

A phylogenetic analysis of 100+ genera and 50+ families of euasterids based on morphological and molecular data with notes on possible higher level morphological synapomorphies

K. Bremer¹, A. Backlund², B. Sennblad³, U. Swenson⁴, K. Andreassen⁵, M. Hjertson¹, J. Lundberg¹, M. Backlund¹, and B. Bremer¹

¹Department of Systematic Botany, Evolutionary Biology Centre, Uppsala University, Uppsala, Sweden

²Department of Medicinal Chemistry, Uppsala University, Uppsala, Sweden

³Stockholm Bioinformatics Center, Stockholm University, Stockholm, Sweden

⁴Department of Botany, University of Stockholm, Stockholm, Sweden

⁵Molecular Systematics Laboratory, Swedish Museum of Natural History, Stockholm, Sweden

Received August 28, 2000

Accepted August 7, 2001

Abstract. A data matrix of 143 morphological and chemical characters for 142 genera of euasterids according to the APG system was compiled and complemented with *rbcL* and *ndhF* sequences for most of the genera. The data were subjected to parsimony analysis and support was assessed by bootstrapping. Strict consensus trees from analyses of morphology alone and morphology + *rbcL* + *ndhF* are presented. The morphological data recover several groups supported by molecular data but at the level of orders and above relationships are only superficially in agreement with molecular studies. The analyses provide support for monophyly of Gentianales, Aquifoliales, Apiales, Asterales, and Dipsacales. All data indicate that Adoxaceae are closely related to Dipsacales and hence they should be included in that order. The trees were used to assess some possible morphological synapomorphies for euasterids I and II and for the orders of the APG system. Euasterids I are generally characterised by opposite leaves, entire leaf margins, hypogynous flowers, “early sympetalous” with a ring-shaped corolla primordium, fusion of stamen filaments with the corolla tube, and capsular fruits. Euasterids II often have alternate leaves, serrate-dentate leaf margins,

epigynous flowers, “late sympetalous” with distinct petal primordia, free stamen filaments, and indehiscent fruits. It is unclear which of these characters represent synapomorphies and symplesiomorphies for the two groups, respectively, and there are numerous expectations to be interpreted as reversals and parallelisms.

Key words: Angiosperms, asterids, euasterids, Asteridae, Apiales, Aquifoliales, Asterales, Dipsacales, Garryales, Gentianales, Lamiales, Solanales, Adoxaceae. Cladistics, phylogeny, morphology, *rbcL*, *ndhF*.

Asterids comprise more than 1/4 of the flowering plants (Bremer et al. 2000). They are often herbaceous plants with sympetalous corollas and stamens in one series. In the classification by the Angiosperm Phylogeny Group (APG 1998), which will be followed here, asterids are grouped in ten orders, viz. Cornales Dumort., Ericales Dumort., Garryales Lindl., Gentianales Lindl., Solanales Dumort., Lamiales Bromhead, Aquifoliales Senft, Apiales Nakai, Dipsacales Dumort., and

Asterales Lindl. The last eight of these constitute the euasterids. Asterids are traditionally known as Sympetalae Rchb., because of the sympetalous corollas. Sympetalous plants were conceived as a group already in the 17th century and they are more or less consistently recognised in flowering plant classification ever since Jussieu 1789 (Wagenitz 1992). Takhtajan (1964, 1969) renamed the group as subclass Asteridae Takht., although he (Takhtajan 1987, 1997) later restricted Asteridae to the core of Asterales as currently understood (APG 1998) and placed the other orders in a subclass Lamiidae Takht. ex Reveal. Before the 1990s (e.g. Cronquist 1981), Asteridae generally comprised plants now classified in Gentianales, Solanales, Lamiales, Dipsacales, and Asterales. Parts of Ericales were earlier considered members of Sympetalae but they were excluded from Asteridae by Takhtajan (1964, 1969). Many groups outside Asteridae have been considered their close relatives and potential candidates for inclusion among the asterids. Mainly due to the presence of polyacetylenes and iridoids, Dahlgren (1989) thus placed Apiales (=Araliales Reveal) and Cornales (including many families now in other asterid orders) close to Asterales and Dipsacales, respectively, and in Dahlgren's diagrams Ericales were surrounded by Cornales, Dipsacales, Gentianales, Lamiales, and Solanales. However, it was not until the breakthrough of molecular information in 1992 and 1993 (Olmstead et al. 1992, 1993; Downie and Palmer 1992; Chase et al. 1993) that asterids became more widely circumscribed.

With cladistic analysis of nucleotide sequences from the *rbcL* gene of the chloroplast genome, it soon became evident that the traditional Asteridae (approximately Gentianales, Lamiales, Solanales, Asterales, Dipsacales) are nested in a larger monophyletic group including also Cornales, Ericales, Garryales, Apiales, and Aquifoliales (Olmstead et al. 1992, 1993, where they are somewhat differently named). It also became evident that there are two major subgroups of asterids, known as Asterid I and II (Chase

et al. 1993) or euasterids I and II (APG 1998), corresponding to I) Garryales, Gentianales, Lamiales, and Solanales, and II) Apiales, Aquifoliales, Asterales, and Dipsacales. Subsequently circumscription of the asterids has been complemented by analyses of extended *rbcL*, *ndhF*, *atpB*, and 18S rDNA data sets with more taxa including whole families revealed to belong among the asterids (Savolainen et al. 1994; Hempel et al. 1995; Gustafsson et al. 1996; Morton et al. 1996; Plunkett et al. 1996; Backlund and Bremer 1997; Soltis and Soltis 1997; Soltis et al. 1997; Backlund et al. 2000; Olmstead et al. 2000; Savolainen et al. 2000a, b; Soltis et al. 2000). Jackknife and bootstrap analyses have corroborated monophyly of asterids, euasterids, euasterids I and II, and the 10 orders recognised by APG (1998). In particular, there is the large jackknife analysis of the *rbcL* gene from 2538 green plants by Källersjö et al. (1998), jackknife analysis of the *rbcL* and *atpB* genes from 357 flowering plants by Savolainen et al. (2000a), bootstrap analysis of the 18S rDNA, *rbcL* and *atpB* genes from 190 flowering plants by Soltis et al. (1998), and jackknife analysis of the same three genes from 545 flowering plants by Soltis et al. (2000).

There have been comparatively few attempts at reconstructing higher-level (suprafamilial and supraordinal) interrelationships of flowering plants by cladistic analysis of morphological data. No doubt this is due to the complex nature of constructing morphological data matrices. Assembling a morphological data matrix of, say, 100 families and 150 characters is normally a much more difficult enterprise than sequencing the *rbcL* gene from 100 species. Hufford (1992) made a morphological cladistic analysis of nearly 70 mostly rosids but also some asterid families. His trees show many similarities with the well-supported phylogenies obtained from the molecular data. However, there are also several gross discrepancies. For example, the asterid Apiales are in Hufford's trees nested in the rosids Malpighiales Mart., illustrating the difficulties with morphological data at higher taxonomic levels. The

morphological data are no more homoplastic than the molecular data, but the number of informative characters is much lower and their pattern of variation is much more complex (e.g. Bremer et al. 1999). This is illustrated also by the large analysis of Nandi et al. (1998). They analysed non-molecular (morphological, chemical, and serological) and *rbcL* data from 161 flowering plant taxa (families and various suprafamilial taxa), among them 1/4 asterids including 14 euasterids (Asterids I and II). Nandi et al.'s morphological trees are similar to the molecular-derived phylogenies but again, as in Hufford's (1992) morphological trees, there are considerable discrepancies. Nandi et al.'s bootstrap analyses of their data set also reveal very weak support for the morphological trees. Other morphological cladistic analyses involving several families of asterids are mostly restricted to single orders or groups of families. Anderberg (1992, 1993) analysed Ericales sensu stricto, Struwe et al. (1994) analysed Gentianales, Anderberg and Ståhl (1995) Primulales Dumort. (now part of Ericales sensu lato), and Gustafsson and Bremer (1995) Asterales. It should be noted that the cladistically obtained morphological phylogenies are much more similar to the well-supported molecular phylogenies than are the intuitively constructed "phylogenetic" classifications (Cronquist 1981, Thorne 1992, Takhtajan 1997). If properly analysed, morphological data certainly have much to contribute to our understanding of phylogeny. Morphological characters are of course also important for predictions of the phylogenetic position of taxa not yet sequenced.

In order to understand better morphology and character evolution, we here present a cladistic analysis of euasterids, representing most of the 77 families of the group as circumscribed by APG (1998). We have compiled a data matrix of 143 morphological and chemical characters, and DNA sequences from the *rbcL* and *ndhF* genes. We use these data and the corresponding parsimony-derived trees for discussing some possible morpholog-

ical synapomorphies for the major euasterid groups of the APG system.

Material and methods

Terminal taxa. The data matrix comprises 142 genera of euasterids. Their classification into families, orders, and the two major groups of euasterids I and euasterids II is shown in Appendix 1 following APG (1998). In general, we have sampled more genera from large and morphologically complex families. Many families are represented by a single genus, in many cases simply because the family is monogeneric. All morphological characters refer to the genus. If there is variation within the genus for a particular character, this is treated as discussed below under morphological data. We have chosen genera as terminal taxa rather than species or families. With species, the morphological variation in the data matrix would have been very sensitive to the taxon sampling, i.e. the particular species that happen to be included, and the results would be heavily dependent on the sampling. With families as terminal taxa, the problems of morphological variation within the families and how to code this variation for the terminals are considerable. The data matrix may become so burdened with morphological polymorphisms that the results of the analysis become obscure. The molecular characters are all from single specimens, from which the sequences were obtained. We assume that the sequences are representative for the genus to which the specimens have been assigned.

Morphological, anatomical, embryological, palynological, chemical, and RFLP data. These characters are listed in Appendix 2 and the data matrix with all the codings in Appendix 3. The morphological characters have been checked on appropriate herbarium specimens or living material. Anatomical, embryological, and chemical characters are taken from standard literature (e.g. Cronquist 1981, Metcalfe and Chalk 1979–1983, Hegnauer 1964–1989, Johri 1984). A comprehensive list of standard literature for the purpose of constructing this type of data matrices is provided by Nandi et al. (1998). Special papers on particular subjects are cited in Appendix 2. The coding of polymorphisms within certain genera poses particular problems. If two (or more) character states are present within one genus and there is information available regarding which state is plesiomorphic

(ancestral) within the genus, it is coded for the plesiomorphic state and the variation is thus ignored. For example, if a particular character state occurs only in one species or a group of species that are known to be nested inside the species phylogeny of the genus, that apomorphic (derived) state may be ignored and the genus coded for the plesiomorphic state. In the absence of such information regarding the states for a polymorphic character in a particular genus, it is coded for both (all) states observed within the genus. There is also a problem in coding complex characters of morphology, anatomy etc. For example the coding of organs that may be absent or present as well as variable is not straightforward. Various coding strategies have been discussed by Pleijel (1995) and Wilkinson (1995). In general we have used composite coding (Wilkinson 1995) and we have used only unordered characters in order to simplify the analyses. The data matrix contains many missing entries. It is not possible to investigate all taxa for all characters, especially regarding features that require microscopy or other methods more complicated than just visual inspection of specimens. Our data are by no means exhaustive but offered as a starting-point for further enquiry into higher level morphological synapomorphies of euasterids.

