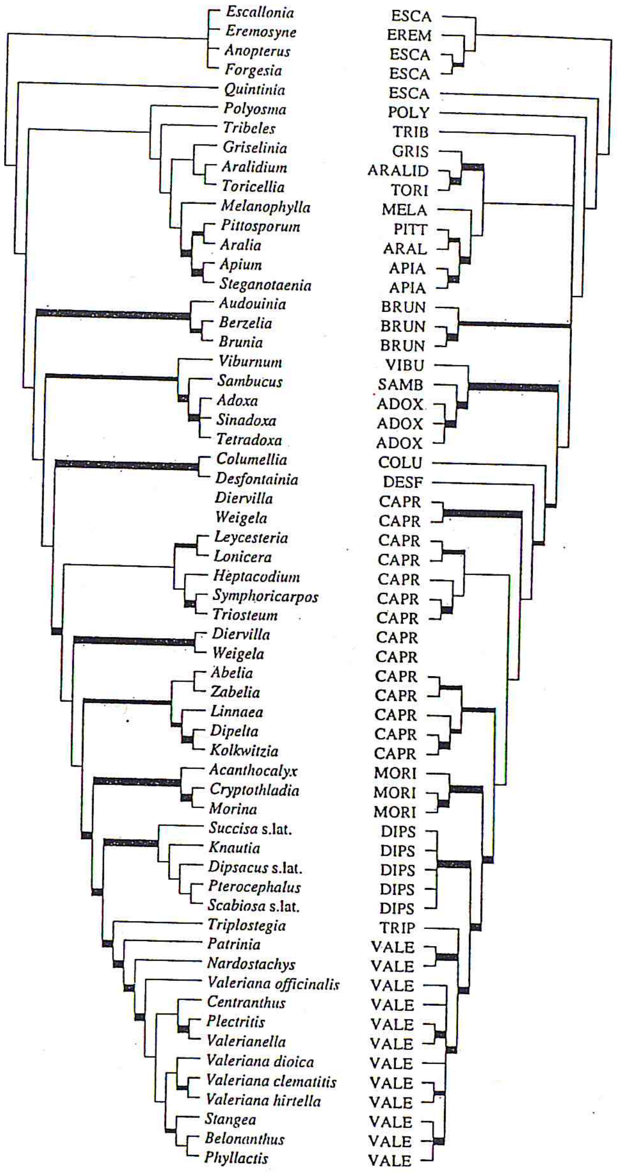


Figure. 3. Strict consensus trees of the 12 equally parsimonious trees from the combined analysis (ALLMATRIX, left) and of the 564 trees from the morphological analysis (MORPHMATRIX, right). Suprageneric taxa follow Takhtajan's system (Takhtajan 1987). Branch thickness is indicative of supporting indices: thin branches = bootstrap values (**bst**) and jackknife fractions (**jac**) both below 50%, and Bremer support (**B s**) below 4. Medium thick branches = one or both of **bst** and **jac** between 50% and 65%, and **B s** above 4. Thick branches = either **bst** or **jac** above 65%, and **B s** above 6.

The MORPHMATRIX analysis with only morphological characters, retained 564 trees of the length 614 steps. The strict consensus tree with the results from the MORPHMATRIXis also found in fig. 3. These two consensus trees are very similar and congruent except for the position of the clade comprising *Diervilla* and *Weigela*. Compared to the earlier analyses of solely molecular data (Backlund et al. 1997) the positions of Adoxaceae s.lat, Bruniaceae and the *Desfontainia-Columellia* clade in the Dipsacales association are prominent changes.

The discussion below will refer to the tree showed in fig. 4, one of the most parsimonious trees obtained from the analysis of the combined datasets. All character state changes on internal nodes are listed in tab. 3a, those of terminal branches in tab. 3b, optimization criterion follows ACCTRAN (accelerated transformation) as implemented in PAUP. Supportive indices are summarized in tab. 4, including branch lengths, bootstrap values, jackknife fractions and Bremer support values.

DISCUSSION

In the Asteridae s.str., or the "asterid II" as defined by Chase et al. (1993) in their broad study of *rbc*L sequences throughout the angioperms, molecular studies have indicated four major evolutionary lineages. These roughly correspond to the orders Asterales, Apiales and Dipsacales and a group commonly referred to as the *Ilex*-clade.

Saxifragaceae-Escallonioideae and the Dipsacales-Apiales complex. The family Saxifragaceae, and its subfamily Escallonioideae, as described by Engler (1930) has repeatedly been subject of reevaluation. The heterogeneity and polyphyly of the family had already at the time of Engler's work been a matter of debate for a considerable time. As Baillon (1872) stated *"il n'y a pas un seul caractère de ceux qui servent à différencier entre elles les familles dicotylédones qui soit constant"* ("There is not one single constant diagnostic character that defines them [Saxifragaceae] from the other dicotyledonous families"). In the classification proposed by Takhtajan (1987), he advocated the elevation of several segregates to family rank, thereby leaving only a small core family Escalloniaceae consisting of seven genera. That the Escalloniaceae even after the reevaluation by Takhtajan (1987) still remain a problem has recently been demonstrated both by molecular studies (i.e. the studies by Morgan and Soltis 1993; Gustafsson et al. 1996, Xiang and Soltis 1995; Backlund et al.

1997), and numerous investigations of morphology, palynology, anatomy and cytology (e.g. Morf 1950; Hamel 1953; Agababian 1964; Wakabayashi 1970; Bensel and Palser 1975; Hideux and Ferguson 1976; Al-Shammary and Gornall 1994). It turns out that even in the restricted sense of Takhtajan the Escalloniaceae, in this analysis represented by the genera *Escallonia, Anopterus, Quintinia* and *Forgesia*, remains a heterogenous group with some taxa instead occupying positions firmly in the order Asterales, viz. *Abrophyllum* and *Cuttsia* of the Abrophyllaceae (Backlund et al. 1997).

The escallonioids confined to Dipsacales, however, do share some general features making this assemblage somewhat homogenous. All the genera are shrubs or small trees with alternate leaves and choripetalous or weakly sympetalous flowers. The flowers are usually pentamerous, except for the genus *Anopterus* and some species of *Quintina* (which have 6-10- or 4-merous flowers, respectively). The number of stamens and carpels and the carpellary organization also vary significantly. Line drawings are supplied of *Escallonia* (after Baillon 1872; figs. 5 A-C), *Anopterus* (original; figs. 6 A-E), and *Forgesia* (original; figs. 7 A-H). In the fields of anatomy and especially palynology (Agababian 1964; Hideux and Ferguson 1976), a close relationship has been suggested between *Anopterus*, *Escallonia* and *Forgesia* on one hand and between *Quintinia* and *Anopterus* on the other. In the vicinity of these taxa was earlier the monotypic genus *Eremosyne* placed (Engler 1930). This small herbaceous plant from Southwest Australia by Takhtajan (1987) recognized as the family Eremosynaceae does, however, share some morphological characteristics with the other escallonioid plants (see figs. 5 D-G after Engler). In spite of these systematic achievements, the suggested relationships between these genera are still poorly supported.

The Apiales Association. Above the basal portions of the tree, two major evolutionary lineages emerge, leading to the Apiales and Dipsacales associations respectively. The first branches in the Apiales association correspond to two former members of the Saxifragaceae s.lat.: *Polyosma* and *Tribeles*. The genus *Polyosma*, by Engler (1930) placed in the subfamily Escalloniaceae tribus Polyosmateae, comprises approximately 60 species from Southeast Asia and the Australo-Pacific region. Representatives of this genus are shrubs or trees, generally with choripetalous or weakly sympetalous tetramerous flowers (see figs. 8 A-E: after Engler 1930). Continuing upwards in the tree in fig. 4 the next branch represents the small monotypic genus *Tribeles*, with its only species *Tribeles australis* growing at high altitudes in southern South America (see figs. 9 A-J: original).

TABLE 3a. Showing synapomorphies for nodes, node numbers and state changes supporting nodes in the tree shown in Fig. 4. Charactes marked with * have CI > 0.7, those with ** have CI = 1.0. Only morphological characters listed.

Node 1	
11	1 → 0
24	1 → 3
39	0 → 1
55	2 → 3
94	1 → 0
104	0 → 1
Node 2	
17	1 → 0
31	1 → 0
59	0 → 1
97	0 → 3
103	1 → 6
Node 3	
12	0 → 2
52	0 → 2
72	0 → 1
74	0 → 5
78	1 → 2
Node 4	
27	0 → 1
34	0 → 1
52	0 → 1
59	0 → 3
61	0 → 1
65	0 → 1
Node 5	
15	2 → 1
20	1 → 0
33	1 → 2
99	1 → 0
Node 6	
7	1 → 2
58	0 → 2
71	1 → 0
Node 7	
11	0 → 1
25	0 → 2
60	1 → 3
Node 8	
32	0 → 1
35	2 → 1
52	1 → 0
56	0 → 2
102	0 → 1**
Node 9	
15	1 → 2
16	1 → 0
17	1 → 3
20	0 → 1
58	2 → 0
63	0 → 1
92	3 → 2
96	1 → 0
Node 10	
19	0 → 1**
24	3 → 0
55	3 → 2
59	3 → 0
76	1 → 0
87	1 → 0
90	0 → 1
95	0 → 1
103	1 → 5
Node 11	
14	0 → 2**
26	1 → 0
29	0 → 1
58	2 → 0
66	0 → 1
71	0 → 1
72	0 → 1
100	0 → 1
Node 12	
9	0 → 1
70	2 → 1
75	2 → 0
Node 13	
10	0 → 2
17	1 → 3
23	1 → 0
29	1 → 2
34	1 → 0
39	1 → 0
59	0 → 2
60	3 → 6
84	1 → 0
Node 14	
16	1 → 0
17	1 → 0
29	0 → 1
67	1 → 0
92	3 → 0
105	0 → 1
Node 15	
3	0 → 2
28	1 → 0
52	1 → 2
60	1 → 0
79	1 → 0
91	0 → 1**
Node 16	
9	0 → 1
23	1 → 2
44	1 → 0
53	1 → 0
55	3 → 1
58	0 → 2
59	3 → 0
60	0 → 5
81	0 → 2
Node 17	
4	2 → 0
5	0 → 1
11	0 → 1
15	2 → 0
24	3 → 2
40	1 → 0
42	0 → 1
50	0 → 1
65	1 → 0
87	1 → 3
95	0 → 1
103	1 → 3
Node 18	
23	1 → 0
25	0 → 2
29	1 → 0
35	2 → 1
60	1 → 3
63	0 → 2
70	2 → 1
72	0 → 1
76	1 → 0
78	1 → 0
89	0 → 1
92	0 → 3
96	1 → 0
109	0 → 1**
Node 19	
1	0 → 1
10	0 → 2
22	0 → 3*
24	2 → 0
26	1 → 0
36	3 → 2
41	2 → 1
47	5 → 4
53	1 → 0
55	3 → 4
63	2 → 3
83	0 → 1**
90	0 → 1
95	1 → 0
Node 20	
3	0 → 2
4	0 → 1
6	2 → 1
11	1 → 2
18	2 → 0
20	1 → 0
31	1 → 0
34	1 → 0
35	1 → 2
44	1 → 2
45	0 → 1
52	1 → 0
59	3 → 1
61	1 → 0
67	0 → 1
89	1 → 0
92	3 → 0
96	0 → 1
Node 21	
21	0 → 1
27	1 → 0
37	0 → 1
42	1 → 2
43	0 → 1
46	0 → 1
50	1 → 2
59	3 → 1
69	0 → 1
93	0 → 1
99	1 → 0
104	1 → 0
106	0 → 1**
108	0 → 3**
Node 22	
4	0 → 2
15	0 → 1
55	3 → 2
59	1 → 2
67	0 → 1
84	1 → 0
103	3 → 1
Node 23	
9	0 → 1
17	0 → 1
33	1 → 2
44	1 → 3
52	1 → 2
58	0 → 2
63	0 → 1
81	0 → 1

TABLE 3A. CONTINUED. Showing synapomorphies for nodes, node numbers and state changes supporting nodes in the tree shown in Fig. 4. Charactes marked with * have CI > 0.7, those with ** have CI = 1.0. Only morphological characters listed.