Molecular data. The molecular characters consist of the sites in the DNA sequences from two genes, *rbcL* and *ndhF*. Some sequences are new, most were obtained from the EMBL/NCBI archives. Sequencing procedures are described by Backlund et al. (2000). Voucher specimens and EMBL/NCBI accession numbers are given in Appendix 1. Alignment was done manually and posed few problems. Differential weighting of the codon positions, primarily down-weighting of third positions, are sometimes applied in cladistic analysis of coding DNA sequences (e.g. Albert et al. 1993) but recent studies indicate that down-weighting third positions is ill-founded, since they may contain considerable phylogenetic information (Sennblad and Bremer 2000). Hence, we applied no weighting schemes for the molecular data. Sequences of the two genes were not available for all genera. The *rbcL* gene has been sequenced and included for 133 of the 142 genera in our sample, and the *ndhF* gene for 97 genera. The *rbcL* and

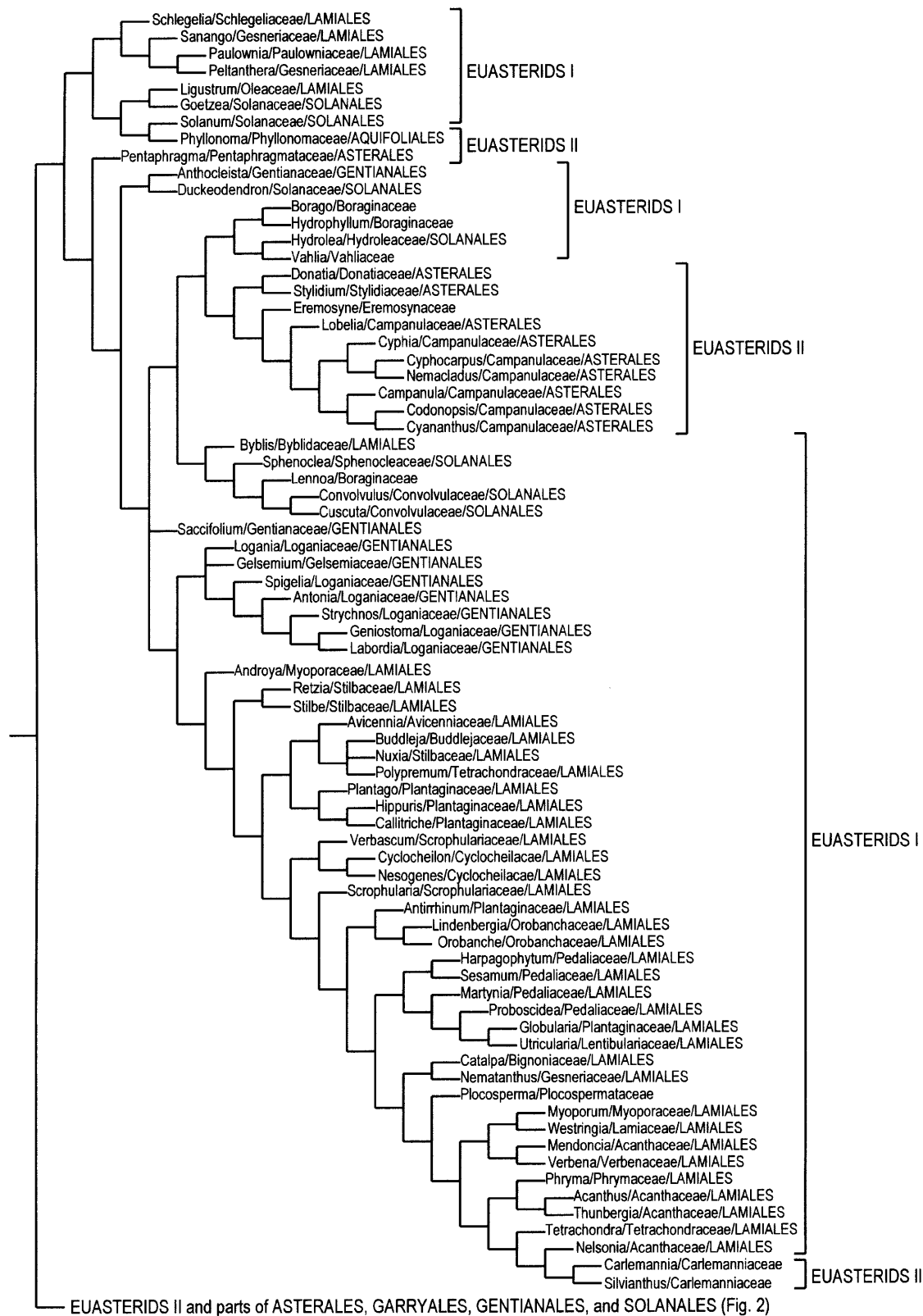
ndhF data comprise 474 and 1028 phylogenetically informative positions, respectively. These figures may be compared to the 143 phylogenetically informative, also frequently multistate characters from the morphological data.

Cladistic analyses. Parsimony analyses were undertaken with the PAUP package (Swofford 1999). Three main analyses were done, first with morphological data, second with molecular data, and third with a combined data set of morphological, *rbcL*, and *ndhF* data. As usual in many combined morphological and molecular analyses, the 143 morphological characters are much fewer than the 1502 phylogenetically informative characters from the molecular sequences. It may be argued that morphological characters are more complex than single sequence positions, so that a differential weighting scheme may be justified. We see no easily justifiable alternative to equal weighting of all characters, however, and morphological and molecular data seem to be complementary rather than contradicting (Donoghue et al. 1991). Several different combinations of heuristic search options were used, including multiple (100) random addition sequences and TBR and SPR branch swapping with MULPARS on. Bootstrap support analyses were done with 1000 replications, random addition of taxa, and SPR branch swapping at each replicate. PAUP was also used to generate character lists, using ACCTRAN optimisation on the trees from the third combined analysis, for clades discussed. Character evolution is thus interpreted from the trees based on all available data, since these trees form the best supported hypothesis of the phylogeny.

Results

The morphological analysis resulted in 824 trees 1558 steps long, consistency index 0.16 and retention index 0.58. The analysis based on molecular data resulted in excessive numbers of equally parsimonious trees and was not run to completion. The numerous (> 100000) shortest trees found were 11643 steps long, consistency index 0.27 (uninformative characters excluded) and retention index 0.55.

Fig. 1. Strict consensus of the 824 trees obtained from parsimony analysis of morphological data, continued in Fig. 2



Bootstrap analysis of the molecular data was completed, however, and the results proved to be very similar to those obtained from bootstrap analysis of combined data. The combined morphological + *rbcL* + *ndhF* analysis gave 920 trees 13403 steps long, consistency index 0.25 (uninformative characters excluded) and retention index 0.55. The strict consensus trees from the analyses are shown in Figs. 1–4. The trees are arranged with an implicit root between euasterids I and II, since previous analyses indicate that both groups are monophyletic (APG 1998; Soltis et al. 2000). The roots shown in Figs. 1–4 are thus only added for clarity; no outgroups outside the asterids were used for these analyses. Bootstrap support values are provided for the combined analysis, but not for the first analysis with morphological characters only, where bootstrap support for most clades is lower than 50%.

The bootstrap values from analysis of molecular data in general support the same clades as those supported by bootstrap analysis of the combined data. There is no case of contradicting bootstrap support in the molecular versus the combined data. Within Lamiales there is some contradicting topology between the trees from the molecular and the combined data, respectively, however only concerning nodes with bootstrap support < 50%. Some clades within the orders receive bootstrap support only from the combined data. Molecular data alone support some clades without bootstrap support from the combined data, especially within some of the orders (Lamiales, Apiales, Asterales, Lamiales), however only with low bootstrap values. Two cases of bootstrap support from molecular data alone are worth mentioning, I) the clade of all euasterids I excluding *Icacina* and Garryales (see Fig. 3), and II) the clade of all euasterids II excluding Aquifoliales (see Fig. 4). These two clades appear in the strict consensus from the combined data, however without bootstrap support. With molecular data alone the two clades, euasterids I sensu stricto and euasterids II sensu

stricto, receive 99% and 56% bootstrap support, respectively.

Discussion

The strict consensus from the morphological analysis is fairly well resolved (Figs. 1–2), although by the nature of the data, the support in terms of number of characters on the branches is low. Cladistic analysis of morphological data does recover several groups now identified and corroborated from analysis of molecular data, but with one exception, Dipsacales, the APG-orders are not recognised. In general, the morphological data seem to identify families and smaller groups of families, supported also by molecular data, but at the level of orders and above, relationships are only superficially in agreement with molecular studies. The distinction between euasterids I and II (APG 1998) becomes clear only after addition of molecular data.

Bootstrap support. The combined analysis of morphology and molecular data (Figs. 3–4) provides strong support for four of the orders. Gentianales are supported by a bootstrap value of 90%, Aquifoliales by 99%, Apiales by 98%, and Asterales by 85%. Garryales are not supported as monophyletic in this analysis. Solanales are monophyletic in all trees but without bootstrap support. Lamiales receive no bootstrap support as monophyletic but it appears as such if Carlemanniaceae are included. Dipsacales are supported as monophyletic only by inclusion of Adoxaceae (84% bootstrap support). Strangely, the combined data place *Lonicera* of Caprifoliaceae together with Adoxaceae whereas the other Caprifoliaceae genus *Triosteum* is clearly within Dipsacales (93% bootstrap support). The distinction of euasterids I sensu stricto, i.e. excluding *Icacina* and Garryales, and euasterids II sensu stricto, i.e. excluding Aquifoliales, is not supported by the combined data, but by the molecular data alone (asterisks in Figs. 3–4). Apparently, homoplasy in morphological characters at this comparatively high taxonomic level, obscures rather than reinforces the identification of these

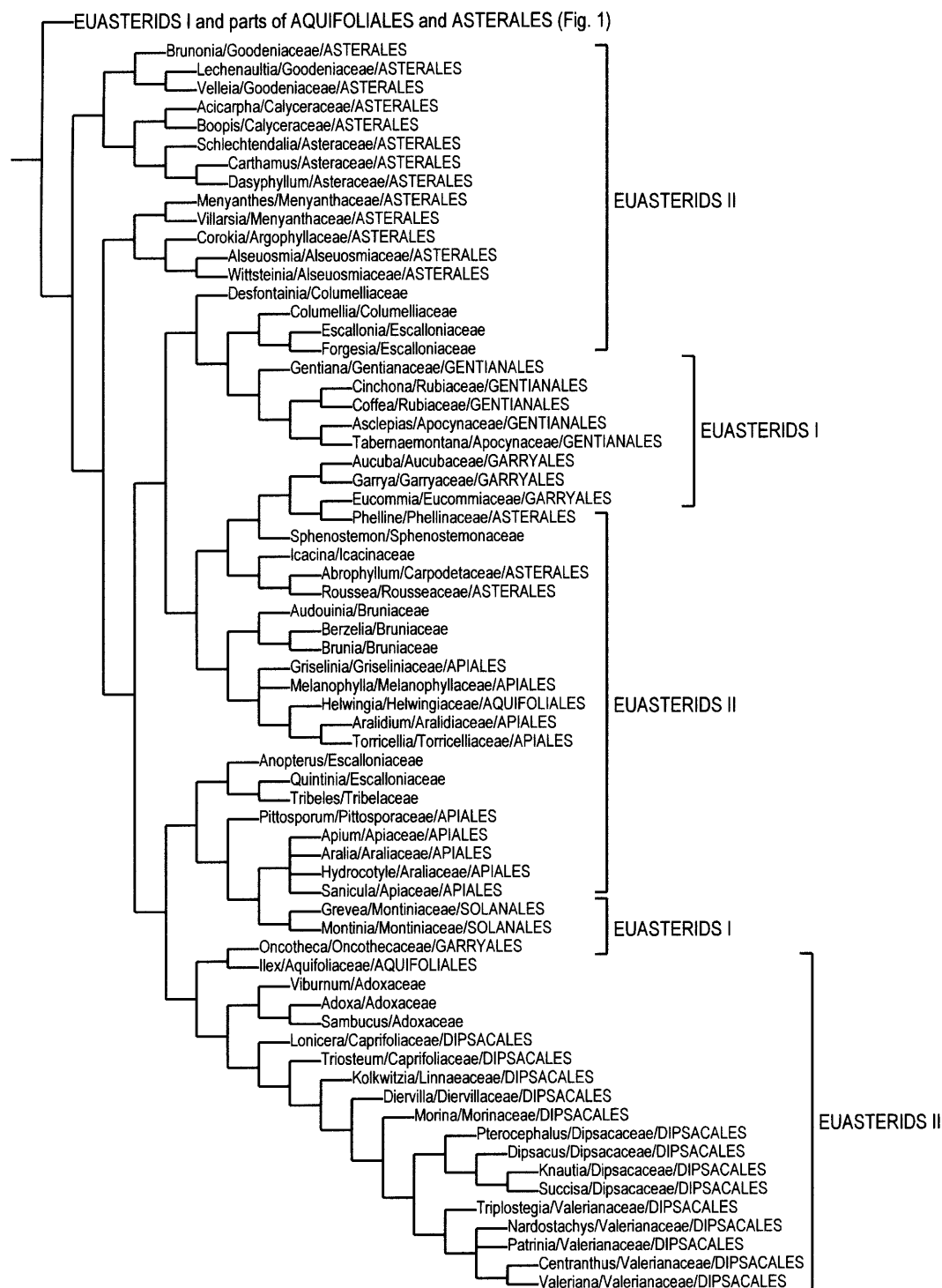


Fig. 2. Strict consensus of the 824 trees obtained from parsimony analysis of morphological data, continued from Fig. 1