Node 24	
11	1 → 0
20	1 → 0
24	2 → 1
29	1 → 2
60	1 → 2
107	0 → 1**
Node 25	
45	0 → 1
61	1 → 0
62	2 → 0
76	1 → 0
Node 26	
28	1 → 0
56	0 → 1
60	2 → 3
80	0 → 1
Node 27	
3	0 → 1
15	0 → 2
17	1 → 0
26	1 → 0
55	3 → 4
81	1 → 0
Node 28	
49	0 → 1
92	0 → 1
Node 29	
24	2 → 3
55	3 → 2
61	1 → 0
62	2 → 0
75	2 → 1
77	0 → 1
79	1 → 0
Node 30	
30	0 → 1
47	5 → 4
48	0 → 2
56	0 → 2
60	1 → 4
Node 31	
15	0 → 2
108	3 → 1**
Node 32	
38	0 → 3
Node 33	
23	1 → 0
76	1 → 0
103	3 → 2
Node 34	
11	1 → 0
43	1 → 2
94	0 → 2
Node 35	
1	0 → 1
3	0 → 2
4	0 → 1
6	2 → 1
9	1 → 0
25	0 → 2
30	1 → 2
31	1 → 0
36	3 → 2
49	1 → 0
52	2 → 0
57	0 → 1
67	0 → 2
80	0 → 1
90	0 → 1
93	1 → 0
99	0 → 1
100	0 → 1
101	0 → 1
Node 36	
7	1 → 2
12	0 → 1
13	0 → 1
28	1 → 2
29	1 → 0
43	1 → 2
69	1 → 2
70	2 → 1
79	1 → 0
81	1 → 0
84	1 → 0
87	3 → 0
95	1 → 0
103	3 → 7
Node 37	
5	1 → 2
17	1 → 2
22	0 → 2*
51	0 → 1**
72	0 → 2
74	0 → 3
75	2 → 1
Node 38	
15	0 → 1
22	0 → 1*
24	2 → 0
35	2 → 1
48	2 → 0
73	0 → 2
75	2 → 0
79	1 → 2
82	0 → 1**
86	0 → 1**
92	1 → 0
104	0 → 1
Node 39	
25	2 → 0
29	1 → 3
38	0 → 2
41	2 → 1
69	1 → 0
84	1 → 2
87	3 → 2
98	0 → 1**
108	3 → 2**
Node 40	
36	2 → 4
43	1 → 2
73	2 → 1
75	0 → 1
Node 41	
37	1 → 2
74	0 → 2
Node 42	
24	0 → 1
41	1 → 2
75	1 → 0
76	1 → 0
Node 43	
24	0 → 1
41	1 → 2
75	1 → 0
76	1 → 0
Node 44	
18	2 → 1
36	2 → 3
38	0 → 3
57	1 → 2
79	2 → 1
80	1 → 0
81	1 → 2
103	3 → 2
Node 45	
Not supported by morphological characters	
Node 46	
6	1 → 2
18	1 → 0
38	3 → 1
47	4 → 3
57	2 → 0
59	1 → 3
81	2 → 1
95	1 → 0
Node 47	
11	1 → 0
57	0 → 1
87	3 → 2
Node 48	
43	1 → 2
79	1 → 2
Node 49	
2	1 → 0
3	2 → 0
4	1 → 3
28	1 → 2
38	1 → 0
57	1 → 2
60	4 → 5
Node 50	
36	3 → 4
Node 51	
24	0 → 1
73	2 → 0
87	2 → 3
Node 52	
1	1 → 0
52	0 → 1
Node 53	
5	1 → 0
6	2 → 0
13	0 → 1
17	1 → 0
54	1 → 0**
Node 54	
32	0 → 2
36	4 → 0
38	1 → 0
41	2 → 0

TABLE 3b. Showing autapomorphies for taxa, character numbers and state changes along terminal branches in the tree shown in Fig. 4. Only morphological characters are listed.

Escallonia	7	1 → 2
	37	0 → 13
	62	2 → 1
Eremosyne	1	0 → 1
	2	1 → 0
	4	2 → 3
	13	0 → 1
	18	2 → 0
	24	1 → 0
	60	1 → 0
	61	0 → 1
	72	0 → 1
	74	0 → 5
	76	1 → 0
	78	1 → 0
	79	1 → 2
Anopterus	33	1 → 0
	36	3 → 4
	37	0 → 1
	39	0 → 1
	41	2 → 4
	44	1 → 0
	58	0 → 2
	61	0 → 1
	62	2 → 0
Forgesia	15	2 → 1
	29	0 → 2
	49	0 → 1
	59	0 → 1
Quintinia	64	0 → 1
	77	0 → 1
	78	1 → 2
Polyosma	30	0 → 1
	36	3 → 2
	37	0 → 13
	39	1 → 0
	41	2 → 1
	42	0 → 2
	47	5 → 4
	49	0 → 1
	55	3 → 1
	59	3 → 1
	60	1 → 2
	62	2 → 1
	74	0 → 5
	75	2 → 1
	78	1 → 2
Tribeles	4	2 → 1
	33	2 → 0
	61	1 → 0
	78	1 → 3
Griselinia	9	0 → 1
	28	1 → 0
	103	1 → 3
Aralidium	10	0 → 2
	11	1 → 2
	14	0 → 1
	23	1 → 0
	26	1 → 0
	40	1 → 0
	71	0 → 1
	80	0 → 1
Toricellia	13	0 → 1
	24	3 → 0
	29	0 → 2
	35	1 → 2
	39	1 → 0
	52	0 → 1
	57	0 → 2
	62	2 → 0
	103	1 → 6
Melanophylla	52	1 → 2
	74	0 → 5
Pittosporum	7	2 → 1
	16	1 → 0
	20	0 → 1
	33	2 → 0
	44	1 → 0
	50	0 → 2
	60	3 → 0
	65	1 → 0
	66	1 → 0
	67	1 → 0
	76	0 → 1
	94	0 → 1
	97	0 → 3
	99	0 → 1
	101	0 → 1
	103	5 → 0
Aralia	8	0 → 123
	35	2 → 1
	57	0 → 2
	61	1 → 0
	63	0 → 1
	71	1 → 0
	81	0 → 1
	84	1 → 3
Steganotaenia	24	0 → 1
	65	1 → 0
Apium	1	0 → 1
	3	0 → 2
	4	2 → 1
	6	2 → 1
	30	0 → 1
	67	1 → 0
Audouinia	7	1 → 0
	13	0 → 1
	18	2 → 1
	29	1 → 2
	30	0 → 1
	56	0 → 2
	57	0 → 2
	63	0 → 1
	75	2 → 0
	77	0 → 1
	87	1 → 0
	103	1 → 5
Berzelia	74	0 → 4
Brunia	48	0 → 1
Viburnum	17	0 → 1
	24	2 → 3
	56	0 → 3
	57	0 → 1
	74	0 → 4
	87	3 → 1
	94	0 → 2
	107	0 → 1
	105	1 → 0
Sambucus	9	0 → 1
	17	0 → 2
	46	0 → 1
	97	0 → 2
Sinadoxa	43	0 → 1
	59	1 → 0
Columellia	29	1 → 0
	37	1 → 0
	46	1 → 0
	53	1 → 0
	87	3 → 0
Desfontainia	8	0 → 1
	12	0 → 1
	23	1 → 0
	24	2 → 3
	27	0 → 1
	28	1 → 0
	31	1 → 0
	33	1 → 0
	55	2 → 5
	60	1 → 2
	61	1 → 0
	69	1 → 0
	71	1 → 0
	77	0 → 1
	80	0 → 1
Leycesteria	20	0 → 1
	55	3 → 45
Lonicera	15	0 → 2
	92	0 → 3
	97	0 → 12

TABLE 3b. CONTINUED. Showing autapomorphies for taxa, character numbers and state changes along terminal branches in the tree shown in Fig. 4.

Heptacodium	13	0 → 1
	23	1 → 2
	30	0 → 1
	52	2 → 0
	56	1 → 2
	57	0 → 2
	75	2 → 1
	77	0 → 1
Symphoricarpos	56	1 → 4
Triosteum	1	0 → 1
	4	0 → 3
	7	1 → 0
	21	1 → 0
	28	0 → 1
	43	1 → 2
	49	0 → 1
Diervilla	3	0 → 1
	23	1 → 0
	97	0 → 2
Weigela	20	1 → 0
	92	1 → 3
	94	0 → 2
Abelia	28	1 → 0
	97	0 → 2
Zabelia	24	2 → 01
	79	1 → 0
	81	1 → 0
Linnaea	3	0 → 1
	4	0 → 2
	17	1 → 0
	28	1 → 0
	49	1 → 0
Dipelta	55	3 → 4
	92	1 → 3
	97	0 → 3
Kolkwitzia	20	1 → 0
	57	0 → 12
	80	0 → 1
Acanthocalyx	20	1 → 0
Morina	37	1 → 2
	81	0 → 2
	97	0 → 2
Succisa s.lat.	3	2 → 1
	4	1 → 3
	103	3 → 2
Knautia	49	0 → 1
	59	1 → 23
	60	4 → 5
	103	3 → 4
Dipsacus s.lat.	17	1 → 2
	60	4 → 6
	73	1 → 2
	79	2 → 1
	96	1 → 0
Pterocephalus	38	2 → 1
	72	0 → 1
Scabiosa s.lat.	36	4 → 3
	37	2 → 1
	59	1 → 2
Triplostegia	30	0 → 3
	73	2 → 0
	76	1 → 0
	85	0 → 1
Patrinia	30	0 → 1
Nardostachys	7	1 → 2
	13	0 → 1
	35	1 → 2
	37	0 → 1
	103	2 → 3
Valeriana officinalis	3	2 → 1
	10	0 → 2
	24	0 → 123
	73	2 → 0
	103	2 → 1
Centranthus	47	3 → 1
	94	0 → 2
Plectritis	48	0 → 1
Valeriana clematitis	32	0 → 2
Valerianella	35	1 → 2
	46	1 → 0
	81	1 → 0
	103	2 → 3
Valeriana dioica	6	2 → 1
	32	0 → 1
	59	3 → 2
Valeriana hirtella	3	2 → 0
	4	1 → 2
	5	1 → 0
	28	1 → 0
Stangea	13	1 → 2
	30	0 → 1
	59	3 → 2
	81	1 → 3
Belonanthus	17	0 → 2
	28	1 → 0
	36	0 → 1
	37	0 → 1
	52	0 → 1
	58	2 → 1
	73	2 → 0
Phyllactis	21	1 → 0
	23	1 → 2
	35	1 → 0
	44	3 → 0
	60	4 → 5

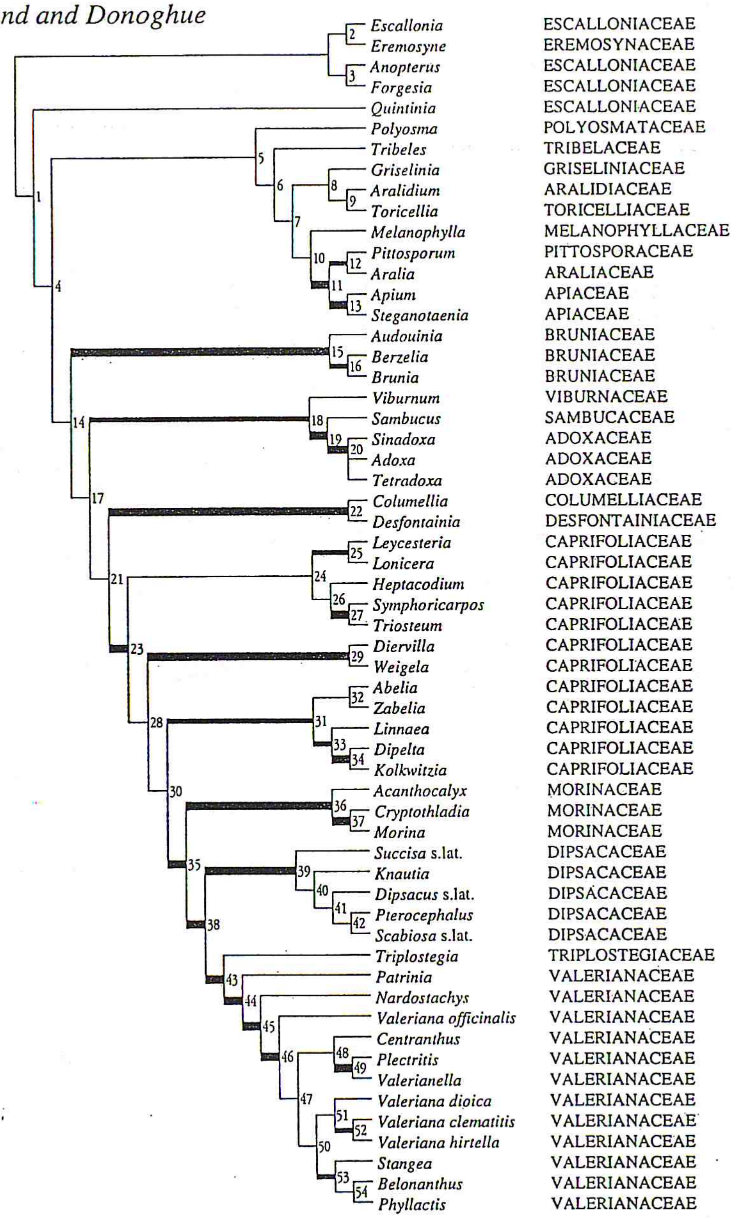


Figure. 4. One of the most parsimonious trees from the combined analysis. Node numbers corresponds to tab. 3a (character state changes along internal branches), tab. 3b (character state changes along terminal branches), and tab. 4 (supportive indices summarized).

TABLE 4. Supportive indices listed according to node numbers in fig. 4.

bl = branch length, total
mor/mol = indicating relative contribution to branch length from morphological and molecular datasets respectively
bst = bootstrap values from 10000 replicates with "quick-swap"
jac = jackknife fractions from 10000 replicates with "quick-swap"
Bs = Bremer support values, number of extra steps to lose a branch

Node nr.	bl	mor/mol	bst	jac	Bs
Node **01**	11	4 - 7	--	--	3
Node **02**	12	7 - 5	--	--	0
Node **03**	23	4 - 19	--	--	0
Node **04**	12	7 - 5	--	--	2
Node **05**	7	4 - 3	--	--	3
Node **06**	14	3 - 11	--	--	3
Node **07**	3	3 - 0	--	--	4
Node **08**	10	5 - 5	--	--	4
Node **09**	11	8 - 3	--	--	5
Node **10**	12	11 - 1	--	--	5
Node **11**	18	8 - 10	72	82	5
Node **12**	8	3 - 5	53	54	5
Node **13**	13	9 - 4	97	99	9
Node **14**	9	6 - 3	--	--	1
Node **15**	30	6 - 24	62	72	3
Node **16**	9	9 - 0	100	100	7
Node **17**	19	12 - 7	--	--	1
Node **18**	23	14 - 9	57	60	7
Node **19**	23	15 - 8	68	72	5
Node **20**	35	18 - 17	90	90	10
Node **21**	17	14 - 3	--	--	1
Node **22**	25	7 - 18	76	86	5
Node **23**	21	8 - 13	64	68	9
Node **24**	19	6 - 13	--	--	4
Node **25**	25	4 - 21	52	53	4
Node **26**	20	4 - 16	--	--	3
Node **27**	6	6 - 0	66	69	5
Node **28**	7	2 - 5	--	--	4
Node **29**	16	7 - 9	80	86	6
Node **30**	7	5 - 2	--	--	4
Node **31**	2	2 - 0	--	54	4
Node **32**	1	1 - 0	--	--	4
Node **33**	3	3 - 0	--	54	6
Node **34**	3	3 - 0	66	72	6
Node **35**	19	19 - 0	59	66	10
Node **36**	25	14 - 11	99	99	13
Node **37**	7	7 - 0	100	99	7
Node **38**	17	13 - 4	62	69	6
Node **39**	17	9 - 8	92	94	6
Node **40**	4	4 - 0	--	--	5
Node **41**	4	2 - 2	--	--	5
Node **42**	16	4 - 12	--	--	5
Node **43**	15	12 - 3	80	85	6
Node **44**	16	8 - 8	79	84	6
Node **45**	13	0 - 13	63	70	6
Node **46**	22	8 - 14	67	72	4
Node **47**	12	3 - 9	--	--	2
Node **48**	33	2 - 31	--	--	1
Node **49**	7	7 - 0	73	78	3
Node **50**	5	1 - 4	--	--	3
Node **51**	23	3 - 20	--	--	6
Node **52**	2	2 - 0	--	59	2
Node **53**	12	5 - 7	--	56	7
Node **54**	4	4 - 0	--	--	1

Tribeles was originally included in the Saxifragaceae by Engler (1930), but its aberrant morphology as a montane cushion-plant with minute flowers and triloculate capsules have promoted suggestions of its transfer to different systematic positions. In various systems *Tribeles* has usually been separated at tribal, subfamilial or even familial level, in the Saxifragaceae sensu Engler (1930), Grossulariaceae sensu Cronquist (1988, together with *Escallonia*, *Pittosporum*, *Argophyllum*, and others), Escalloniaceae (e.g. Melchior 1964), or Tribelaceae (Takhtajan 1987).

No molecular information is at present available for *Tribeles*, but a detailed study of the genus, including molecular sequencing, is in progress (A. Backlund, unpublished data). Notable is that both Agababian (1964) and Hideux and Ferguson (1976) suggested some palynological resemblance between *Tribeles*, *Quintinia* and to some extent *Polyosma*, an interpretation compatible with the present hypothesis of their relationships.

The large clade including Apiales s.str. and a number of additional taxa in this analysis corresponds closer to its traditional circumscription than in previously reported results from analyses of molecular data (Backlund et al 1997). The Adoxaceae s.lat., by *rbc*L-data indicated as a part of the Apiales association, is now repositioned in the Dipsacales.

In the Apiales we find indications of two lineages. One consists of undisputed members of this order such as *Apium*, *Conium*, and *Aralia*. The family Pittosporaceae, represented in the analysis by *Pittosporum*, clearly occupies a place close to the Apiaceae. The close relationship between Apiaceae and Pittosporaceae is shown repeatedly in studies of molecular data (e.g., Plunkett et al. 1992, 1996) as well as anatomy (Tieghem 1885; Rodríguez 1971) and secondary chemistry (e.g. Hegnauer 1964; 1969, and references therein, Swain 1975). Results in this portion of the tree are partly incongruent with those obtained from a much wider sampling in the Apiaceae and related taxa by Plunkett et al. (1996). Presumably due to scarce sampling in the present study, our results are partly incongruent with those of Plunkett et al. We therefore argue for caution regarding the relationships in this part of the tree and refer to the previously mentioned study. The core-group of Apiales is successively followed by *Melanophylla* (see fig. 10 A: after Wangerin, 1910, B: original), albeit with significantly lower supportive indices. *Melanophylla* was previously placed in the Cornaceae sensu Wangerin (1910)

The other lineage consists of the genera *Griselinia*, *Aralidium* and *Toricellia*, largely in concordance with the studies by Xiang and Soltis (1995) and Backlund et al. (1997) on *rbc*L sequence data. These taxa were earlier also believed to be parts of the Cornaceae (Wangerin 1910), or systematically positioned close to that family (Dahlgren 1975; 1980; 1989). Some earlier studies have indicated a low degree of similarity between Griselinia and Cornaceae s.str. (e.g. Brunner 1978), but without suggesting an alternative systematic position.

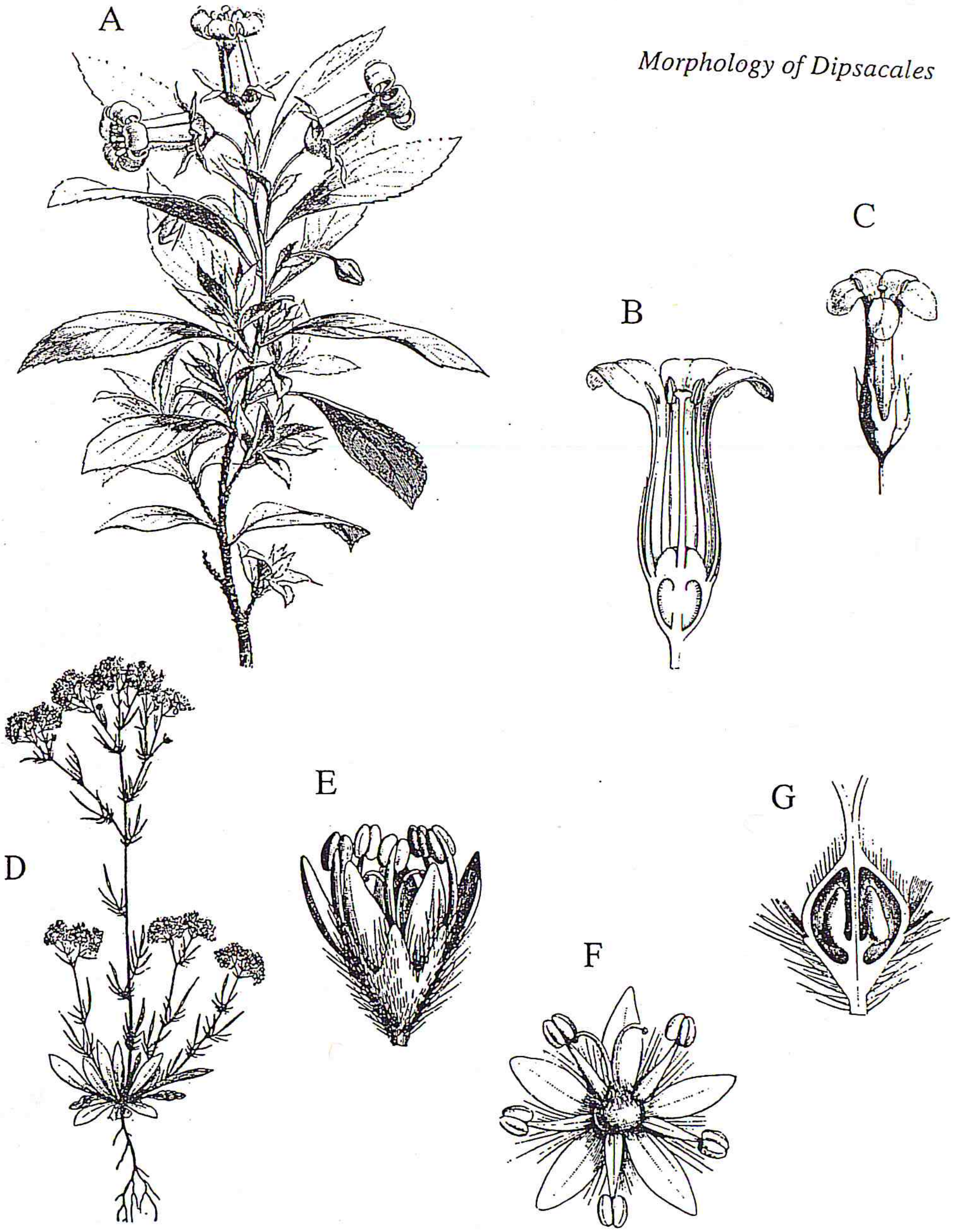


Figure 5. A-C. *Escallonia rubra*, from Baillon (1872). A - habitus, flowering branch, B - single flower, longitudinal section, C - single flower. D-G. *Eremosyne pectinata*, from Engler (1930). D - habitus, E - single flower in horizontal projection, F - d:o in vertical projection, G - gynoecium in longitudinal section.

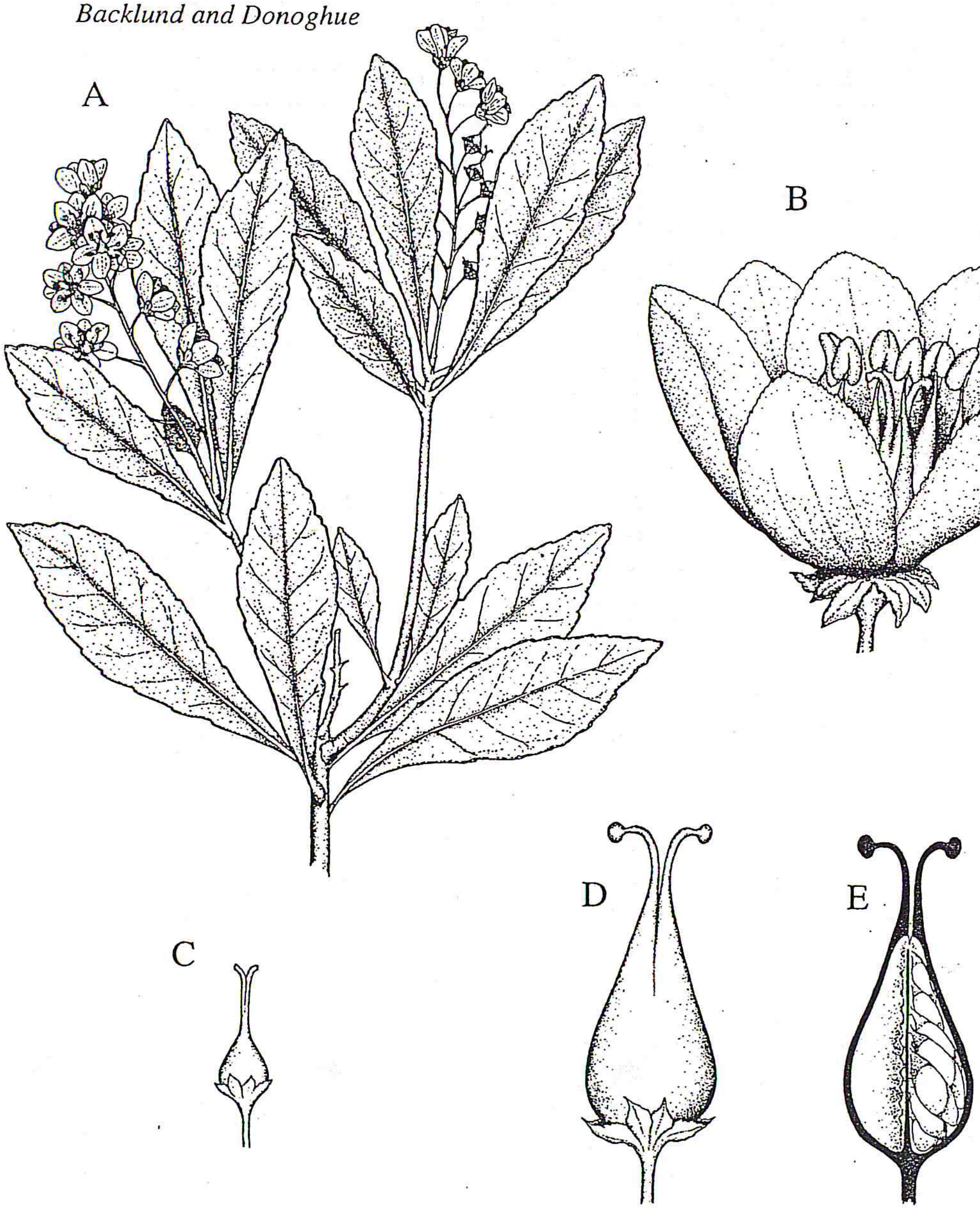


Figure 6. A-E. *Anopterus glandulosus*, original drawing. A - habitus, flowering branch, B - single flower, C - gynoecium at anthesis, D - ripe fruit before dehiscence, E - ripe fruit before dehiscence, longitudinal section.