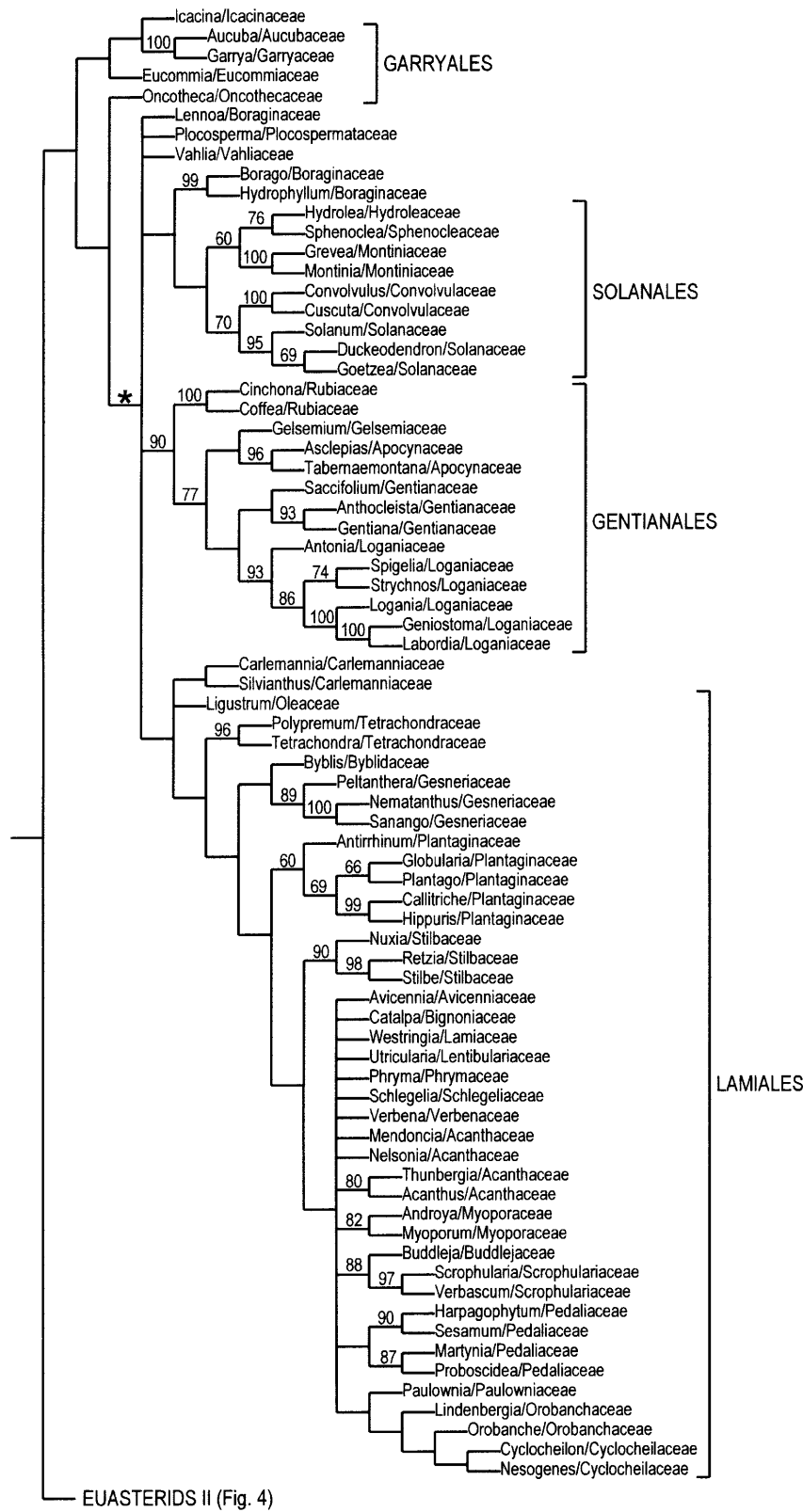


Fig. 3. Strict consensus of the 920 trees obtained from parsimony analysis of morphological, *rbcL*, and *ndhF* data, continued in Fig. 4. Bootstrap support is reported for nodes supported by a value above 50%. The clade of euasterids I sensu stricto, marked with an asterisk, receives 99% bootstrap support in the analysis of molecular data alone

two clades. The two clades have also been identified in other molecular analyses (Soltis et al. 2000). In particular, euasterids I sensu stricto are strongly supported (99%).

Euasterids I and II. As noted under Results, the trees are arranged with an implicit root between euasterids I and II, both groups presumably being monophyletic (APG 1998). A number of morphological features do distinguish the two groups but due to the considerable variation in their sister group (Cornales, Ericales, or both; APG 1998; Soltis et al. 2000), character polarities cannot be distinguished. Opposite leaves characterise most euasterids I, Columelliaceae, Adoxaceae, and Dipsacales. Excluding the latter three, euasterids II are mostly alternate-leaved. Leaf position is variable in other asterids (Cornales and Ericales) so the plesiomorphic condition within euasterids is unclear. Either opposite leaves are a synapomorphy for euasterids I with reversals within Lamiales and Solanales, or alternate leaves are a synapomorphy for euasterids II with reversals in Columelliaceae and Adoxaceae + Dipsacales. Entire leaf margins are more common among euasterids I and serrate-dentate leaf margins are more common among euasterids II. In our analysis, the leaf margin character distinguishes euasterids I and II, with a number of reversals within both groups. Again, it is unclear whether entire leaf margins are a synapomorphy for euasterids I or serrate-dentate leaf margins are a synapomorphy for euasterids II. Furthermore, the homology of characters such as leaf margins in different taxa often requires more detailed investigations.

Hypogynous flowers predominate in euasterids I and epigynous flowers in euasterids II. Epigynous flowers may then be interpreted as a synapomorphy for euasterids II (hypogynous flowers being plesiomorphic, found in other asterids) but there are many reversals to hypogynous flowers among euasterids II and there are parallelisms in epigynous flowers among euasterids I. The optimisation of this character is thus much dependent on the topology of the tree and the uncertain rela-

tionships among the major groups within both euasterids I and II. Two types of development of the corollas have been described, “early sympetaly” with a ring-shaped corolla primordium and “late sympetaly” with distinct petal primordia (Erbar and Leins 1996). Early sympetaly characterises euasterids I and late sympetaly euasterids II, however with exceptions in Oleaceae (Lamiales) and Rubiaceae (Gentianales). Both conditions are known from other asterids, early sympetaly in Cornales and late sympetaly in Ericales so it is unclear which type represents a synapomorphy. One possible synapomorphy for euasterids I is the fusion of the stamen filaments with the corolla. This is characteristic of most euasterids I with rather few exceptions but it is much more rare in other asterids, where it is found, e.g. in part of Asterales and in Columelliaceae, Adoxaceae, and Dipsacales. Fusion of stamen filaments and corolla may thus be interpreted as a synapomorphy for euasterids I with parallelisms within euasterids II. The fruits of euasterids I are frequently septicidal or loculicidal capsules but there are also many indehiscent fruit types. The fruits of euasterids II are mostly indehiscent, or more rarely capsules opening irregularly, by lids, septicidally or loculicidally. Thus there seems to be a distinction between dehiscent fruits in euasterids I and indehiscent fruits in euasterids II but the optimisation is uncertain (as with hypogynous versus epigynous flowers) as is determination of the plesiomorphic and apomorphic states.

Garryales. In the APG (1998) system Garryales comprise Aucubaceae, Garryaceae, Eucommiaceae and Oncothecaceae. In the tree based on combined morphological and molecular data *Aucuba*, *Garrya*, and *Eucommia* form a clade together with *Icacina*. *Oncotheca* is sister to the remaining euasterids I rather than to Garryales. The position of *Icacina* in Garryales deserves further investigation (cf. Savolainen et al. 2000b). Unisexual flowers and apical placentation are present in Garryales, and these features may be regarded as probable synapomorphies for Garryales, with

parallelisms within Aquifoliales (*Ilex*, *Helwingia*) and within Apiales (*Aralidium*, *Griselinia*, *Torriceilia*) of euasterids II.

Gentianales. Interpetiolar stipules with colleters (glands) are present in many Gentianales but absent from other asterids. These features are synapomorphies for Gentianales, although secondarily absent in some of the representatives, e.g. in Gentianaceae (cf. Backlund et al. 2000). There are also some synapomorphies from wood anatomy. Interxylary phloem and tracheary elements with vested pits are present in most Gentianales but rare in other asterids (interxylary phloem, e.g. in some Acanthaceae, Convolvulaceae, Solanaceae, and Styliaceae; vested pits in Montiniaceae and *Phyllonoma*). Intraxylary phloem on the other hand seems to be a synapomorphy for a subgroup, i.e. Gentianales excluding Rubiaceae. Alkaloids are common in Gentianales but also in several other asterids, and it is unclear whether the types found in Gentianales stem from one ancestral type and may be interpreted as a synapomorphy for the group.

Lamiales. Zygomorphic flowers with reductions in stamen number are common in Lamiales (found also in Dipsacales). Most Lamiales have four or two stamens but there are also many with five stamens. Reductions in stamen number are coupled to the specialised zygomorphic corollas (also in Dipsacales) and parsimoniously interpreted as a synapomorphy for Lamiales, however with several reversals to actinomorphic corollas with five stamens. Reversals to actinomorphic flowers with five stamens are now known to be triggered by simple genetic changes (e.g. Cubas et al. 1999). There are different types of zygomorphic flowers and the stamen reductions involve not only the number of fertile stamens but also differences in their length and transformations to staminodia. The precise nature of the first zygomorphic flowers in Lamiales are not known and the evolution of different types with their stamen modifications requires further investigation. Furthermore, classification within Lamiales is currently under substantial revision

(Olmstead and Reeves 1995, Wagstaff and Olmstead 1997, Wagstaff et al. 1998, Oxelman et al. 1999, Reveal et al. 1999), and should facilitate our understanding of morphological evolution within the group. Petal veins anastomosing between the petals are found in many Lamiales, in Dipsacales and Asterales of euasterids II, but not in other euasterids I. They are also absent from many Lamiales but are parsimoniously interpreted as a synapomorphy for Lamiales with secondary reversals within the group.

Solanales. In the APG system Solanales comprise Solanaceae, Convolvulaceae, Hydroleaceae, Montiniaceae, and Sphenocleaceae (cf. Olmstead et al. 1993). The circumscription was based on a three-gene analysis (APG 1998; Soltis et al. 1999, 2000), which supported the group as monophyletic although not recognised as such in earlier studies. The order is identified also by our data, albeit without bootstrap support. There are few if any morphological synapomorphies for Solanales. Alternate leaves are present in all five families (*Grevea* has opposite leaves) and may be one synapomorphy (with a reversal in *Grevea*). Other euasterids I generally have opposite leaves (cf. discussion above). There are synapomorphies for Convolvulaceae and Solanaceae, e.g. wood with inter- and intraxylary phloem and presence of similar alkaloids, but these features are not shared by the other families.