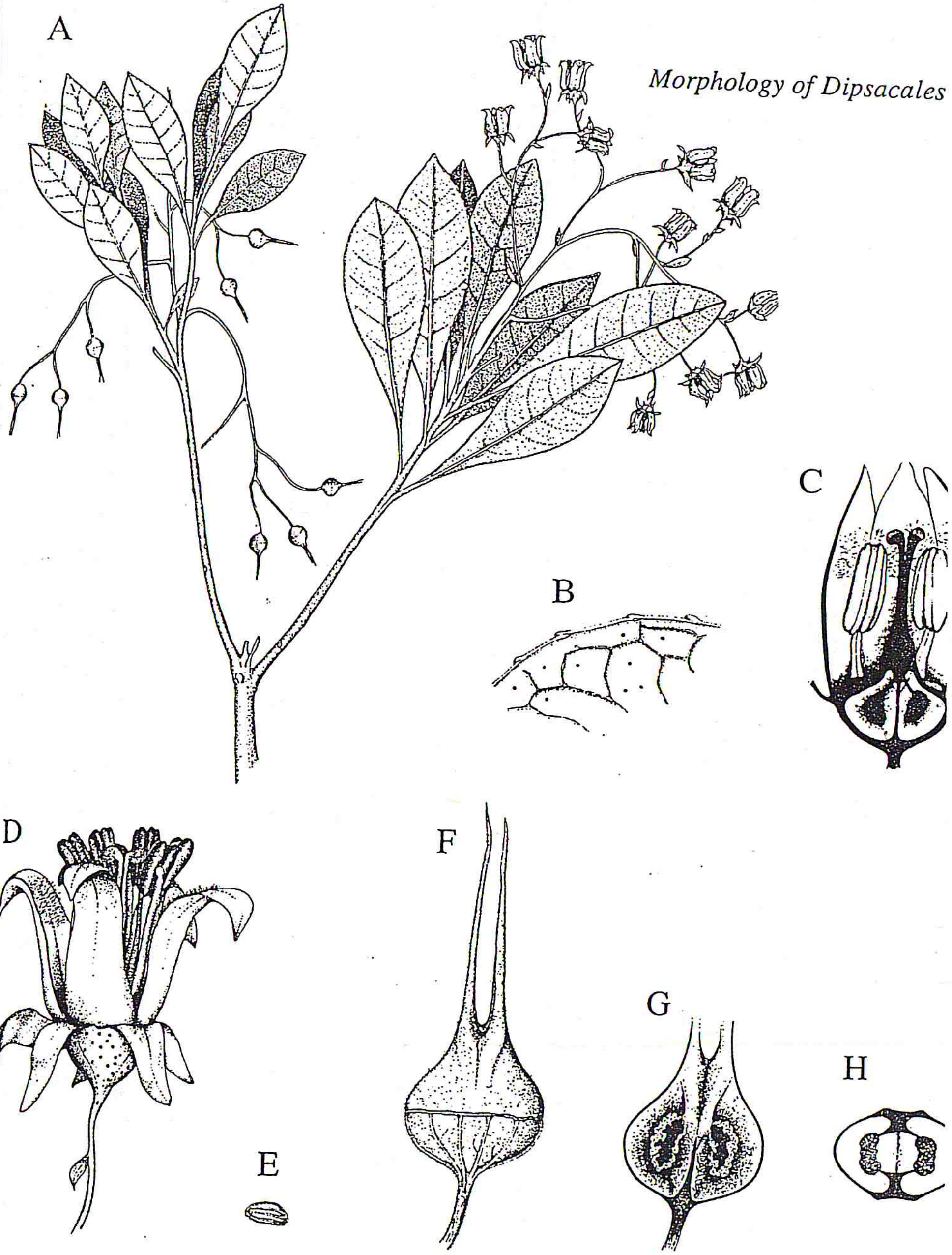


Figure 7. A-H. *Forgesia borbonica*, original drawing. A - habitus, flowering branch, B - leaf margin, C - bud, longitudinal section, D - single flower, E - seed F - ripe fruit, G - gynoecium, longitudinal section, H - gynoecium, cross section.

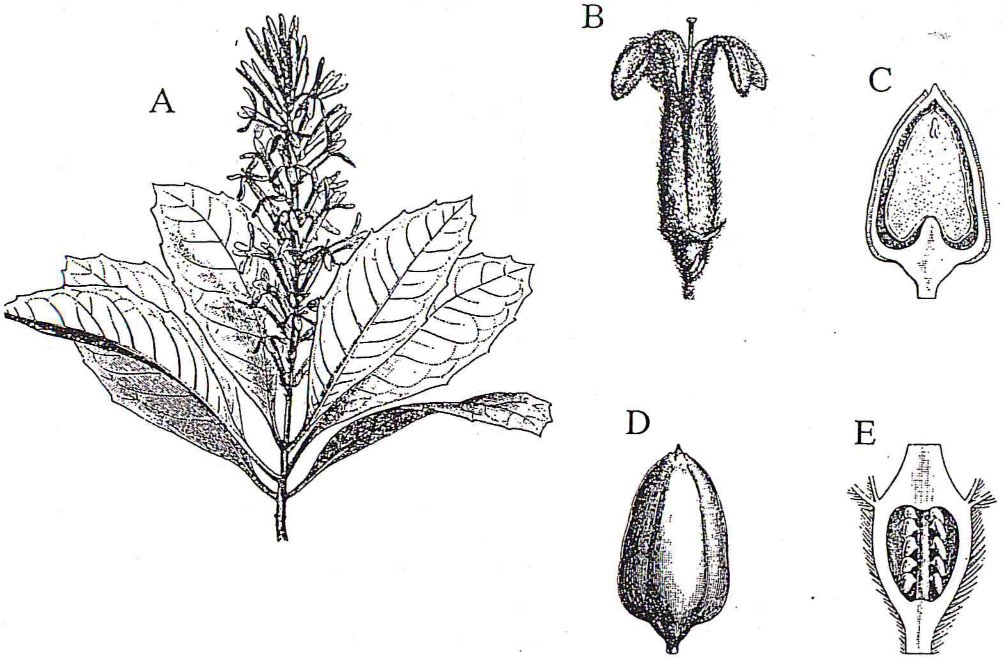


Figure 8. A-E. *Polyosma ilicifolia*, after Engler (1930). A - habitus, flowering branch, B - single flower, C - gynoecium, longitudinal section, D - ripe fruit, E - ripe fruit, longitudinal section.

The Dipsacales Association. The basalmost group of the Dipsacales, and sistergroup to the rest of the order, is the exclusively South African family Bruniaceae, represented in the analysis by the genera *Audouinia*, *Berzelia* and *Brunia*. The monophyly of this family is strongly supported both by morphology (Saxton 1910; Niedenzu and Harms 1930; Pillans 1947; Carlquist 1991) and molecular data. Somewhat more weakly so is the placement in the Asteridae s.str., as well as in the Dipsacales-Apiales complex. Neither the exact position in the complex is well established and even though the results from the parsimony analysis are unambigous in that respect, the supportive indices for the suggested placement are low.

Further upwards the tree we find a group corresponding to Adoxaceae s.lat. (Donoghue 1985, Donoghue et al. 1992, Judd et al. 1994) including five taxa.

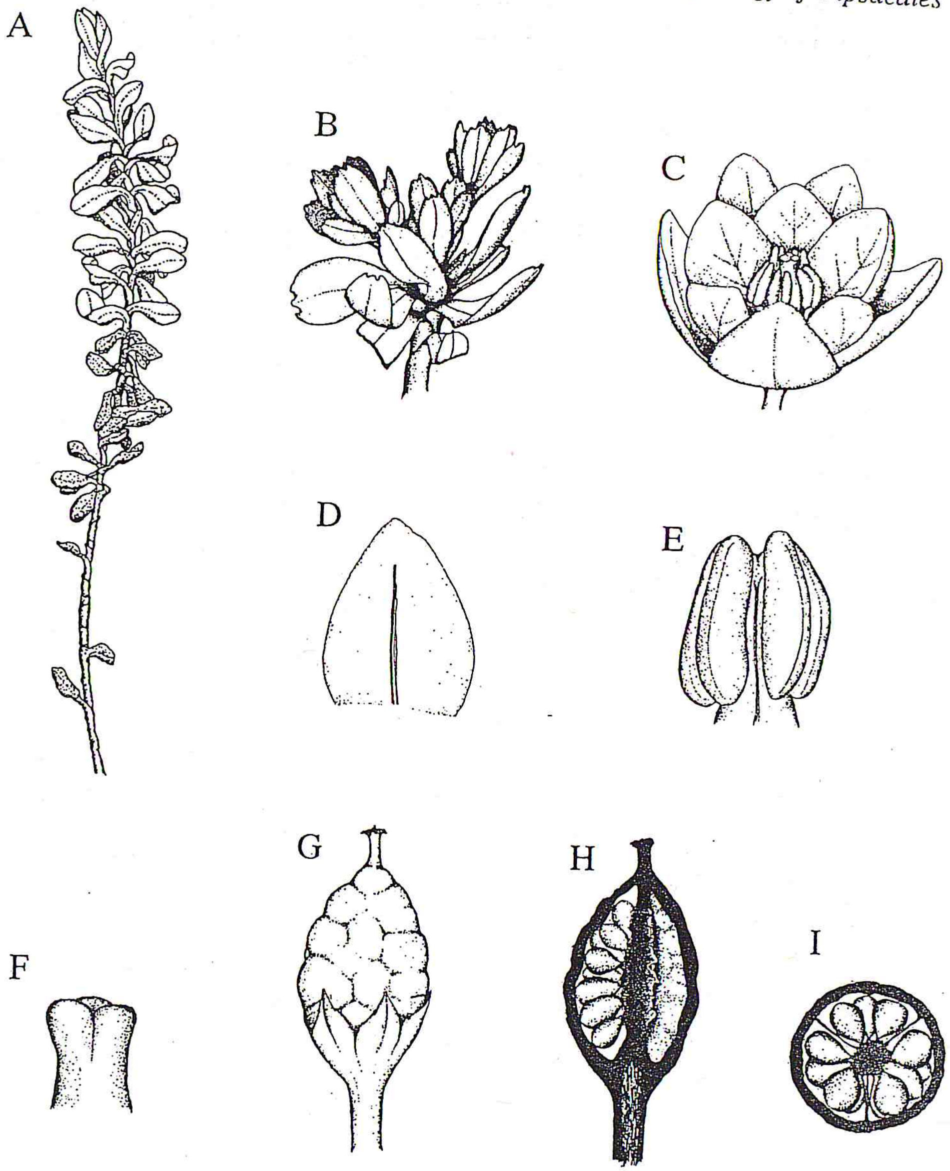


Figure 9. A-J. *Tribeles australis*, original drawing. A - habitus, single shoot, B - shoot apex with flower buds, C - single flower, D - petal, E - anther, F - style, G - ripe fruit, H - ripe fruit in longitudinal section, I - ripe fruit in cross section.

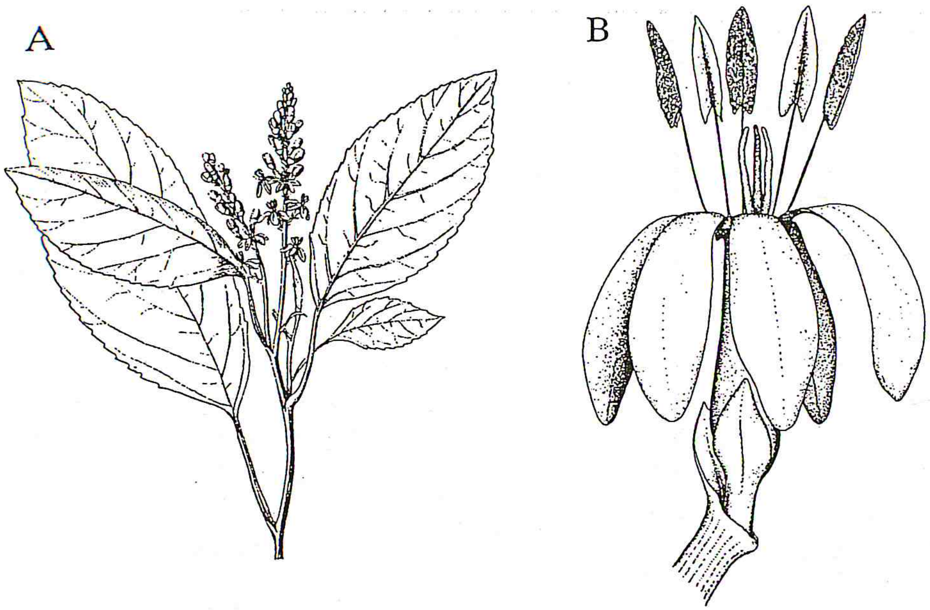


Figure 10. A-B. *Melanophylla, A - M. crenata*, after Wangerin (1910), habitus with flowering branch. B - *M. alnifolia*, original, single flower.

The controversial position in the Apiales association of this entire family, earlier indicated by *rbc*L-data but with low supportive indices (**bst** < 50 %, **jac** < 50 %, **bl** 2, **Bs** 1 in Backlund et al. 1997) again becomes reversed. The support for this traditional position of the Adoxaceae as sister group to the Dipsacales is still weak, with trees allowing for inclusion in the Apiales being six steps longer. The recent karyosystematic studies by Benko-Iseppon (1992) have shown a strong difference in karyomorphology between the traditional Caprifoliaceae s.str. on one hand and *Viburnum* and *Sambucus* on the other, strongly supporting the exclusion of the latter from the vicinity of the Caprifoliaceae. Information from anatomical data (Metcalfe and Chalk 1950), secondary chemistry (Hegnauer 1964; 1969), and serological investigations (Hillebrand and Fairbrothers 1970) also have been suggestive of a more remote position of these taxa compared to the Caprifoliaceae.

Between Adoxaceae s.lat. and the core of the order Dipsacales, a small but stable clade containing the two South American genera *Desfontainia* and *Columellia* attaches. Earlier systematic positions of *Columellia* have included a wide variety of families from different parts of the system. Combining morphological information with the *rbc*L nucleotide sequence for *Columellia* supports the placement of *Columellia* as sister group to *Desfontainia*, in a position within Asteridae s.str. The genus *Desfontainia* was earlier considered to be the single member of the tribe Desfontainieae of the Loganiaceae, or of the monogeneric family Desfontainiaceae. Several morphological character state changes support the *Columellia-Desfontainia* relationship, including the evergreen habit, conduplicate vernation, two carpels and bilobate stigmas, Solanad embryogeny and the chromosome base number $x=7$. An additional 18 molecular synapomorphies gives this branch moderately high supportive indices: branch length (**bl**) 25, bootstrap (**bst**) 76%, jackknife (**jac**) 86%, Bremer support (**Bs**) 5.

The core of the order Dipsacales traditionally includes the four families Caprifoliaceae, Morinaceae, Dipsacaceae, and Valerianaceae. The branch leading to the core of the order is well supported by the combined morphological and molecular data (**bl** 21 [8 morph, 13 molec], **bst** 64 %, **jac** 68 %, **Bs** 9), as well as by each dataset separately. Within this core-group it is evident that some taxonomic rearrangements will be necessary, at least partly opposing traditional views.