Apiales. A sheathing petiole is found in most Apiales and it is a characteristic synapomorphy for this group. Sympetaly is probably a synapomorphy for all asterids so secondarily free petals (choripetaly) are synapomorphies for various groups within the asterids. Apiales are one such group. They have a ring-shaped corolla primordium (“early sympetaly” according to Erbar and Leins 1996) but the developed corolla consists of free petals. It is possible that secondarily free petals are a synapomorphy for a large group euasterids II including not only Apiales but some of the families not classified to order, e.g. Bruniaceae, also with free petals. Plunkett et al. (1996) listed several similarities between the smaller families (Araldiaceae,

Griselinaceae, Melanophyllaceae, Torricelliaceae) and Apiaceae + Araliaceae but it is difficult to point out further morphological synapomorphies for the group as a whole.

Aquifoliales. Stipules are rare in asterids but found in Aquifoliales and constitute a possible synapomorphy. Stipules also occur in Bruniaceae, part of Apiales and Gentianales, but in the latter group mostly of the different interpetiolar type. One synapomorphy may be the unisexual flowers found in most Aquifoliales, if the bisexual flowers of *Phyllonoma* are interpreted as a reversal. Fleshy fruits may be another synapomorphy for Aquifoliales. Fleshy fruits occur also within all the other orders but they are parsimoniously interpreted as independent parallelisms.

Asterales. Valvate corolla aestivation is a probable synapomorphy for Asterales, with a reversal in Donatiaceae and Stylidiaceae to the more general imbricate condition. Valvate aestivation occurs also in many other euasterids, e.g. in Gentianales and Garryales, but is most parsimoniously interpreted as independent parallelisms from a plesiomorphic imbricate aestivation. A basic chromosome number of $x = 9$ may be interpreted as a synapomorphy for Asterales with several modifications inside the order (e.g. *Donatia* and *Stylidium* $x = 8$, Campanulaceae variable). The storage carbohydrate inulin occurs in many Asterales and is another probably synapomorphy. It is otherwise only known from a few scattered genera of euasterids (Porembski and Koch 1999). Secondary pollen presentation is considered characteristic of Asterales but the mechanisms are of different types and characterise subgroups of Asterales, not the whole order as presently circumscribed (Leins and Erbar 1990; Gustafsson and Bremer 1995, 1997; Gustafsson et al. 1996; Kårehed et al. 2000). Secondary pollen presentation is also present in one subfamily of Rubiaceae.

Dipsacales. Zygomorphic flowers are perhaps the most conspicuous morphological synapomorphy of the Dipsacales, although there are reversals to actinomorphic flowers, e.g. in Valerianaceae. Zygomorphic flowers are

otherwise found within specialised families and genera among other euasterids II, and generally in Lamiales of the euasterids I. The anther tapetum in most Dipsacales consists of three to four cell layers, an uncommon condition among euasterids II and found elsewhere in some families of Apiales. *Lonicera* of the Caprifoliaceae, however, has two cell layers as most other euasterids, so the three- to four-layered tapetum is best interpreted as a synapomorphy for a major subgroup of Dipsacales, excluding Caprifoliaceae and also with some reversals within Dipsacaceae. The tapetum is amoeboid, another uncommon character among euasterids and probably a synapomorphy for Dipsacales. It is found elsewhere, e.g. in *Adoxa* and *Columellia*. Pericyclic cork origin characterises Dipsacales (reversal in *Knautia*). It is rare in other euasterids and seems to provide a synapomorphy for Dipsacales, although it occurs also in Stylidiaceae.

Adoxaceae + Dipsacales. Corolla nectaries occur in Dipsacales and in *Adoxa* and some *Viburnum*. They are absent from most other euasterids (present within several Asterales) and thus parsimoniously interpreted as a synapomorphy for Adoxaceae and Dipsacales, with some reversals. The homology of these nectaries requires further investigation. Most euasterids have two carpels although there are increases to three or more carpels in several groups (they may also be seen as reversals to a more general three- to five-carpellate condition among eudicots in general). Dipsacales generally have three carpels (variable in Caprifoliaceae, two only in *Diervilla*) and three to five carpels occur in all Adoxaceae. Three or more carpels are thus interpreted as a synapomorphy for Adoxaceae and Dipsacales with reversals in *Diervilla* and some *Lonicera*.

Traditionally Adoxaceae and all its genera have been included in Dipsacales (e.g. Cronquist 1981). When the APG (1998) system was put together, there was no conclusive molecular support for a position of Adoxaceae in Dipsacales, and hence the family was left unclassified with respect to order. Adoxaceae sensu APG (1998) are well supported as

monophyletic from several types of data (e.g. cytology, Benko-Iseppon and Morawetz 2000). Given the bootstrap support for Adoxaceae and Dipsacales in the morphology + *rbcL* + *ndhF* analysis and the morphological synapomorphies hypothesised above, we here suggest that Adoxaceae are included in Dipsacales.

We thank Mats H.G. Gustafsson, Olof Ryding, and Lena Struwe who took part in the earlier preparations of the morphological data matrix. The study was supported by Swedish Natural Science Research Council grants to Kåre Bremer and Birgitta Bremer, respectively, and by a Helge Ax:son Johnson grant to Anders Backlund for computer hardware.

Appendix 1. Taxa and EMBL/NCBI accession numbers for the *rbcL* and *ndhF* sequences, and authors responsible for codings of morphological data (see author list for explanation of abbreviations). The classification follows APG (1998), except that several genera of Scrophulariaceae s.l. have been reclassified to Plantaginaceae and Orobanchaceae (Reveal et al. 1999). Also, several genera of Buddlejaceae have recently been reclassified to other families of Lamiales (Oxelmann et al. 1999)

Taxon	<i>rbcL</i>	<i>ndhF</i>	Authors
Euasterids I without order			
1. <i>Borago</i> /Boraginaceae	L11680	L36393	KA, AB
2. <i>Hydrophyllum</i> /Boraginaceae	L01927	AF047811	KA, AB
3. <i>Lennoa</i> /Boraginaceae	–	–	AB
4. <i>Plocosperma</i> /Plocospermataceae	Z68829	AJ011985	MB, US, AB
5. <i>Vahlia</i> /Vahliaceae	L11208	AJ236273	AB
Garryales			
6. <i>Aucuba</i> /Aucubaceae	L11210	AF060158	KA, US, AB
7. <i>Eucommia</i> /Eucommiaceae	L01917	–	KA
8. <i>Garrya</i> /Garryaceae	L01919	AF147714	KA, US
9. <i>Oncotheca</i> /Oncothecaceae	AJ131950	–	AB
Gentianales			
10. <i>Asclepias</i> /Apocynaceae	X91774	–	BS
11. <i>Tabernaemontana</i> /Apocynaceae	X91772	–	BS
12. <i>Gelsemium</i> /Gelsemiaceae	AJ011984	AF130170	MB
13. <i>Anthocleista</i> /Gentianaceae	L14389	AF235829	MB
14. <i>Gentiana</i> /Gentianaceae	L14398	L36400	MB, BB
15. <i>Saccifolium</i> /Gentianaceae	AJ242609	–	MB
16. <i>Antonia</i> /Loganiaceae	AJ235817	AJ235832	MB
17. <i>Geniostoma</i> /Loganiaceae	Z68828	AJ235835	MB
18. <i>Labordia</i> /Loganiaceae	AJ235820	AJ235836	MB
19. <i>Logania</i> /Loganiaceae	Z68826	AJ235837	MB
20. <i>Spigelia</i> /Loganiaceae	Y11863	AJ235840	MB
21. <i>Strychnos</i> /Loganiaceae	L14410	AJ235841	MB
22. <i>Cinchona</i> /Rubiaceae	AJ233990	AJ235843	KA
23. <i>Coffea</i> /Rubiaceae	X83631	AJ236290	KA
Lamiales			
24. <i>Acanthus</i> /Acanthaceae	L12592	–	BB
25. <i>Mendoncia</i> /Acanthaceae	–	–	AB
26. <i>Nelsonia</i> /Acanthaceae	L01935	–	AB
27. <i>Thunbergia</i> /Acanthaceae	L12596	AJ235844	BB
28. <i>Avicennia</i> /Avicenniaceae	U28868	–	AB
29. <i>Catalpa</i> /Bignoniaceae	L11679	L36397	MH, AB
30. <i>Buddleja</i> /Buddlejaceae	AJ001757	AF130143	MB, AB, MH

Appendix 1 (continued)

Taxon	<i>rbcL</i>	<i>ndhF</i>	Authors
31. <i>Byblis</i> /Byblidaceae	L01891	–	AB
32. <i>Cyclocheilon</i> /Cyclocheilaceae	U28871	–	AB
33. <i>Nesogenes</i> /Cyclocheilaceae	–	–	AB
34. <i>Nematanthus</i> /Gesneriaceae	L36466	AF130157	MH, AB
35. <i>Peltanthera</i> /Gesneriaceae	AJ001762	AF027281	MB, AB
36. <i>Sanango</i> /Gesneriaceae	AJ001763	AF027283	AB
37. <i>Westringia</i> /Lamiaceae	Z37474	–	MH, AB
38. <i>Utricularia</i> /Lentibulariaceae	L13190	–	MH, AB
39. <i>Androya</i> /Myoporaceae	AJ001756	AF027276	MB, AB
40. <i>Myoporum</i> /Myoporaceae	L36445	L36403	AB
41. <i>Ligustrum</i> /Oleaceae	L11686	AJ130164	BB, AB
42. <i>Lindenbergia</i> /Orobanchaceae	AJ001768	AF123686	MH
43. <i>Orobanche</i> /Orobanchaceae	U73970	–	MH
44. <i>Paulownia</i> /Paulowniaceae	L36447	L36406	AB
45. <i>Harpagophytum</i> /Pedaliaceae	L01923	–	BB, AB
46. <i>Martynia</i> /Pedaliaceae	–	AF190906	BB, AB
47. <i>Proscidea</i> /Pedaliaceae	L01946	AF123690	BB, AB
48. <i>Sesamum</i> /Pedaliaceae	L14408	L36413	BB
49. <i>Phryma</i> /Phrymaceae	U28881	–	AB
50. <i>Antirrhinum</i> /Plantaginaceae	L11688	L36392	MH
51. <i>Callitriche</i> /Plantaginaceae	L11681	L47330	BS, AB
52. <i>Globularia</i> /Plantaginaceae	AJ001764	AF123681	AB
53. <i>Hippuris</i> /Plantaginaceae	L36443	L36401	AB
54. <i>Plantago</i> /Plantaginaceae	L36454	AF130151	AB
55. <i>Schlegelia</i> /Schlegeliaceae	L36448	L36410	MH, AB
56. <i>Scrophularia</i> /Scrophulariaceae	L36449	L36411	MH, AB
57. <i>Verbascum</i> /Scrophulariaceae	L36452	L36452	MH, AB
58. <i>Nuxia</i> /Stilbaceae	AJ001761	AF027280	MB, AB
59. <i>Retzia</i> /Stilbaceae	Z29669	AF147716	MB
60. <i>Stilbe</i> /Stilbaceae	Z68827	AF027287	MB, BB
61. <i>Polypremum</i> /Tetrachondraceae	AJ011989	AJ011986	MB, AB
62. <i>Tetrachondra</i> /Tetrachondraceae	U28885	AF027272	AB
63. <i>Verbena</i> /Verbenaceae	Z37473	L36418	MH, AB
Solanales			
64. <i>Convolvulus</i> /Convolvulaceae	L11683	AJ236243	BS, AB
65. <i>Cuscuta</i> /Convolvulaceae	X61698	–	AB
66. <i>Hydrolea</i> /Hydroleaceae	L14293	AF013999	AB
67. <i>Grevea</i> /Montiniaceae	AJ315130	AJ315131	BS, AB
68. <i>Montinia</i> /Montiniaceae	L11194	AF130178	BS, AB
69. <i>Duckeodendron</i> /Solanaceae	Y14760	–	AB
70. <i>Goetzea</i> /Solanaceae	AF035738	–	AB
71. <i>Solanum</i> /Solanaceae	M76402	U47427	KA, AB
72. <i>Sphenoclea</i> /Sphenocleaceae	L18798	–	AB
Euasterids II without order			
73. <i>Adoxa</i> /Adoxaceae	L01883	AF060156	AB
74. <i>Sambucus</i> /Adoxaceae	L14066	AF130196	AB
75. <i>Viburnum</i> /Adoxaceae	X87398	AF027273	AB