The family Caprifoliaceae in its traditional sense (including *Viburnum* and *Sambucus*) is obviously both poly- and paraphyletic, a view earlier advocated by Donoghue et al. (1992) and Judd et al. (1994). These results are concordant in all retrieved trees, both from the combined and the morphological datasets. The ”Caprifoliaceae s.str” are by the available data fragmented in three entities, all of which would have to be assigned the rank of family. The composition of these three entities and their relations to each other are still somewhat unstable, justifying the use of the informal name caprifolioids (analogous to escallonioids), and at present judged as not providing sufficient ground for a formal erection of new families. Preliminary analyses of additional *rbc*L and *ndh*F sequences (Olmstead and Donoghue, Jansen and Kim, and Roels and Pyck, respectively, all unpublished data) may supply adequate support for a less tentative solution, however.

Above the caprifolioids, we encounter a clade consisting of the three genera *Acanthocalyx*, *Cryptothladia* and *Morina*, forming the Morinaceae. This small family, distributed from continental Southeast Asia to eastern Europe, has traditionally been placed as a sister group to – or occasionally even part of – the Dipsacaceae (e.g. Caputo and Cozzolino 1994; Backlund and Bremer 1996, and references therein). The entire issue have more or less been founded on one single feature, namely the presence in both Morinaceae and Dipsacaceae of a so called epicalyx or 'Aussenkelch'. A wide variety of detailed studies from several different fields (e.g. Vinokurova 1959, Vijayaraghavan and Sarveshwari 1968, Verlaque 1977, Kamelina 1980 1983, Blackmore and Cannon 1983, Cannon and Cannon 1984, Benko-Iseppon 1992) have unanimously rejected the inclusion of Morinaceae under Dipsacaceae, and instead pointed to similarities with parts of the Caprifoliaceae. The herein obtained position basal to both Dipsacaceae and Valerianaceae and close especially to the Linnaeae-clade of the caprifolioids is congruent with earlier presented results from analyses of molecular data (Backlund et al. 1997).

Continuing from the Morinaceae remains only the two families Dipsacaceae and Valerianaceae, the latter here taken to include also the genus *Triplostegia*. The close relation between these two families is widely accepted, but the placement of *Triplostegia* has posed an intricate problem. A thorough discussion concerning the classification and affinities of *Triplostegia* is given in Backlund and Bremer (1996) and additional details on its palynology in Backlund and Nilsson (1996). The indication from molecular data of a closer relation between *Triplostegia* and the family Valerianaceae is further supported by the addition of morphological evidence. This is significant as most arguments for a connection to the Dipsacaceae have originated in the so called "double epicalyx" of *Triplostegia*. Several recent studies (e.g. Hofmann and Göttmann 1990, Roels and Smets 1996) have indicated that the epicalices found in Morinaceae, Dipsacaceae and *Triplostegia* all result from the fusion of bracteoles and supernumerary sterile bracts of the inflorescence. Thus they are homologous to the bracteoles and bracts found in the inflorescences of Caprifoliaceae and Valerianaceae, and not necessarily constituting a unique and derived specific organ but instead a fusion of several well known and characterized parts.

The relationships found in the Dipsacaceae are consistent with the tribal delimitations suggested by Ehrendorfer (1964), and largely congruent with the suggested evolutionary pattern of fruits and chromosome numbers in the same study, as well as with preliminary results from studies in progress of morphology and the *atp*B-*rbc*L intergenic spacer (a-r-IGS; Veronika Mayer, personal communication). The extensive study by Caputo and Cozzolino (1994) based on a parsimony analysis of 45 morphological characters from 30 taxa in the Dipsacaceae and related families provides, however, a conflicting hypotesis. Apparently more complete with respect to the taxon sampling in the Dipsacaceae, the matrix presented by Caputo and Cozzolino nevertheless contain 61 states coded as unknown or "polymorphic". By addition of recently obtained information, these unknown states can to a large extent be completed. A subsequent recoding of the polymorphic states, for usage with an analytical tool handling polymorphic character states, in this case increases the number of equally parsimonious solutions (giving 42 equally parsimonious trees). Reinterpreting the homology of the epicalyx according to theories put forward by Roels and Smets (1996) further pronounces this tendency. The incongruence between the study by Caputo and Cozzolino (1994) and the present analysis, regarding the intrafamilial relationships of the Dipsacaceae, thereby decreases (as the obtained consensus tree gets more collapsed) but remains significant. The situation calls for a detailed, combined, molecular and morphological approach for elucidating the phylogeny of the Dipsacaceae. It should be noted, however, that even though the infrafamilial relations of the Dipsacaceae are less well supported in this study, the monophyly of the family and its position in relation to the Valerianaceae and Morinaceae is very strongly supported.

The relationships indicated in the Valerianaceae are congruent with previous results from the analysis of *rbc*L sequence data. The increased sampling has added some presumed members of the *Valerianella*-lineage, and further enabled an enhanced coding of the polymorphic genus *Valeriana*. Results consistently support the basal placement of the genus *Triplostegia* in the Valerianaceae, and the positions of the genera *Patrinia* and *Nardostachys* as parts of a basal grade. In combination with the recently demonstrated presence of valepotriates (cyclopenta-[c]-pyran derivatives) also in the genera *Triplostegia, Patrinia* and *Nardostachys* (Backlund and Moritz 1996) these results give no support to the traditionally circumscribed tribe Patrinieae of the Valerinaceae.

Instead these highly specific compounds should be understood as a synapomorphy for the entire Valerianaceae. In the branches above *Nardostachys* we encounter a fairly well supported node defining the old tribe Valerianeae, **bl** 22, **bst** 67%, **jac** 72%, **Bs** 4. This former tribe has, usually on the basis of pollen data, been subdivided in two major entities: the *Valeriana*-group and the *Valerianella*-group (Clarke and Jones 1977; Clarke 1978; Patel and Skvarla 1979).

The *Valeriana*-group would according to palynology include - apart from *Valeriana* itself - mainly the South American taxa of which *Stangea*, *Belonanthus* and *Phyllactis* are included in this study. In the *Valerianella*-group on the other hand, where *Valerianella*, *Centranthus* and *Plectritis* belongs, several of the genera have comparably large, showy flowers, though not *Valerianella* itself. The flowers are often strongly zygomorphic, and the pollen wall has prominently branched columellae.

The support in the analysis for these two groups is weak as indicated by the estimated indices, for the *Valeriana*-group: **bl** 5 (1 morph, 4 molec), **bst** and **jac** below 50%, **Bs** 3, and for the *Valerianella*-group **bl** 23 (2 morph, 21 molec), **bst** and **jac** below 50%, **Bs** 6. The circumscription of the genus *Valeriana* with reference especially to the South American taxa has become a controversial question. Several suggestions of lumping most of the South American genera into a large, widely circumscribed, genus *Valeriana* have been put forward (Larsen 1986; Eriksen 1989). In congruence with the previously presented results from the analysis of *rbc*L sequence data, the herein obtained results contradict such an approach. The frequently disputed genera *Stangea*, *Belonanthus* and *Phyllactis* form a monophyletic sister group to a few *Valeriana* species. The widespread *Valeriana officinalis* (the type species) occupies a position basal not only to these two groups but also to the *Valerianella*-group. Attempting to lump the South American taxa included in this analysis into the genus *Valeriana* would simultaneously demand the reduction of the genera *Centranthus*, *Plectritis* and *Valerianella* under *Valeriana*. This would not only create an unnecessary instability in the classification, but also a large heterogenous taxon. Considering, however, that the supportive indices for most nodes in this entire clade are comparably weak, strong recommendations on treatment of these genera are premature. Instead this calls for further investigation of the inter- and intrageneric relationships within the Valerianaceae.

Hypotheses of character evolution: flower morphology. The entire group studied, here referred to as the Dipsacales-Apiales complex, is morphologically heterogenous. In the basal clades all taxa are woody shrubs or small trees with alternate leaves and an apparently choripetalous corolla, sometimes connate at the base. Studies performed on members of Dipsacales, Apiales and Asterales all indicate that these groups are characterized by a corolla initiated by a ring-shaped primordium ("early sympetaly"). This is true also for apparently choripetalous members of e.g. Apiaceae and the subfamily Apioideae (Erbar 1988; 1991; Roels 1993; Erbar 1994; Roels and Smets 1995; 1996). The conclusion and most parsimonious explanation must be that the syndrome of "early sympetaly" has arisen already before the split of Asteridae s.str. into the Asterales and Dipsacales-Apiales clades. Consequently, the flowers of e.g. *Forgesia* could be technically regarded as sympetalous, albeit their mature petals are not united. This has, however, not yet been studied from an ontogenetic view.

Also more general trends in flower and inflorescence morphology encountered elsewhere in the angiosperms can be demonstrated. Examples are a shift in several lineages from monotelic over truncated monotelic to polytelic inflorescences (e.g. Weberling 1961; 1965; 1982 1983; 1992), from a few large flowers to numerous small, and from actinomorphic to zygomorphic flowers. The reduction in floral parts is prominent in the Dipsacales. Number of stamens decrease in all lineages from five (occasionally up to ten) in the basal taxa, and down to one in some Valerianaceae. The trend is further expressed by a decrease in carpel number, carpel fertility and number of ovules from two or three in the basalmost taxa of the Dipsacales-Apiales complex to one fertile carpel with a single pendulous ovule in Dipsacaceae and Valerianaceae.

Secondary Chemistry. Apart from the similarities in flower morphology, shared traits of the entire Dipsacales-Asterales complex are the possession of a wide variety of sophisticated chemical compounds. Notable in this context are the iridoids, seco-iridoids, sesquiterpenes and polyacetylenes. The biosynthesis and trends in modifications of iridoid compounds have been studied by Kaplan and Gottlieb (1982) and Rosendal Jensen (1992). Kaplan and Gottlieb suggested that iridoids become increasingly oxidated in more derived groups of plants. Comparing estimated oxidation values (OV) with averaged Sporne indices of groups delimited according to Dahlgren's system (Dahlgren 1980) they obtained a fair correlation. Using more recently hypothesized phylogenies based on cladistic analyses these figures match even better.

Palynology. Studies available in palynology (e.g. Blackmore and Cannon 1983; Clarke and Jones 1977; Clarke 1978; 1981; Clarke and Jones 1981; Hideux and Ferguson 1976; Patel and Skvarla 1979; Backlund and Nilsson 1997) evaluated in light of the proposed phylogenetic hypothesis are suggestive of trends in pollen evolution. All pollen grains in the Dipsacales-Apiales association are triaperturate, with the notable exception of some species of *Quintinia* (varying between three and five apertures) and *Abelia* (frequently tetraaperturate). In the more basal taxa the pollen grains are commonly semi-tectate, clearly so in Adoxaceae, changing into tectate pollen sometimes with microperforations in the caprifolioids and higher taxa. Parallel with the closure of the exine, echinae and microechinae become more common, eventually also verrucae in some Valerianacean taxa.

Systematic Conclusions. The phylogenetic hypotheses obtained from solely molecular (Backlund et al. 1997), morphological, and the combination of both types of data are are largely congruent. Furthermore, a significantly increased support especially at the familial level of several groups is noted. The major inconsistency from the obtained results is the position of the family Adoxaceae, which by pure molecular data was placed closer to the Apiales, albeit weakly supported. The current position in the basal portion of the Dipsacales but clearly separated from caprifolioids conforms to the suggestions put forward by e.g. Donoghue et al. (1992) and Donoghue and Judd (1994). The phylogeny of the caprifolioids indicates an arrangement with the former tribes Lonicereae and Triosteae forming one lineage and Linneae forming another. Between these attach the Diervilleae, weakly supported. It is evident that the caprifolioids neither on molecular nor on morphological grounds can be defended as a monophyletic entity, and the erection of at least one new family will be necessary. The positions of Morinaceae and *Triplostegia* are completely congruent in both molecular and morphological aspects, with Morinaceae as the sister group of the Dipsacaceae-Valerianaceae clade and with *Triplostegia* included in the Valerianaceae. Also the sister group relation between the genera *Desfontainia* and *Columellia*, suggested by molecular data and their position basal to the caprifolioids is confirmed. Following the reasonings by Backlund and Bremer (1996), these two taxa ought to be included in the same family to maximise information content in the system. Priority should in this case be given to Columelliaceae described in 1828, Desfontainiaceae was not conceived until 1841 (Reveal 1993, and references therein). We therefore consider the genus *Desfontainia* included in Columelliaceae, and consequently the family Desfontainiaceae becomes reduced.

Results from this study confirm earlier observations that a large number of Englerian (Engler 1930) Saxifragaceae apparently belong in all four major lineages of the Asteridae s.str as basal branches. (Doboghue et al. 1992; Olmstead et al. 1993; Xiang et al. 1993; Gustafsson et al. 1996; Xiang and Soltis 1995). At these positions taxa like *Helwingia*, *Phyllonoma*, *Quintinia*, *Escallonia*, *Anopterus* and *Polyosma* clearly are of prime importance for understanding the basal relationships of the Asteridae s.str, as well as the Dipsacales-Apiales complex.

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APPENDIX A.

Drawings of corollary vascular supplies in 33 taxa included in the analysis, and three additional. Taxa depicted are listed below, plate number indicated in parentheses. All drawings are original, in scale, and with scale-bar divisions in mm. Some drawings show only part of a corolla.

Adoxaceae s.lat (5) – *Adoxa moschatellina, Sambucus nigra, Viburnum sieboldii, Viburnum ferarai.*
Alseuosmiaceae (1) – *Alseuosmia quercifolia, Alseuosmia liniarifolia.*
Bruniaceae (1) – *Berzelia intermedia.*
Caprifoliaceae (2) – *Abelia tetrasepala, Dipelta yunnanensis, Kolkwitzia amabilis, Linnaea borealis, Zabelia integrifolia.*
(3) – *Diervilla lonicera, Heptacodium jasminoides, Leycesteria formosa, Lonicera pyrenaica, Symphoricarpos albus, Triosteum sinuatum.*
Columelliaceae (5) – *Desfontainia spinosa.*
Dipsacaceae (3) – *Dipsacus asper, Knautia arvensis, Pterocephalus lasiospermus, Scabiosa palaestinacum, Succisa pratensis.*
Morinaceae (5) – *Acanthocalyx nepalensis, Morina coulteriana.*
Pittosporaceae (1) – *Pittosporum crispulum.*
Valerianaceae (3) – *Centranthus ruber, Nardostachys jatamansii, Patrinia scabiosaefolia, Phyllactis rigida, Plectritis sp., Triplostegia glandulifera, Valeriana officinalis, Valerianella locusta.*

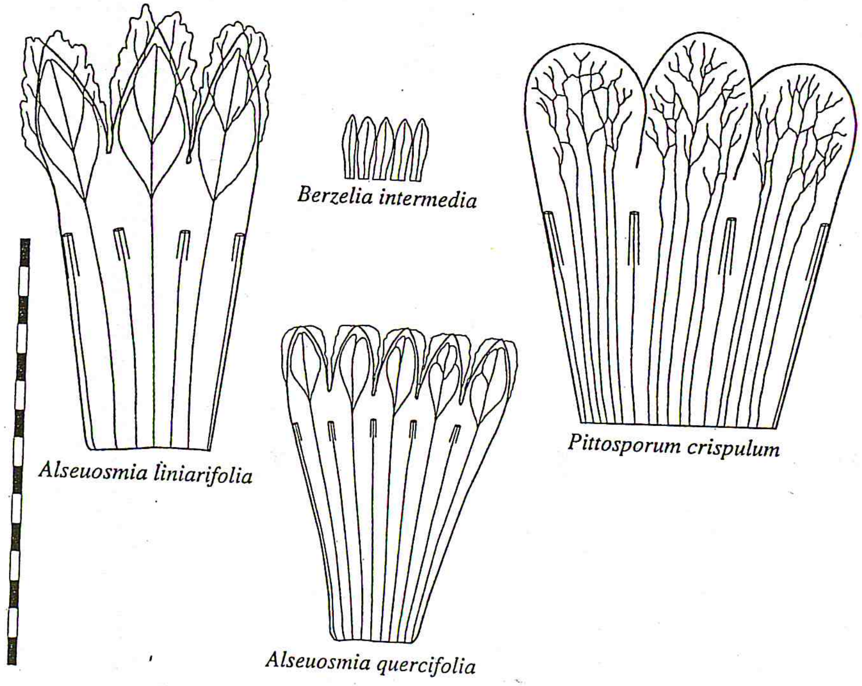
Alseuosmia liniarifolia
Berzelia intermedia
Alseuosmia quercifolia
Pittosporum crispulum

Plate 1. Taxa illustrated: *Alseuosmia quercifolia, Alseuosmia liniarifolia, Pittosporum crispulum, Berzelia intermedia.*

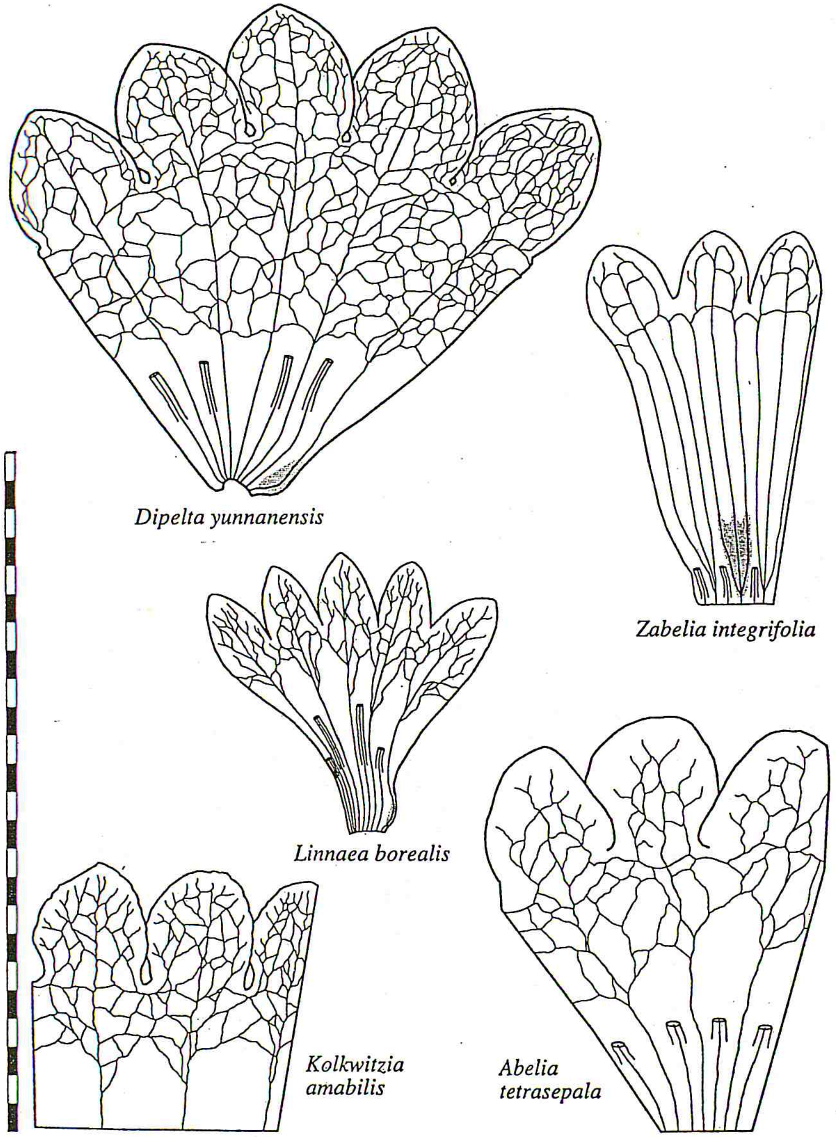

Plate 2. Taxa illustrated: *Dipelta yunnanensis, Zabelia integrifolia, Linnaea borealis, Kolkwitzia amabilis, Abelia tetrasepala.*

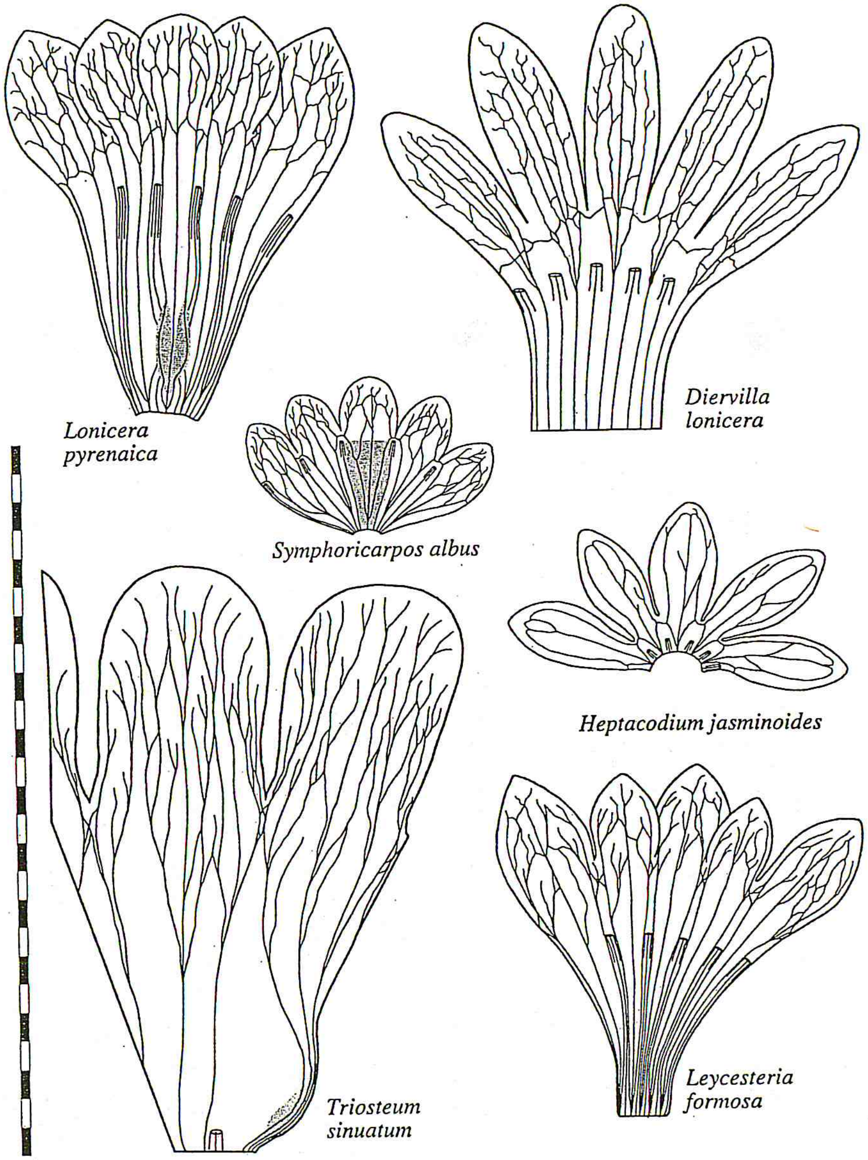

Plate 3. Taxa illustrated: *Lonicera pyrenaica, Diervilla lonicera, Symphoricarpos albus, Heptacodium jasminoides, Triosteum sinuatum, Leycesteria formosa.*

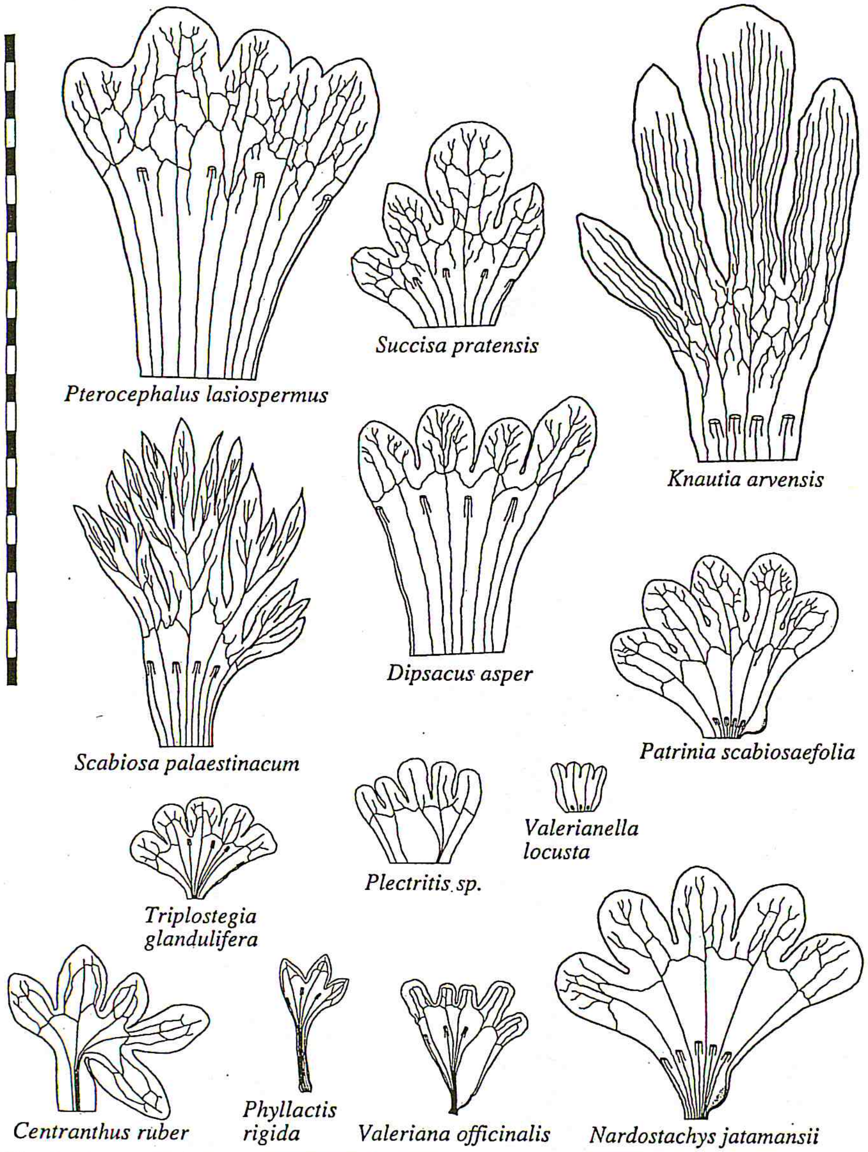

Plate 4. Taxa illustrated: *Pterocephalus lasiospermus, Succisa pratensis, Knautia arvensis, Dipsacus asper, Scabiosa palaestinacum, Patrinia scabiosaefolia, Valerianella locusta, Plectritis sp., Triplostegia glandulifera, Centranthus ruber, Phyllactis rigida, Valeriana officinalis, Nardostachys jatamansii.*