Appendix 1 (continued)

Taxon	<i>rbcL</i>	<i>ndhF</i>	Authors
76. <i>Audouinia</i> /Bruniaceae	–	–	AB, US
77. <i>Berzelia</i> /Bruniaceae	L14391	AJ236241	AB, US
78. <i>Brunia</i> /Bruniaceae	Y10674	AF060159	AB, US
79. <i>Carlemannia</i> /Carlemanniaceae	AJ402937	–	AB
80. <i>Silvianthus</i> /Carlemanniaceae	–	–	AB
81. <i>Columellia</i> /Columelliaceae	Y10675	AF060160	AB
82. <i>Desfontainia</i> /Columelliaceae	Z29670	AJ011988	AB
83. <i>Eremosyne</i> /Eremosynaceae	L47969	AJ236272	AB
84. <i>Anopterus</i> /Escalloniaceae	Y10673	AJ292984	AB
85. <i>Escallonia</i> /Escalloniaceae	L11183	AJ236251	AB
86. <i>Forgesia</i> /Escalloniaceae	[AB unpubl.]	–	AB, JL
87. <i>Quintinia</i> /Escalloniaceae	X87394	AJ238344	AB, JL
88. <i>Icacina</i> /Icacinaceae	X69743	AJ400888	MB, AB
89. <i>Sphenostemon</i> /Sphenostemonaceae	AJ403005	–	US, AB, JL
90. <i>Tribeles</i> /Tribelaceae	AJ403010	–	AB
Apiales			
91. <i>Apium</i> /Apiaceae	L01885	–	KB, AB
92. <i>Sanicula</i> /Apiaceae	L11170	–	KB
93. <i>Aralia</i> /Araliaceae	L11166	–	KB, AB
94. <i>Hydrocotyle</i> /Araliaceae	U50236	–	KB
95. <i>Aralidium</i> /Aralidiaceae	AF299087	–	KB
96. <i>Griselinia</i> /Griselinaceae	L11225	AF130285	KB
97. <i>Melanophylla</i> /Melanophyllaceae	U50254	AJ236244	KB
98. <i>Pittosporum</i> /Pittosporaceae	U50261	AF130201	KB, AB
99. <i>Torricellia</i> /Torricelliaceae	AF299089	–	AB
Aquifoliales			
100. <i>Ilex</i> /Aquifoliaceae	M88583	AF130206	US, AB, JL
101. <i>Helwingia</i> /Helwingiaceae	L11226	AF130207	US
102. <i>Phyllonoma</i> /Phyllonomaceae	L11201	AF130208	US, AB
Asterales			
103. <i>Alseuosmia</i> /Alseuosmiaceae	X87377	AJ236239	JL
104. <i>Wittsteinia</i> /Alseuosmiaceae	X87399	AJ238345	JL
105. <i>Corokia</i> /Argophyllaceae	L11221	AF130182	JL
106. <i>Carthamus</i> /Asteraceae	L13862	L39417	KB
107. <i>Dasyphyllum</i> /Asteraceae	L13863	L39392	KB
108. <i>Schlechtendalia</i> /Asteraceae	–	–	KB
109. <i>Acicarpha</i> /Calyceraceae	X87376	–	JL
110. <i>Boopis</i> /Calyceraceae	L13860	L39384	JL
111. <i>Campanula</i> /Campanulaceae	L13861	L39387	JL
112. <i>Codonopsis</i> /Campanulaceae	L18797	AF130185	JL
113. <i>Cyananthus</i> /Campanulaceae	L18795	AF130186	JL
114. <i>Cyphia</i> /Campanulaceae	L18796	AJ238339	JL
115. <i>Cyphocarpus</i> /Campanulaceae	L18792	–	JL
116. <i>Lobelia</i> /Campanulaceae	L13930	AF130187	JL
117. <i>Nemacladus</i> /Campanulaceae	L18791	–	JL
118. <i>Abrophyllum</i> /Carpodetaceae	X87375	AJ238333	JL

Appendix 1 (continued)

Taxon	<i>rbcL</i>	<i>ndhF</i>	Authors
119. <i>Donatia</i> /Donatiaceae	X87385	AJ225074	JL, US
120. <i>Brunonia</i> /Goodeniaceae	X87380	–	JL
121. <i>Lechenaultia</i> /Goodeniaceae	X87388	–	JL
122. <i>Velleia</i> /Goodeniaceae	X87396	–	JL
123. <i>Menyanthes</i> /Menyanthaceae	L14006	L39388	JL
124. <i>Villarsia</i> /Menyanthaceae	L11685	AF130180	JL
125. <i>Pentaphragma</i> /Pentaphragmataceae	L18794	AF130183	JL
126. <i>Phelline</i> /Phellinaceae	X69748	AJ238342	JL
127. <i>Rousseia</i> /Rousseaceae	AF084477	AJ277384	JL
128. <i>Stylidium</i> /Stylidiaceae	L18790	AF130188	JL
Dipsacales			
129. <i>Lonicera</i> /Caprifoliaceae	X87389	AF027274	AB
130. <i>Triosteum</i> /Caprifoliaceae	–	AF161292	AB
131. <i>Diervilla</i> /Diervillaceae	Z29672	AF060164	AB
132. <i>Dipsacus</i> /Dipsacaceae	L13864	AF130190	AB
133. <i>Knautia</i> /Dipsacaceae	Y10698	AF161298	AB
134. <i>Pterocephalus</i> /Dipsacaceae	Y10702	–	AB
135. <i>Succisa</i> /Dipsacaceae	–	AF130191	AB
136. <i>Kolkwitzia</i> /Linnaeaceae	AJ315129	AF161294	AB
137. <i>Morina</i> /Morinaceae	Y10706	–	AB
138. <i>Centranthus</i> /Valerianaceae	AJ277857	AF161297	AB
139. <i>Nardostachys</i> /Valerianaceae	Y10705	–	AB
140. <i>Patrinia</i> /Valerianaceae	Y10704	AF161296	AB
141. <i>Triplostegia</i> /Valerianaceae	Y10700	–	AB
142. <i>Valeriana</i> /Valerianaceae	L13934	AF130192	AB

Appendix 2. Morphological, anatomical, embryological, palynological, chemical, chromosomal, and macromolecular characters**Vegetative morphology and anatomy**

- Habit, 0 = herbaceous, 1 = woody, 2 = suffrutescent.
- Duration, 0 = perennial, 1 = annual.
- Phyllotaxy, 0 = alternate, 1 = opposite, 2 = verticillate.
- Leaf arrangement, 0 = not rosulate, 1 = rosolute only, 2 = leaf rosette and leaves along stem.
- Petiole, 0 = absent, 1 = present and not sheathing, 2 = present and sheathing.
- Stipules, 0 = absent, 1 = present and free, 2 = present and fused pairwise, interpetiolar, 3 = present and fused to a sheath.
- Leaf shape, 0 = simple, 1 = palmately lobed, 2 = pinnately lobed, 3 = palmately compound, 4 = pinnately compound.
- Leaf margin, 0 = entire, 1 = serrate or dentate, 2 = spinulose.
- Primary leaf venation, 0 = pinnately veined, 1 = palmately veined, 2 = unbranched.
- Secondary leaf venation, 0 = craspedodromous, 1 = camptodromous. See Hickey & Wolfe (1975).
- Colleters, 0 = absent, 1 = ordinary, 2 = feather-like. Colleters are glands of the stipules and calyx lobes in many Gentianales.
- Stomata type, 0 = anomocytic, 1 = paracytic, 2 = anisocytic, 3 = diacytic, 4 = tetracytic.
- Leaf vernation, 0 = conduplicate, 1 = circinate, 2 = involute, 3 = supervolute, 4 = plicate, 5 = flat/curved.
- Calcified trichomes, 0 = absent, 1 = present.

Appendix 2 (continued)

-
15. Silicified trichomes, 0 = absent, 1 = present.
 16. Nodes, 0 = unilacunar, 1 = trilacunar, 2 = multilacunar.
 17. Leaf hypodermis, 0 = absent, 1 = present.
 18. Hydatodes, 0 = absent, 1 = present.
 19. Star-shaped idioblasts, 0 = absent, 1 = present.
 20. Ca-oxalate crystals in wood, 0 = absent, 1 = present.
 21. Endodermis in stem, 0 = absent, 1 = present.
 22. Casparian thickening in endodermis, 0 = absent, 1 = present.
 23. Vestured pits, 0 = absent, 1 = present. Vestured pits have outgrowths from the secondary wall covering the tracheary element pit cavities (Bailey 1933).
 24. Intraxylary phloem, 0 = absent, 1 = present.
 25. Interxylary phloem, 0 = absent, 1 = present.
 26. Latex cells, 0 = absent, 1 = single, 2 = forming lysigenous ducts, 3 = forming schizogenous ducts.
 27. Resins cells, 0 = absent, 1 = single, 2 = forming lysigenous ducts, 3 = forming schizogenous ducts.
 28. Domatia, 0 = absent, 1 = present.
 29. Vessel element perforations, 0 = scalariform, 1 = simple.
 30. Tracheary element pits, 0 = simple, 1 = bordered. The tracheary elements (vessels and tracheids) are interconnected by pits, which may be bordered, i.e., provided with a secondary wall partly covering the pit cavity.
 31. Tracheary element pit arrangement, 0 = scalariform, 1 = opposite, 2 = alternate. The pits may be arranged in diagonal rows (alternate), in horizontal rows (opposite), or they may be horizontally elongated and arranged in a ladder-like (scalariform) fashion.
 32. Apotracheal wood parenchyma, 0 = present and diffuse, 1 = present and banded, 2 = absent. Apotracheal wood parenchyma is not associated with the vessels. It may consist of single cells or strands of few cells (diffuse), or of whole layers of cells (banded).
 33. Paratracheal wood parenchyma, 0 = present and scanty, 1 = present and unilateral, 2 = present and vasicentric, 3 = absent. Paratracheal wood parenchyma is distinctly associated with the vessels. It may consist of discontinuous strands of cells (scanty), continuous strands along one side of the vessel (unilateral) or of whole sheaths around the vessel (vasicentric).
 34. Wood rays, 0 = heterocellular, 1 = homocellular. This character refers to whether the parenchymatic wood rays consist of the same or of different cell types.
 35. Wood rays, 0 = uniseriate, 1 = pluriseriate. The rays may consist of single rows or of several parallel rows and cells.
 36. Cork origin, 0 = pericyclic, 1 = superficial.
 37. Septate wood fibres, 0 = absent, 1 = present.
 38. Vascular flankbridge in stem, 0 = absent, 1 = present.

Flowers

39. Bracteole pair beneath flower, 0 = absent, 1 = present and one, 2 = present and supernumerary, 3 = present and forming an epicalyx.
 40. Sex distribution, 0 = unisexual flowers, 1 = bisexual flowers.
 41. Perianth position, 0 = hypogynous, 1 = semiepigynous, 2 = epigynous.
 42. Perianth composition, 0 = sepals and petals, 1 = sepaloid, 2 = petaloid.
 43. Sepal bud aestivation, 0 = valvate, 1 = imbricate, 2 = right-contorted, 3 = left-contorted, 4 = open.
 44. Sepal fusion, 0 = fused, 1 = free.
 45. Sepal number, 0 = two, 1 = three, 2 = four, 3 = five, 4 = numerous.
 46. Petal bud aestivation, 0 = valvate, 1 = imbricate, 2 = right-contorted, 3 = left-contorted.
 47. Petal apex, 0 = flat and straight, 1 = with inflexed tips.
-

Appendix 2 (continued)

-
48. Petal fusion, 0 = fused, 1 = free.
 49. Petal primordium, 0 = ring-shaped, 1 = distinct and free, 2 = ring-shaped of type II. Development of the corollas are either from a ring-shaped corolla primordium (“early sympetaly”) or from distinct petal primordia (“late sympetaly”; Erbar 1991, Erbar & Leins 1996). A second type of ring-shaped primordium was described by Roels & Smets (1994, 1996).
 50. Petal numbers, 0 = two, 1 = three, 2 = four, 3 = five, 4 = numerous.
 51. Petal symmetry, 0 = actinomorphic, 1 = zygomorphic of *Lamium*-type, 2 = zygomorphic of *Cyphia*-type.
 52. Corolla orientation, 0 = abaxial of *Lamium*-type, 1 = adaxial of *Cyphia*-type. The corollas of euasterids are usually five-lobed and many are zygomorphic and two-lipped. In *Lamium* (Lamiaceae) and many other euasterids the upper lip is two-lobed and the lower lip is three-lobed with the middle lobe oriented downwards along a perpendicular plane. In *Cyphia* and other Campanulaceae the lower lip is two-lobed and the upper lip is three-lobed with the middle lobe oriented upwards along a perpendicular plane. Hence there is a distinction not only between the number of lobes in the lips of five-lobed corollas, but also in the orientation of the corolla, so that it is the lowermost lobe that is oriented along the perpendicular plane in *Lamium*, whereas it is the uppermost lobe that is oriented along the perpendicular plane in *Cyphia*. This distinction is visible also in actinomorphic corollas and the character is thus applicable, albeit sometimes difficult to observe, in plants with five-lobed, actinomorphic corollas. Note that in *Lobelia* and its relatives (Campanulaceae-Lobelioideae) the flowers are resupinate so that the flowers seem to be of the *Lamium*-type, although they are actually of the *Cyphia*-type, which becomes evident when the resupination is taken into account. Resupination is an autapomorphy for *Lobelia* in our sample of taxa, and hence not included in our set of characters.
 53. Petal wings, 0 = absent, 1 = present.
 54. Petal hairs, 0 = absent, 1 = present.
 55. Petal appendages, 0 = present as a corona, 1 = present as protrusions in the petal lobe sinuses, 2 = absent.
 56. Petal venation, 0 = anastomosing between petals, 1 = not anastomosing. This character is reviewed by Gustafsson (1995).
 57. Floral nectar disc, 0 = absent, 1 = present and intrastaminal, 2 = present and extrastaminal.
 58. Corolla nectaries, 0 = absent, 1 = present.

Androecium

59. Androecium orientation, 0 = central, 1 = abaxial, 2 = adaxial. This character refers to the general position of the stamens in the flower. They may form a central bundle so that access to the inside of the flower is between the stamens and the corolla wall or they may be peripherally oriented so that access to the flower is inside the ring of stamens. In zygomorphic flowers, the stamens may be abaxially or adaxially oriented, i.e., towards the lower or upper wall of the corolla.
 60. Stamen number, 1 = one, 2 = two, etc. 9 = \geq nine
 61. Stamen length, 0 = all equal, 1 = unequal.
 62. Stamen position, 0 = alternisepalous, 1 = oppositisepalous.
 63. Stamens adnate to style, 0 = no, 1 = yes.
 64. Staminodes, 0 = absent, 1 = present.
 65. Filament fusion, 0 = free, 1 = forming a tube.
 66. Filament hairs, 0 = absent, 1 = present.
 67. Filament fused to corolla, 0 = no, 1 = yes.
 68. Anther attachment, 0 = dorsifixed, 1 = basifixed, not sagittate, 2 = basifixed, sagittate. Thecae of basifixed anthers are sometimes prolonged below the connective and the attachment point to the filament. The anthers then become sagittate and superficially similar to dorsifixed anthers although they are actually basifixed.
 69. Anther fusion, 0 = free, 1 = connivent, 2 = entangled, 3 = agglutinated
-

Appendix 2 (continued)

-
70. Anther opening, 0 = extrorse, 1 = latrorse, 2 = introrse.
 71. Anther hairs, 0 = absent, 1 = present.
 72. Number of sporangia in each theca, 0 = one, 1 = two.
 73. Apical anther appendage, 0 = absent, 1 = present, 2 = present and glandular.

Gynoecium

74. Carpel number, 0 = > nine, 1 = one, 2 = two, 3 = three, etc.
75. Ovary locules, 0 = unilocular, 1 = bilocular, 2 = trilocular, 3 = plurilocular.
76. Placentation, 0 = axile, 1 = parietal/marginal, 2 = basal, 3 = apical, 4 free-central.
77. Placenta upcurved, 0 = no, 1 = yes.
78. Placenta intrusion, 0 = not intrusive, 1 = intrusive.
79. Style, 0 = absent, 1 = present, one per carpel, 2 = present, single. Euasterids have at least two carpels. If there are several styles, there is one per carpel. If there is a single style, it consists of fused parts from the different carpels.
80. Style hairs beneath the stigma, 0 = absent, 1 = present.
81. Secondary pollen presentation, 0 = absent, 1 = present. For a review of this character, see Leins & Erbar (1990)
82. Style attachment, 0 = terminal, 1 = basal (gynobasic), 2 = lateral.
83. Stigma shape, 0 = entire, 1 = lobed, 2 = capitate.
84. Stigma surface, 0 = dry, 1 = wet.
85. Placenta texture in fruit, 0 = dry, 1 = fleshy.
86. Fruit wall, 0 = fleshy, 1 = dry.
87. Endocarp, 0 = not sclerified, 1 = sclerified.
88. Fruit dehiscence, 0 = indehiscent, 1 = septicidal, 2 = loculicidal, 3 = both septicidal and loculicidal, 4 = irregular, 5 = by lids.
89. Ovule number, 0 = one per carpel, 1 = two per carpel, 2 = > two per carpel.
90. Endocarp and seed coat fusion, 0 = absent, 1 = present.
91. Seed dispersal adaptations, 0 = none, 1 = wings, 2 = plumes.
92. Fruit dispersal adaptations, 0 = none, 1 = plumes, 2 = awns and bristles, 3 = wings.

Embryology and palynology

93. Anther epidermis, 0 = persistent, 1 = degenerating.
 94. Endothecium with fibrous thickenings, 0 = absent, 1 = present.
 95. Number of middle layers in anther wall, 0 = none, 1 = one, 2 = two, 3 = three, 4 = > three.
 96. Tapetum type, 0 = glandular, 1 = amoeboid.
 97. Number of tapetum cell layers, 0 = one, 1 = two, 2 = three, 3 = four, 4 = numerous.
 98. Number of nuclei in tapetum cells, 0 = mononucleate, 1 = binucleate, 2 = multinucleate.
 99. Arrangement of microspores, 0 = tetrahedral, 1 = isobilateral, 2 = decussate, 3 = T-shaped, 4 = linear.
 100. Number of cells in male gametophyte, 0 = two-celled, 1 = three-celled.
 101. Pollen shape, 0 = prooblate, 1 = oblate, 2 = spheroid, 3 = prolate, 4 = perprolate. Pollen terminology generally follows Erdtman (1952).
 102. Aperture number, 1 = one, 2 = two, 3 = three, 4 = four, 5 = five, 6 = six, 7 = numerous.
 103. Amb type, 0 = sharply angulaperturate, 1 = angulaperturate, 2 = standard, 3 = planaperturate, 4 = sinaperturate, 5 = fossaperturate. The amb type refers to the position of the apertures along the equator of the pollen grain, i.e., as seen in equatorial cross-section. If this cross-section is angular or even star-shaped, the apertures may be situated on the edges (angulaperturate and sharply angulaperturate, respectively), on the flat sides (planaperturate), or in the more or less deeply concave sides seen in cross-section (sinaperturate to fossaperturate). In the common situation with rounded or globose pollen grains with a circular cross-section, no such distinction can be made (standard type).
-

Appendix 2 (continued)

-
104. Aperture type, 0 = leptate, 1 = trichotomocolpate, 2 = colpate, 3 = porate, 4 = colporate, 5 = pororate.
105. Equatorial constrictions on colpi, 0 = absent, 1 = present.
106. Exine type, 0 = crassinexinous, 1 = crassisexinous, 2 = isoexinous.
107. Columella layer, 0 = absent, 1 = reduced, 2 = prominent and unbranched, 3 = prominent and branched.
108. Tectum, 0 = semitectate, 1 = tectate.
109. Microperforations, 0 = absent, 1 = present.
110. Exine sculpturing, 0 = smooth, 1 = granulose, 2 = verrucose, 3 = microechinate, 4 = echinate.
111. Ovule type, 0 = amphitropous, 1 = anatropous, 2 = hemianatropous, 3 = campylotropous, 4 = orthotropous.
112. Nucellus type, 0 = tenuinucellate, 1 = crassinucellate, 2 = pseudocrassinucellate
113. Integument number, 0 = unitegmic, 1 = bitegmic.
114. Hypostase, 0 = absent, 1 = present.
115. Endothelium, 0 = absent, 1 = present.
116. Obturator, 0 = absent, 1 = present.
117. Parietal tissue, 0 = absent, 1 = present.
118. Embryo sac formation, 0 = *Polygonum* type, 1 = *Adoxa* type, 2 = *Drusa* type.
119. Embryogeny type, 0 = Solanad, 1 = Caryophyllad, 2 = Asterad, 3 = Onagrad, 4 = Piperad, 5 = Chenopodiad.
120. Endosperm formation, 0 = cellular, 1 = nuclear, 2 = helobial.
121. Terminal endosperm haustoria, 0 = absent, 1 = present.
122. Chalazal endosperm haustoria, 0 = absent, 1 = present.
123. Suspensor, 0 = absent, 1 = present.
124. Endosperm in seed, 0 = absent, 1 = present and scanty, 2 = copious.
125. Endosperm storage compounds, 0 = starch, 1 = fat, 2 = protein.
126. Chlorophyll in embryo, 0 = absent, 1 = present.
127. Embryo shape, 0 = straight, 1 = curved.
128. Embryo storage compounds, 0 = starch, 1 = fat, 2 = protein.
129. Seed coat type, 0 = exotestal, 1 = mesotestal, 2 = endotestal, 3 = exotegminal, 4 = mesotegminal, 5 = endotegminal. The different seed coat types are described by Corner (1976).

Chemical, chromosomal, and macromolecular data

130. Cephalaroside, 0 = absent, 1 = present.
131. Aucubine, 0 = absent, 1 = present.
132. Polyacetylenes, 0 = absent, 1 = present.
133. Iridoids, 0 = absent, 1 = present.
134. Saponins, 0 = absent, 1 = present.
135. Proanthocyanidins, 0 = absent, 1 = delphinidin, 2 = cyanidin.
136. Alkaloids, 0 = absent, 1 = present.
137. Myreticin, 0 = absent, 1 = present.
138. Flavonols, 0 = absent, 1 = quercetin, 2 = kaempferol, 3 = both quercetin and kaempferol.
139. Coumarines, 0 = absent, 1 = present.
140. Grisenoliside, 0 = absent, 1 = present.
141. Inulin, 0 = absent, 1 = present.
142. Chromosome bas number, a = 4, b = 5, c = 6, d = 7, e = 8, f = 9, g = 10, h = 11, i = 12, j = 13, k = 15, l = 16, m = 17, n = 18, p = 21, q = 22, r = 23, s = 25, t = 26, u = 27.
143. CIR regions, 0 = absent, 1 = present. CIR regions are cold-induced undercontracted chromosome regions described by Benko-Iseppon & Morawetz (1993).
-

Appendix 2 (continued)

144–147. RFLP data. 0 = absent, 1 = present. Restriction fragment length polymorphism data from the chloroplast DNA are taken directly from the tables in Downie & Palmer (1992) complemented for some taxa not represented in those tables (S. Downie pers. comm.). The data have been interpreted as absence/presence of three deletions of 600, 400 and 500 bp, respectively. (Characters 144, 145, 147) and a 500 bp insertion (character 146).