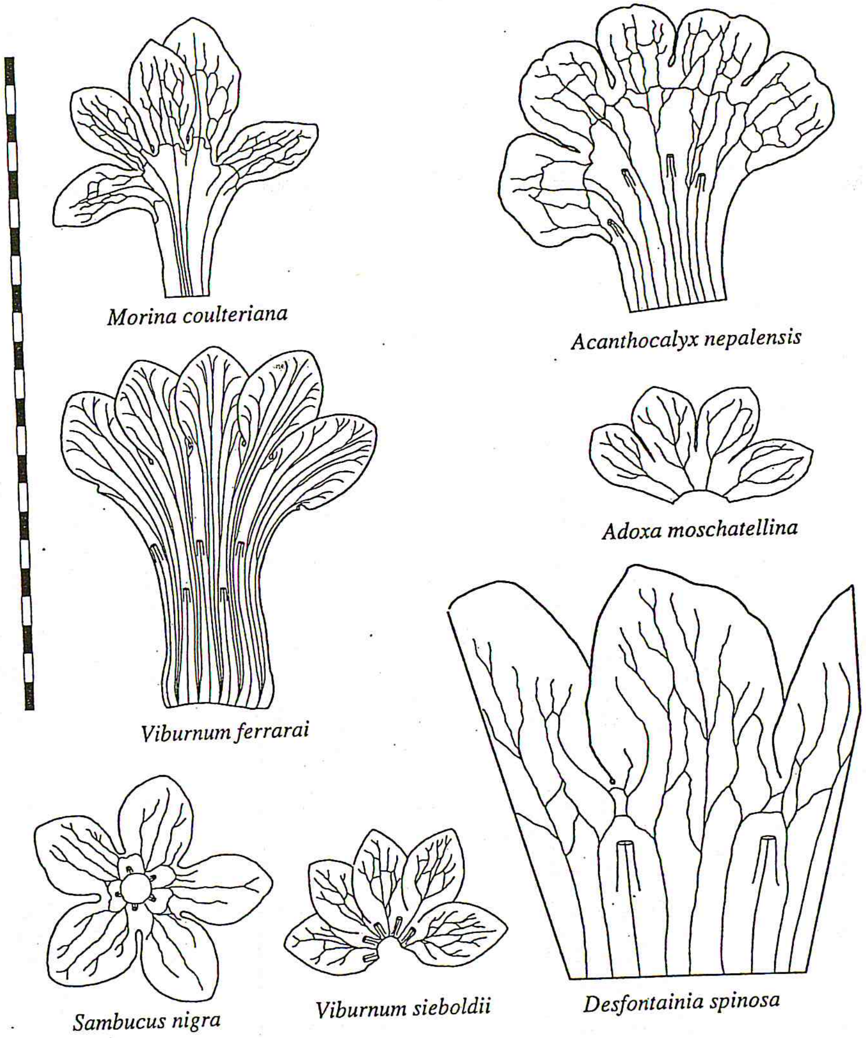

Plate 5. Taxa illustrated: *Viburnum ferrarai, Sambucus nigra, Viburnum sieboldii, Adoxa moschatellina, Acanthocalyx nepalensis, Morina coulteriana, Desfontainia spinosa.*

CHARACTER 017

THOUVENIN, M., 1890; VIDAL, L., 1903; • 8; • 19; • 28; MOHANA RAO, P.R., 1972; ERNET, D., 1977; NEUBAUER, H.F., 1978; • 10; CRONQUIST, A., 1981; • 14; LÖRCHER, H. AND WEBERLING, F., 1984; • 29; • 7

CHARACTER 019

THOUVENIN, M., 1890; • 3; SOLEREDER, H., 1899; VIDAL, L., 1903; GUNDERSEN, A.-L., 1910; • 8; METCALFE, C.R., 1952; • 12; • 28; FUKUOKA, N., 1974; DAHLGREN, R., 1975; • 10; CARLQUIST, S., 1981; CRONQUIST, A., 1981; CARLQUIST, S., 1982; CARLQUIST, S., 1991; • 29

CHARACTER 020

TIEGHEM, P.V., 1885; SZABO, Z., 1905; MOHANA RAO, P.R., 1972

CHARACTER 021

TIEGHEM, P.V., 1885; THOUVENIN, M., 1890; • 2; TIEGHEM, P.V., 1903; SZABO, Z., 1905; GUNDERSEN, A.-L., 1910; COOPER, T.B., 1939; • 8; ERNET, D., 1977; VERLAQUE, R., 1977; • 10; • 7

CHARACTER 022

THOUVENIN, M., 1890; VIDAL, L., 1903; PHILIPSON, W.R., 1947; • 8; • 28; BENSEL, C.R. AND PALSER, B.F., 1975; MENNEGA, A.M.W., 1980; • 10; • 7

CHARACTER 023

THOUVENIN, M., 1890; PHILIPSON, W.R., 1947; • 28; HOWARD, R.A., 1970; ERNET, D., 1977; NEUBAUER, H.F., 1978; • 7

CHARACTER 024

SOLEREDER, H., 1899; SZABO, Z., 1905; • 8; LI, H.-L., 1954; PHILIPSON, W.R., 1967; • 28; PHILIPSON, W.R. AND BUTTERFIELD, B.G., 1980; CARLQUIST, S., 1981; OGATA, K., 1988; CARLQUIST, S., 1992

CHARACTER 025

SZABO, Z., 1905; ADAMS, J.E., 1949; • 8; • 8; DEVOS, F., 1951; • 28; • 22; MENNEGA, A.M.W., 1980; PHILIPSON, W.R. AND BUTTERFIELD, B.G., 1980; CARLQUIST, S., 1981; CRONQUIST, A., 1981; CARLQUIST, S., 1982; LÖRCHER, H. AND WEBERLING, F., 1984; OGATA, K., 1988; LÖRCHER, H. AND WEBERLING, F., 1990; CARLQUIST, S., 1992; HUFFORD, L., 1992; • 29; BREMER, B., ET AL., 1994

CHARACTER 026

THOUVENIN, M., 1890; • 8; • 28; PHILIPSON, W.R. AND BUTTERFIELD, B.G., 1980; CARLQUIST, S., 1981; CARLQUIST, S., 1984; LÖRCHER, H. AND WEBERLING, F., 1984; TAKHTAJAN, A., 1987; LÖRCHER, H. AND WEBERLING, F., 1990; CARLQUIST, S., 1992; HUFFORD, L., 1992; BREMER, B., ET AL., 1994; • 7

CHARACTER 027

THOUVENIN, M., 1890; SOLEREDER, H., 1899; VIDAL, L., 1903; NIEDENZU, F. AND HARMS, H., 1930; • 8; DEVOS, F., 1951; PHILIPSON, W.R., 1967; • 28; CARLQUIST, S., 1981; TAKHTAJAN, A., 1987; OGATA, K., 1988; • 18; • 7

CHARACTER 028

THOUVENIN, M., 1890; JORICA, H.S., 1921; NIEDENZU, F. AND HARMS, H., 1930; • 8; METCALFE, C.R., 1952; • 19; • 15; ERNET, D., 1977; • 10; CRONQUIST, A., 1981; • 14; • 23; TAKHTAJAN, A., 1987; LÖRCHER, H. AND WEBERLING, F., 1990; • 7

CHARACTER 029

BENTHAM, G. AND MUELLER, F., 1864; • 1; • 2; • 4; KLETT, W., 1924; SPRAGUE, T.A., 1927;
20; • 24; NIELSEN, S.D., 1949; ADAMSON, R.S. AND SALTER, T.M., 1958; BRIZCKY, G.K., 19
• 11; WEBERLING, F., 1965; FUKUOKA, N., 1969; • 16; ERNET, D., 1977; • 22; • 14; WEBERLIN
F., 1982a; LARSEN, B.B., 1986; HOFMANN, U. AND GÖTTMANN, J., 1990; • 6; • 18; • 25; ERBA
C., 1994; WEBERLING, F., 1996

CHARACTER 030

BAILLON, H., 1862-1863; • 1; • 2; HALLIER, H., 1910; • 4; • 20; • 24; NIELSEN, S.D., 1949; • 11; •
GANDERS, F.R., ET AL., 1976; ERNET, D., 1977; • 10; • 14; WEBERLING, F., 1982; • 21; • 17;
HOFMANN, U. AND GÖTTMANN, J., 1990; • 6; • 18; • 25; • 9

CHARACTER 031

• 2; • 4; DOLL, W., 1927; • 20; PHILIPSON, W.R., 1947; • 24; BRIZCKY, G.K., 1961; • 11; • 15;
ERNET, D., 1977; • 22; • 10; • 14; • 23; • 17; HOFMANN, U. AND GÖTTMANN, J., 1990; • 6; • 18;
25

CHARACTER 032

• 1; THOUVENIN, M., 1890; • 2; SZABO, Z., 1905; • 24; • 11; LEVYNS, M.R., 1966; • 12; • 15; • 28;
16; GANDERS, F.R., ET AL., 1976; • 22; • 14; WEBERLING, F., 1982; • 23; • 21; LARSEN, B.B.,
1986; • 17; • 13; • 6; • 7; PLUNKETT, G.M., ET AL., 1996

CHARACTER 033

BENTHAM, G. AND MUELLER, F., 1864; • 1; • 2; GÜNTHART, A., 1904; HALLIER, H., 1910; • 4;
JORICA, H.S., 1921; • 24; • 11; LEVYNS, M.R., 1966; • 12; • 28; • 16; GANDERS, F.R., ET AL.,
1976; • 10; • 14; • 26; • 23; • 21; DONOGHUE, M.J., 1985; LARSEN, B.B., 1986; • 17; • 13; BREMER
B., ET AL., 1994; • 25; • 9

CHARACTER 034

• 1; • 4; • 10; ERBAR, C. AND LEINS, P., 1988; ERBAR, C., 1994; • 7

CHARACTER 035

• 1; • 2; • 4; JORICA, H.S., 1921; NIELSEN, S.D., 1949; BRIZCKY, G.K., 1961; • 11; NAPPER, D.M.
1968; • 12; • 15; • 16; GANDERS, F.R., ET AL., 1976; • 22; • 10; • 14; • 26; • 23; • 21; LARSEN, B.B.,
1986; • 17; • 6; • 18; • 25; • 9; • 7

CHARACTER 036

BENTHAM, G. AND MUELLER, F., 1864; • 1; THOUVENIN, M., 1890; • 2; VIDAL, L., 1903;
GRAEBNER, P., 1906; TIEGHEM, P.V., 1909; • 4; JOHNSTON, A.M., 1931; NIELSEN, S.D., 1949;
BRIZCKY, G.K., 1961; • 11; LEVYNS, M.R., 1966; NAPPER, D.M., 1968; • 12; • 15; FUKUOKA, N.,
1972; KAO, M.-T. AND DEVOL, C., 1973; RICHARDSON, I.B.K., 1975; • 16; ENGEL, K., 1976; • 22
• 10; • 14; • 26; • 23; • 21; LARSEN, B.B., 1986; • 17; MABBERLEY, D.J., 1990; • 13; • 6; • 18;
ERBAR, C., 1994

CHARACTER 037

HALLIER, H., 1910; • 4; • 24; BAKSAY, L., 1952; FERGUSON, I.K., 1966; BENSEL, C.R. AND PALSER, B.F., 1975; • 16; ERNET, D., 1977; • 22; • 10; HARA, H., 1981; • 14; LARSEN, B.B., 1986; HOFMANN, U. AND GÖTTMANN, J., 1990; • 13; BOLLI, R., 1994; • 25; • 9

CHARACTER 038

• 1; • 2; • 4; BAILEY, L.H., 1929; • 24; BRIZCKY, G.K., 1961; EHRENDORFER, F., 1964; • 11; NAPPER, D.M., 1968; • 15; RICHARDSON, I.B.K., 1975; • 16; ERNET, D., 1977; • 22; • 10; • 14; • 21; LARSEN, B.B., 1986; • 17; CARLQUIST, S., 1991; • 13; • 6; BOLLI, R., 1994; • 25

CHARACTER 039

BENTHAM, G. AND MUELLER, F., 1864; • 1; • 2; • 4; HORNE, A.S., 1914; SPRAGUE, T.A., 1927; • 20; • 24; BRIZCKY, G.K., 1961; AIRY-SHAW, H.K., 1964; FERGUSON, I.K., 1965; BORSINI, O.E., 1966; KOKAWARO, J.O., 1968; VERDCOURT, B., 1968; • 15; • 22; • 10; CRONQUIST, A., 1981; • 14; • 23; • 21; MABBERLEY, D.J., 1990; • 18; • 9

CHARACTER 040

BENTHAM, G. AND MUELLER, F., 1864; • 2; • 4; HANNAH, M., 1916; SZABÓ, Z., 1923; • 20; • 24; LEVYNS, M.R., 1966; • 28; • 10; • 26; ERBAR, C., 1991; • 6

CHARACTER 041

BENTHAM, G. AND MUELLER, F., 1864; • 1; • 2; TIEGHEM, P.V., 1909; • 4; SZABÓ, Z., 1923; NIELSEN, S.D., 1949; BAKSAY, L., 1952; BRIZCKY, G.K., 1961; • 11; LEVYNS, M.R., 1966; • 12; • 15; • 16; GANDERS, F.R., ET AL., 1976; • 22; • 10; • 26; WEBERLING, F., 1982; • 23; • 21; LARSEN, B.B., 1986; • 17; MABBERLEY, D.J., 1990; • 13; • 6; • 25; ERBAR, C., 1994; PENG, C.-I., ET AL., 1995

CHARACTER 042

• 2; • 4; • 20; • 24; NIELSEN, S.D., 1949; BRIZCKY, G.K., 1961; • 11; VERDCOURT, B., 1968; • 12; • 15; RICHARDSON, I.B.K., 1975; • 16; GANDERS, F.R., ET AL., 1976; • 10; • 14; • 26; • 23; • 21; LARSEN, B.B., 1986; • 17; • 13; • 6; • 18