Appendix 3. Data matrix for the taxa listed in Appendix 1 and the 147 characters listed in Appendix 2, a = 01, b = 02, c = 03, d = 04, e = 12, f = 012, g = 23, h = 123, i = 0123, j = 023, k = 13, l = 134, m = 14, n = 013, o = 024, p = 0124, q = 0123, r = 1234, s = 035, t = 0235, u = 24, v = 34, w = 45, x = 2345, y = 246, z = 12345, A = 235, B = 567890, C = 234, D = 1?, E = 3456, F = 034, G = 014, H = 345, I = 56, J = 456, K = 458, L = 124, M = 135, N = 25, O = 123456, P = 34567, Q = 67, R = 234567, S = 35, T = 07, U = 36, V = 567, W = 4567, X = 145, Z = 89, # = 56789, § = 4689, & = 012345. This coding does not apply to character 142 which has more than 10 states coded by letters

1. <i>Borago</i> /Boraginaceae				0aabf00a01	000110000r	00a000001a
2a0f1a1001	00m03h0013	0000111005	0100001a12	01021b0020	0100010010	0001e0??a1
g724010100	e0011a005a	1012?0a?00	00000a?300	1e00000		
2. <i>Hydrophyllum</i> /Boraginaceae				000210p0a1	0001000001	1000000011
203b?10001	00103k0013	0000110005	0100011a02	0102aa0120	0000010Ce0	00??10?0?0
331u1101?0	1000100001	1102e00?00	000a000101	0f?????		
3. <i>Lennoa</i> /Boraginaceae				01000000??	0??00?0000	00?000001?
?23????011	00a0va001v	0?002?00a#	1100001?02	010B300020	00e?010410	000010????0
23N4012100	1000000010	0012000030	000?000000	0f?????		
4. <i>Plocosperma</i> /Plocospermataceae				1010?000?0	00?10?0000	00???0001?
?????????a	0010v100?v	0?002?100I	1100001002	01020100e0	001?010ea0	20?????????
?3?4??2???	?0?????????	???1??0?0	0?0?????????	?????????		
5. <i>Vahlia</i> /Vahliaceae				0a10?000??	0??00?000?	00?00000??
????1???1	20013101?3	0?0?211005	0100000002	010g030110	001?010r20	00???0?1a0
??????????	101?1?0010	010??????0	0??????????	?????????		
6. <i>Aucuba</i> /Aucubaceae				1010100a01	00?0010001	000000000a
1200110?a0	2041200102	0?00211004	0100000002	010e030010	0020?00000	00?????????
232400?0?0	11001?10?0	???20?0?0	1?1?0?21?1	?e?0000		
7. <i>Eucommia</i> /Eucommiaceae				100010010?	003aa00000	0000010011
?a3?a1?000	0?????????	??????0?0#	0?0000?10?	0112130?20	001?010010	0301e0?e00
3344110100	1100001000	00122?0?0	001?200h01	0m?????		
8. <i>Garrya</i> /Garryaceae				1010100001	0100011011	0000000001
e020a10?00	21002?????	??????0?04	000000?102	010g030110	0000010000	0001e1??00
2324011100	1101011001	00120?00?0	101?110000	0???????		
9. <i>Oncotheca</i> /Oncothecaceae				1000100001	0a?0021011	00???0000?
?00??1?011	00113100?3	0?000?0?05	01000011b0	00a53c0010	000?0010a0	00?????????
23541?2110	1000000???	0002??0?0	0??????????	?s?????		
10. <i>Asclepias</i> /Apocynaceae				f0e0an000?	1f500a0001	10111h0111
?a20a1?001	00a0320023	000?2?0005	01101001?2	00121a0020	1021010120	2000m0h041
?E??0?0?00	1000000001	001e1100?0	00?0010300	0(ghi)00100		
11. <i>Tabernaemontana</i> /Apocynaceae				1010ag0001	110000000e	00110h0110
?230a11?11	00103g0023	000?e?1005	01100a1102	01e21c0021	a0fa00?f20	000140?0f1
ev240?????	1000100011	00021000?0	001af1?i00	0(efghi)00000		

Appendix 3 (continued)

12. <i>Gelsemium</i> /Gelsemiaceae				1010120001	1150000000	000100001?
22b1a10?11	00113100?3	0?002?0005	0100001201	0102100020	001?010020	00????????
g324112110	1000000030	11a2000?0	0?1a01????	?e0????		
13. <i>Anthocleista</i> /Gentianaceae				1010100000	0??00??0??	?????000??
???????11	00112g00?4	0?000???0Z	0?00001102	0104k00120	002?101020	00????????
e32v00a100	100????0??	??????????	?1????????	???????		
14. <i>Gentiana</i> /Gentianaceae				0aeb0b0001	abs00fa00r	10a110001?
?23200??11	00m0vh001v	000011a003	0100001f02	0102010a20	0011010120	000111?0a1
hO?C?1????	1001100001	0002100000	0?1001????	? (fg) 00000		
15. <i>Saccifolium</i> /Gentianaceae				1000100010	02?00?0000	00???0000?
?23????001	00103100?3	0?0?2?00?5	010000110e	0112a00?20	001?????2?	??????????
?3????????	000???????	?????????0	0?1?0?0???	???????		
16. <i>Antonia</i> /Loganiaceae				1010120a0?	1a?00?????	?11100?11
?03?0??21	00Ga3000?3	0??2?a005	010000100e	0102100?20	00e?111120	10????????
232400?1?0	100000003a	11021?0?0?	?0?0?0???	?h?????		
17. <i>Geniostoma</i> /Loganiaceae				e010ag000a	1?500?????	?11100?1?
?af?a?1?1a	00103h00?3	0001210005	0000001102	a11210012a	00b?111m20	00????????
ep?300?110	1000000030	1102100?0?	?1?1?a????	?g?????		
18. <i>Labordia</i> /Loganiaceae				e010ag000a	1??00?????	?11100?0?
?af?a?1?1a	00103g00?3	0001210005	0000001102	a11ge0012a	00b?111m20	00????????
e413001110	1000000030	1102100?0?	?1?1?a????	?g?????		
19. <i>Logania</i> /Loganiaceae				a010ag000?	1?000f0000	00a110001?
2200a10?11	0010g100?g	01002?000w	0100001102	0102100020	00f?010120	00????????
e314a12110	1000000030	11a2100?00	001a010??0	??0????		
20. <i>Spigelia</i> /Loganiaceae				ba10a20000	10?0000010	0011000011
2231010?01	00aa3000?3	0?002?1005	0100011e02	010210012a	00b?010M20	00??0?0???
e31202?110	200000003a	1102110?00	0?????????	??00000		
21. <i>Strychnos</i> /Loganiaceae				10101b0000	11?0001010	0011100a11
2b2aa10?01	001ag000?g	000a2?000w	01000a12a2	a112100020	00e?10a0f0	00?1e001b1
eCe4022?10	1000000031	11021?0?00	0?1101????	??00000		
22. <i>Cinchona</i> /Rubiaceae				1010120001	110000?10v	1110100111
20cb1a0?11	2040300003	000121100w	0100001002	0112100120	001?010120	100110?0f0
2324020110	1000a10001	00a2100000	0010a11a?0	1m00000		
23. <i>Coffea</i> /Rubiaceae				1010120001	110000?103	111010aa11
2??011??11	2040g3000r	000021100w	0100001002	0112100120	101?100000	000110?0?0
2v240201?0	1000a10001	00?2100000	0010a11a?0	0h00000		
24. <i>Acanthus</i> /Acanthaceae				101a100100	030000101u	0001?00110
?20b0110e1	004agD001h	10002010b4	0100001002	1102100020	0010010210	000110?e?1
33220?21?4	h001010000	111110a000	0?1a01?c?0	?(eh)00000		
25. <i>Mendoncia</i> /Acanthaceae				1010?000?0	03?00?0000	000000001?
???????11	00403v0013	10?02?10?w	110a001?0?	01021a0020	001??010a0	0?????????
2524001110	n00101?0?0	111110?000	?1????????	???????		
26. <i>Nelsonia</i> /Acanthaceae				0010100001	03?00?0000	00?1000010
?0?????01	0010210013	1000200?22	0100011200	1102100020	001?010220	000110?e?0
3324?1?1?0	0001110030	1111101000	0?1??????0	?n?????		
27. <i>Thunbergia</i> /Acanthaceae				a0101001a0	03000?000e	10?11000??
?????1??11	0040v30003	a0002010a5	110a001002	11a210002a	0011010210	0000100?00
21?01????	k0010100?0	1011101000	0?100?????	?c?????		

Appendix 3 (continued)

28. <i>Avicennia</i> /Avicenniaceae				10101000??	03?00?100?	000??0001?
?af1????11	00103100?2	0?002?0004	a100001?0?	01021?0?20	00???10z10	0???g0???0
23240e?1?0	1000a00030	11?0?1?0?0	0???0?0?0	?c?????		
29. <i>Catalpa</i> /Bignoniaceae				101010raa0	0a00000000	0000000110
?2b0aaa?01	00403a0013	10002?1025	1101001202	0a02100a20	0011010h20	a00a41??00
232u0101?0	e001100030	1110?00?00	001a0a?a?0	0d00100		
30. <i>Buddleja</i> /Buddlejaceae				10e0120a01	0?000?000r	000000001a
?200a0a?a1	0010210012	00012?a004	01000a1202	0104300120	002?010220	a001100?b0
g32402?110	e001100030	1101100?00	101100?b00	0o00000		
31. <i>Byblis</i> /Byblidaceae				a000100000	01100?0000	00000000a?
?23????001	00103h00?3	0?002?0?05	01000011a?	0102100?20	002?010220	00?????????
e322?2????	1010100?0	11?2?00000	110?0?????	???????		
32. <i>Cyclocheilon</i> /Cyclocheilaceae				0010100100	0?00?0?0??	?????000??
??????011	02???100?3	0000210004	1100011202	01020a0121	000?0102e0	00?????????
232201?111	?????????	???0?????0	0?????????	???????		
33. <i>Nesogenes</i> /Cyclocheilaceae				0?10100100	0?00?0?0??	?????000??
??????01	00?03100?3	0?0?2?0?04	1?000?120?	0102100020	002?010000	00?????????
232201?111	?????????	???2?????0	0?????????	???????		
34. <i>Nematanthus</i> /Gesneriaceae				a010100a00	02200faaaa	aa00000010
?2cb?a??01	0000310013	100a2?1025	1101001ea2	a102010120	001a010220	000110?2b0
?3?4??????	100a100030	11021000?0	0?0000?0?0	?000000		
35. <i>Peltanthera</i> /Gesneriaceae				1010100a0?	0?00??????	?????000??
????????01	000a3000?3	0?01211005	010000110?	0002100120	002?011220	10?????????
??????????	??????????	??????????	??????????	???????		
36. <i>Sanango</i> /Gesneriaceae				1010120a??	02?002100m	0000000001
22201?1111	00?03100?3	1001211005	0101011102	0102100120	001?011320	0011???????
e3?4??????	1?????????0	???2??0???	?0?????????	?1?????		
37. <i>Westringia</i> /Lamiaceae				aa10a0da01	0300001a01	a100001010
?200aa1?01	00m0310013	100a2?1024	110a0a1ba2	0102120020	0a10010010	000110?2b0
kU220bea10	1001110030	110e100e?0	0?100a?0?0	?(bcdefgh)00000		
38. <i>Utricularia</i> /Lentibulariaceae				000010000?	0000000000	00?00000??
??????0a1	00m0j10013	10002?00?4	110a001002	0102040020	0011010o20	000110?ef1
372401?1??	10011000S0	11001100?0	101?0a0000	0e?????		
39. <i>Androya</i> /Myoporaceae				1010100000	0?00?0?0??	?????000??
????????01	00113100?3	0?00210005	0100001101	1102100120	001?010220	00?????????
??????????	??????????	??????????	??????????	???????		
40. <i>Myoporum</i> /Myoporaceae				1000a00a0?	0?00000001	000000101?
?2fa?1??01	0010310013	100020010w	a10a001a02	0102100020	0020001010	00???0???0
33520b200a	1000100030	1111?0?0?0	001a0a?000	0u00000		
41. <i>Ligustrum</i> /Oleaceae				1010100001	00?0000000	00a00001a0
?bfa?1??01	0000200002	0a00201002	0100001002	01021c0020	001000a010	000110??a0
232u0101??	a0011000a0	1002100e00	0?1a0a?i?0	?r00100		
42. <i>Lindenbergia</i> /Orobanchaceae				fa10100a0?	0?000000??	?0?000?1?
????????01	0040310013	1001201024	11000a1002	0000130?1a	0010010320	0001e0??f?
h324???????	100a100030	111e1??0?0	101?0?0000	01?0000		
43. <i>Orobanche</i> /Orobanchaceae				01000000??	0?0000?0a?	?????000??
????????001	00dag100?3	10012?1024	110a0010a2	01ag010?10	0010000220	0001r0??f0
g3240e?1?0	1000100030	1112100?00	?0100a0000	0(inop)?0000		