CHARACTER 043

• 1; • 2; • 4; • 24; NIELSEN, S.D., 1949; • 19; • 11; • 12; • 15; • 28; FAGERSTRÖM, K., 1975; RICHARDSON, I.B.K., 1975; • 16; GANDERS, F.R., ET AL., 1976; • 22; • 10; • 14; • 26; • 23; HSU, P.-S., 1983; • 21; LARSEN, B.B., 1986; • 17; • 13; • 6; • 18; • 9; • 7

CHARACTER 044

LINDLEY, J., 1836; • 1; • 3; VIDAL, L., 1903; • 4; BROWN, W.H., 1938; BAKSAY, L., 1952; RAZI, B.A. AND SUBRAMANYAM, K., 1952; FAHN, A., 1953; • 15; • 28; BENSEL, C.R. AND PALSER, B.F., 1975; GANDERS, F.R., ET AL., 1976; • 10; • 21; • 18; BOLLI, R., 1994; ERBAR, C., 1994; PENG, C.-I., ET AL., 1995; ROELS, P. AND SMETS, E., 1996

CHARACTER 045

• 1; • 3; • 4; NIELSEN, S.D., 1949; RAZI, B.A. AND SUBRAMANYAM, K., 1952; • 28; BENSEL, C.R. AND PALSER, B.F., 1975; • 10; • 26; • 23; • 21; • 18; ERBAR, C., 1994; • 9

CHARACTER 046

• 2; • 4; • 20; • 24; • 19; FUKUOKA, N., 1974; • 10 ; • 14; SHI-YOU, L. AND ZHU-HUA, N., 1987; HOFMANN, U. AND GÖTTMANN, J., 1990; • 6; • 18

CHARACTER 047

BENTHAM, G. AND MUELLER, F., 1864; • 1; • 2; • 4; JORICA, H.S., 1921; SZABÓ, Z., 1923; • 24; NIELSEN, S.D., 1949; • 11; LEVYNS, M.R., 1966; • 12; • 15; • 28; FUKUOKA, N., 1974; RICHARDSON, I.B.K., 1975; • 16; GANDERS, F.R., ET AL., 1976; • 22; KAMELINA, O.P., 1980; • 10; • 14; • 26; • 23; • 21; LARSEN, B.B., 1986; • 17; MABBERLEY, D.J., 1990; • 13; • 6; • 25; • 7

CHARACTER 048

• 1; • 2; • 3; • 4; BRIZCKY, G.K., 1961; • 11; • 12; RICHARDSON, I.B.K., 1975; • 16; GANDERS, F.R., ET AL., 1976; • 22; KAMELINA, O.P., 1980; • 10; • 14; • 26; • 23; • 21; • 17; • 13; • 6

CHARACTER 049

• 2; • 4; • 20; HANDEL-MAZZETTI, H., 1936; • 24; • 19; BRIZCKY, G.K., 1961; • 11; • 15; • 22; • 10; • 14; • 26; • 23; • 21; CHEN, H.B. AND CHENG, C.R., 1991; • 13; • 6; • 18; AL-SHAMMARY, K.I. AND GORNALL, R.J., 1994

CHARACTER 050

• 1; • 2; • 4; • 20; • 24; BRIZCKY, G.K., 1961; • 11; • 12; • 15; • 16; GANDERS, F.R., ET AL., 1976; • 22; • 10; • 14; • 26; • 23; • 21; • 17; • 13; • 6

CHARACTER 051

• 1; THOUVENIN, M., 1890; • 2; • 4; • 24; • 19; BRIZCKY, G.K., 1961; • 11; • 12; • 15; • 16; GANDERS, F.R., ET AL., 1976; • 10; • 14; • 21; • 17; • 13; • 6

CHARACTER 052

LINDLEY, J., 1836; • 1; • 2; • 4; SZABÓ, Z., 1923; • 24; • 11; • 15; • 16; GANDERS, F.R., ET AL., 1976; • 10; • 14; • 23; • 21; LARSEN, B.B., 1986; • 17; • 13; • 6; HUFFORD, L., 1992

CHARACTER 053

• 1; THOUVENIN, M., 1890; • 2; VIDAL, L., 1903; • 4; JOHNSTON, A.M., 1931; • 24; BRIZCKY, G.K., 1961; • 11; • 15; FUKUOKA, N., 1972; • 22; • 10; • 14; • 26; • 23; • 21; TAKHTAJAN, A., 1987; • 17; • 13; • 6; BOLLI, R., 1994; ERBAR, C., 1994; • 9; • 7

CHARACTER 054

LINDLEY, J., 1836; • 1; • 2; TIEGHEM, P.V., 1903; • 4; • 24; MEYER, F.G., 1951; DAVIES, G.L., 1966; • 12; • 15; • 16; GANDERS, F.R., ET AL., 1976; • 22; • 10; • 14; • 23; • 17; • 13; • 6; • 7

CHARACTER 055

BENTHAM, G. AND MUELLER, F., 1864; • 1; THOUVENIN, M., 1890; • 2; • 3; SAXTON, W.T., 1910; HORNE, A.S., 1914; JOHNSTON, A.M., 1931; • 24; NIELSEN, S.D., 1949; MORF, E., 1950; MEYER, F.G., 1951; ADAMSON, R.S. AND SALTER, T.M., 1958; AIRY-SHAW, H.K., 1964; • 11; FERGUSON, I.K., 1966; • 15; • 28; FAGERSTRÖM, K., 1975; KAMELINA, O.P., 1980; • 14; • 26; • 23; • 21; LARSEN, B.B., 1986; • 17; HUFFORD, L., 1992; • 18; ROELS, P., 1993; ERBAR, C., 1994; • 9; PENG, C.-I., ET AL., 1995; • 7; PLUNKETT, G.M., ET AL., 1996

CHARACTER 056

• 1; • 2; • 3; VIDAL, L., 1903; • 4; SPRAGUE, T.A., 1927; JOHNSTON, A.M., 1931; • 24; NIELSEN, S.D., 1949; MORF, E., 1950; ADAMSON, R.S. AND SALTER, T.M., 1958; • 11; • 15; • 28; FAGERSTRÖM, K., 1975; • 16; • 22; KAMELINA, O.P., 1980; • 10; • 14; • 26; • 23; • 21; LARSEN, B.B., 1986; • 17; MABBERLEY, D.J., 1990; LANGE, J.H.D., ET AL., 1993b; ROELS, P., 1993; • 9

CHARACTER 057

• 1; • 2; VIDAL, L., 1903; • 4; ASPLUND, E., 1920; SPRAGUE, T.A., 1927; JOHNSTON, A.M., 1931; • 24; NIELSEN, S.D., 1949; ADAMSON, R.S. AND SALTER, T.M., 1958; BRIZCKY, G.K., 1961; • 11; • 16; • 22; • 10; • 14; • 26; • 23; • 17; SCHULTES, R.E., 1989; LANGE, J.H.D., ET AL., 1993b; • 25

CHARACTER 058

SAXTON, W.T., 1910; ASPLUND, E., 1920; WILKINSON, A.M., 1948a; WILKINSON, A.M., 1948c; WILKINSON, A.M., 1948b; WILKINSON, A.M., 1949; PHILIPSON, W.R., 1967; • 28; FUKUOKA, N., 1972; BENSEL, C.R. AND PALSER, B.F., 1975; • 10; CRONQUIST, A., 1981; LARSEN, B.B., 1986; • 9

CHARACTER 059

BENTHAM, G. AND MUELLER, F., 1864; • 1; • 2; TIEGHEM, P.V., 1909; • 4; SZABÓ, Z., 1923; SPRAGUE, T.A., 1927; • 24; NIELSEN, S.D., 1949; • 19; • 11; FERGUSON, I.K., 1966; VERDCOURT, B., 1968; • 15; • 28; FUKUOKA, N., 1972; RICHARDSON, I.B.K., 1975; GANDERS, F.R., ET AL., 1976; • 22; • 10; • 14; • 26; • 23; • 21; LARSEN, B.B., 1986; • 13; • 18; • 25; • 7

CHARACTER 060
BENTHAM, G. AND MUELLER, F., 1864; • 1; THOUVENIN, M., 1890; • 2; • 3; • 4; • 24; NIELSEN, S.D., 1949; • 19; BRIZCKY, G.K., 1961; • 11; LEVYNS, M.R., 1966; • 12; • 15; • 28; RICHARDSON, I.B.K., 1975; GANDERS, F.R., ET AL., 1976; • 10; • 14; • 23; • 21; LARSEN, B.B., 1986; • 17; MABBERLEY, D.J., 1990; • 13; • 6; • 18; • 25; ERBAR, C., 1994

CHARACTER 061
VIDAL, L., 1903; SAXTON, W.T., 1910; HORNE, A.S., 1914; ASPLUND, E., 1920; SZABÓ, Z., 1923; LAVIALLE, P., 1925; • 20; WILKINSON, A.M., 1948a; WILKINSON, A.M., 1948c; WILKINSON, A.M., 1948b; WILKINSON, A.M., 1949; PHILIPSON, W.R., 1967; • 12; • 28; FUKUOKA, N., 1972; FUKUOKA, N., 1974; • 10; CRONQUIST, A., 1981; KAMELINA, O.P., 1983; • 9

CHARACTER 062
• 2; • 3; VIDAL, L., 1903; SAXTON, W.T., 1910; • 4; HORNE, A.S., 1914; SZABÓ, Z., 1923; WILKINSON, A.M., 1948a; WILKINSON, A.M., 1948c; WILKINSON, A.M., 1948b; WILKINSON, A.M., 1949; JOHRI, B.M., 1963; • 28; FUKUOKA, N., 1972; FUKUOKA, N., 1974; BENSEL, C.R. AND PALSER, B.F., 1975; • 16 ; • 22; • 10; KAMELINA, O.P., 1983; SCHULTES, R.E., 1989; • 9

CHARACTER 063
• 1; • 2; • 4; • 24; • 10; LANGE, J.H.D., ET AL., 1993b; ERBAR, C., 1994; • 7

CHARACTER 064
MOHANA RAO, P.R., 1972; PHILIPSON, W.R., 1974; JOHRI, B.M., ET AL., 1992; LANGE, J.H.D., ET AL., 1993c

CHARACTER 065
MOHANA RAO, P.R., 1972; PHILIPSON, W.R., 1974; JOHRI, B.M., ET AL., 1992

CHARACTER 066
• 5

CHARACTER 067
KAPIL, R.N. AND TIWARI, S.C., 1978; JOHRI, B.M., ET AL., 1992

CHARACTER 068
DAVIES, G.L., 1966; • 12; KAMELINA, O.P., 1980; • 21; MALDONADO DE MAGNANO, S., 1986; JOHRI, B.M., ET AL., 1992; LANGE, J.H.D., ET AL., 1993b; PENG, C.-I., ET AL., 1995

CHARACTER 069
DAVIES, G.L., 1966; • 12; KAMELINA, O.P., 1980; KAMELINA, O.P., 1983; • 21; MALDONADO DE MAGNANO, S., 1986; JOHRI, B.M., ET AL., 1992; ERBAR, C., 1994; • 9; PENG, C.-I., ET AL., 1995; • 7

CHARACTER 070
DAVIES, G.L., 1966; • 12; KAMELINA, O.P., 1980; KAMELINA, O.P., 1983; • 21; MALDONADO DE MAGNANO, S., 1986; JOHRI, B.M., ET AL., 1992; PENG, C.-I., ET AL., 1995

CHARACTER 071
DAVIES, G.L., 1966; • 12; KAMELINA, O.P., 1980; • 21; MALDONADO DE MAGNANO, S., 1986; JOHRI, B.M., ET AL., 1992; PENG, C.-I., ET AL., 1995; • 7

CHARACTER 072
DAVIES, G.L., 1966; BREWBAKER, J.L., 1967; • 12; KAMELINA, O.P., 1980; • 21; MALDONADO DE MAGNANO, S., 1986; JOHRI, B.M., ET AL., 1992; PENG, C.-I., ET AL., 1995; • 7

CHARACTER 073
CHAO, C.-Y., 1954; • 11; ERDTMAN, G., 1966; LEENHOULTS, P.W., 1967; PHILIPSON, W.R., 1967; SLEUMER, H., 1968; BASSETT, I.J. AND CROMPTON, C.W., 1970; WAKABAYASHI, M., 1970; • 30; CLARKE, G.C.S. AND JONES, M.R., 1977; CLARKE, G., 1978; TSENG, C.C., 1980; CLARKE, G.C.S., 1981; • 14; • 26; BLACKMORE, S. AND CANNON, M.J., 1983; HOC, P.S. AND BRAVO, L.D., 1984; DONOGHUE, M.J., 1985; LANGE, J.H.D., ET AL., 1993; • 9

CHARACTER 074
CHAO, C.-Y., 1954; AGABABIAN, V.S., 1964; • 11; ERDTMAN, G., 1966; LEENHOULTS, P.W., 1967; SLEUMER, H., 1968; WAKABAYASHI, M., 1970; CLARKE, G.C.S. AND JONES, M.R., 1977; CLARKE, G., 1978; PATEL, V.C. AND SKVARLA, J.J., 1979; TSENG, C.C., 1980; CLARKE, G.C.S., 1981; • 14; • 26; • 21; VERLAQUE, R., 1986; LANGE, J.H.D., ET AL., 1993

CHARACTER 075
CHAO, C.-Y., 1954; AGABABIAN, V.S., 1964; • 11; ERDTMAN, G., 1966; LEENHOULTS, P.W., 1967; SLEUMER, H., 1968; • 30; CLARKE, G., 1978; TSENG, C.C., 1980; CLARKE, G.C.S., 1981; • 14; • 26; BLACKMORE, S. AND CANNON, M.J., 1983; • 21; LANGE, J.H.D., ET AL., 1993; • 25

CHARACTER 076
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