Appendix 3 (continued)

44. <i>Paulownia</i> /Paulowniaceae				10?0?0000?	?b?000????	??0?00?1?
???11????1	?0a03a00?3	a00?2?1004	?1000?1?02	?10210012?	?0a?011220	13??e0???0
332401?1?0	h0001000a1	?021????00	??1?0?0???	??00000		
45. <i>Harpagophytum</i> /Pedaliaceae				001010f000	00?00?0a00	00?000001?
???b?1??11	00103100?3	1000201005	1101011002	0122100020	0011010220	0001g0??i0
3V2201?1?0	1001100030	111a1?0000	0?100?????	???????		
46. <i>Martynia</i> /Pedaliaceae				0aa01000??	00?00?0000	00??00001?
???b??0?1	0010310013	10002?1005	1101001?0?	0102010120	001?010220	0?0110??f1
2T2??12??0	1000100030	1111??0??0	001?000001	0???????		
47. <i>Proboscidea</i> /Pedaliaceae				01a010f000	00?00?0a00	00?000001?
???b?1?011	0010310013	10002?1025	1101011012	0102010120	0011000020	000110?1f1
20???????	1001100030	11011?01?0	00100?????	??00000		
48. <i>Sesamum</i> /Pedaliaceae				0aa0100000	00?00?0a00	00?000001?
???b?1??11	00103100?3	10002?1005	1101011002	0122100020	0011010220	0001g0??i0
3Q220????2	1001100030	111a1?0100	0?110?????	?(j1)?0100		
49. <i>Phryma</i> /Phrymaceae				0010100100	0j?00?0000	00?00000??
??????11	00?03?00?3	100?2????4	110000100?	?10202002?	0b1?010000	00??????1
3322012110	u001a00000	0111??10?0	0?1000????	??00000		
50. <i>Antirrhinum</i> /Plantaginaceae				f0a0a0000?	0??000?00?	??0??0001?
??????01	00103100?3	10012?1024	1101001002	0102100?10	002?010520	0001e0????
23?4??hl??	100?1??0c0	11?2f0?0?	001?010200	0(e1)?0000		
51. <i>Callitriche</i> /Plantaginaceae				011000000?	0h?00??000	00??0000??
??????10	2?????????	??????0?01	??000?10a	01021c0010	000?011010	0301?0?e?1
231001100o	1000100030	1111100??0	0?1?00????	?b?00000		
52. <i>Globularia</i> /Plantaginaceae				a00a10000?	0n00000010	000000001?
?230?0011	0010310013	10002?1004	110a001?0?	0102030020	00e?010000	0????????0
g32401???	1000100030	11021?0??0	101?000000	0e?00000		
53. <i>Hippuris</i> /Plantaginaceae				002000002?	0i?00?0000	00??0000??
??????0a	20?0c?????	??????0001	0?0000000?	0101030010	0000011020	0??110??1
1J?u?????	1000010030	1101?0?0?	001?000001	0e?????		
54. <i>Plantago</i> /Plantaginaceae				0a0ab000a0	0c?00f0100	00??00001?
????a?0aa	001a2a0012	0?002?0?04	010000a002	0112100021	00100105f0	00??0????a
27250?1100	1000100030	1102?0a0?0	0?1a0a????	?(bc)?????		
55. <i>Schlegelia</i> /Schlegeliaceae				101010000	??????????	??????????
??????11	00?0?00?3	0?01?????	??????0?	01?2a??12?	?0??000020	00?????????
?????????	h0001000?0	11?????????	???????????	???????		
56. <i>Scrophularia</i> /Scrophulariaceae				A010100100	0b?000000?	000000001?
?23????01	00a03a00?3	10002?10a4	1101001132	0102100120	001?01?120	0001e0??f0
hR2u02????	h00a100030	111210?000	??1?0?0???	?n?????		
57. <i>Verbascum</i> /Scrophulariaceae				0a0b100a01	0b0000aa0r	0000000010
2bcbaa0011	00a03a0013	10002?100w	1100011202	0102100120	002a010z20	000120??f0
23240e????	h00a100030	1112100000	001a0a00?0	?c00000		
58. <i>Nuxia</i> /Stilbaceae				1010100a01	0??00?????	????0000??
??????11	00?02000?2	000101??04	010000110?	010?????20	00e?01??0?	???????????
g324?2e1?0	?????????0	??1?0?0???	???????????	???????		
59. <i>Retzia</i> /Stilbaceae				1020100000	00?00?0000	00000000a?
2230a?0?11	00a0300013	00000?1005	a100001202	0102000020	001?0101e0	00?0???????
2324a1211b	10011000?0	11020?0??0	0?1????????	???????		

Appendix 3 (continued)

60. <i>Stilbe</i> /Stilbaceae				1020100000	00?00?0000	00000000a?
2230a?0?11	00a03100?3	100a010005	010a001002	0002120020	000?010b00	00?0??????
g324012110	10011000?0	11021?0?0	0?1???????	???????		
61. <i>Polypremum</i> /Tetrachondraceae				0a100200??	??00?????	?????00???
????1??21	a0102100?2	0?012?0?04	0100001002	01021b0120	002?011320	00????????
g3240221?0	1000100030	11021?0?0?	?0???????	???????		
62. <i>Tetrachondra</i> /Tetrachondraceae				00101001??	0??00?0000	00??0000??
?????????1	00102?00?2	01002????4	0100001002	0??2120020	010?010110	00????????
332402?1?0	1?????????	?????????0	0?????????	???????		
63. <i>Verbena</i> /Verbenaceae				a0f0a0d000	0?00000000	000000011?
?23a?1?001	00m0310013	10012?10b4	1100001ba2	01021b0020	0011001010	000110??f0
23041?11?0	1000100030	110a?000?0	0?1a0a?0?0	?(bcd)00000		
64. <i>Convolvulus</i> /Convolvulaceae				fa00a0f0a1	0100000001	11011h0011
220baa0011	0011320013	00002?1005	0100011101	01121200e0	00f0?10o10	0011100ef1
33120eg11a	1a10011031	101e0110?0	0001e10311	0g?1101		
65. <i>Cuscuta</i> /Convolvulaceae				01000000??	0??00?0000	00??k001?
?????011	0010g1000g	00002?000w	0000001002	0102ab0010	00b0010510	0001100101
g3120e21?0	10000100a1	101e0110?0	0001210301	0d?0000		
66. <i>Hydrolea</i> /Hydroleaceae				f000a00a00	001000???	?????00?1?
?0??1?01	00113100?3	0000210005	0000001001	0102000a10	0000011L20	00????????0
33240221?0	1000100000	00021?0?00	?0a00?3??	?g?????		
67. <i>Grevea</i> /Montiniaceae				1010100000	0b?0010001	001000001a
?2b1a?0?10	2040h101?h	000021100x	??a00000a	0102aa012?	001??0?020	00????????
23241e2100	1?????????	??2??0?0	0?????????	???????		
68. <i>Montinia</i> /Montiniaceae				1000100000	00?0010004	0010000010
?0b0a?00?0	2040h101?h	000?21100H	0101000000	0102100120	00110102e0	10????????
2324012100	1?????????	??a??0?0	0?1?e??0	??0????		
69. <i>Duckeodendron</i> /Solanaceae				10001000??	0??00?0000	00?1?00011
2120a??0?1	0010310013	0?002?1005	0100001002	01021?0?20	001??01000	00????????0
3324021100	1?0???????	??11?1?0	0?????????	???????		
70. <i>Goetzea</i> /Solanaceae				100010000?	00?00?000k	000100001?
??a0??0?1	0000C0001C	a??02?100J	a?0000100?	010ea20020	00e??00010	0?????????
e3e20011?4	??0???????	??0?????0	0?????????	???????		
71. <i>Solanum</i> /Solanaceae				aa0010da00	0f0000000m	a001100a11
2b0f0a1001	00003j0013	0000211005	01000a1112	0102100120	001a10a020	0001h0?1f0
g324010101	h001100000	0102a01000	000ae1ai?0	li00000		
72. <i>Sphenoclea</i> /Sphenocleaceae				0100100000	04?00?0001	0000000011
?2????011	10103100?3	0?0021?005	0100001?02	0102100120	002?010520	000110?100
g324?????0	1000100030	1111?0?0	0????????0	li0????		
73. <i>Adoxa</i> /Adoxaceae				0012104100	0020000100	0000000010
?2b0?1?101	1010a1000g	01002a010w	0100001000	010w3a0020	0020001000	0001111101
3324022000	1000100120	0002100??0	0?1?010010	?f10000		
74. <i>Sambucus</i> /Adoxaceae				a01010d100	0a2002000a	a000000010
?00001a111	1040h0000h	000020000H	010000110b	010Hgc000?	0010001000	00?1101e01
3324022000	1000100120	00021000?0	001?0103a0	?f10000		
75. <i>Viburnum</i> /Adoxaceae				101010ba00	0a2001000a	1000000a01
?00001001a	e010310003	0000210a05	0100001102	010320002a	0010001000	00?1101e01
33N4022000	1a00101020	0002100??0	0011ba0300	?(ef)10000		

Appendix 3 (continued)

76. <i>Audouinia</i> /Bruniaceae				1000a1002?	003001001m	00?000?001
a030110021	10103101?3	000a21a005	0100000202	010Hg0020	001?010000	00?1?1?1???
2322a20100	122110102?	00020000?0	00a0200100	0h0????		
77. <i>Berzelia</i> /Bruniaceae				1000a100b?	003001001m	00?000?001
a030110001	10103101?3	000a21a005	0100000202	01010a0020	00a?010000	00?1??????
2324a2010b	122110102?	00020000?0	00a0e01100	0g0????		
78. <i>Brunia</i> /Bruniaceae				1000a100b?	00?001001m	00?000?001
a030110001	10103101?3	000a21a005	a100000202	01021a0020	00a?010000	00?1??????
2U2412010b	122110102?	00020000?0	00a0e01100	0h0????		
79. <i>Carlemania</i> /Carlemaniaceae				b01010010?	0??00?0001	?0??0001?
?????1a?01	20mlg100?2	a000201002	010000101e	01021b0020	00e?010220	0?????????
1I240e21?0	?00?00????	?????????0	0????0????	???????		
80. <i>Silvianthus</i> /Carlemaniaceae				10101a0101	0??00?0001	?0??0001?
?????a?01	2040g000?3	10002?1002	0100001112	01021b0020	000?010220	0?????????
132201?1?0	??????????	?????????0	0?????????	???????		
81. <i>Columellia</i> /Columelliaceae				1010100a00	0000001001	10??00001
2??0?00011	10a03100?3	000021100N	0100001100	0102010020	001?010120	00?1?112?1
e3240e2100	1000100????	0002?00?00	000?0?0?00	???????		
82. <i>Desfontainia</i> /Columelliaceae				10101b0200	0000000001	1000000001
10a0010011	00103100?3	0000201005	0100001e02	0105010120	00e1000020	00?1?0ve0?
e324022110	100010000?	0002?00?00	0?1?a??00	?d?????		
83. <i>Eremosyne</i> /Eremosynaceae				010010001?	00300?0000	10??000011
???????001	10003001?3	0101210005	010000000e	01021b00e0	002??10200	00?0?01???
33?40?1?00	1000?00?01	??2??0?00	0?????????	???????		
84. <i>Anopterus</i> /Escalloniaceae				1000100100	0030010001	10?0000001
?23??00001	00?04101?4	0100210005	0?00000102	0102110010	000?010120	00?11?e?1
2324002100	?0001000?1	?02?00?00	0???e?03?0	???????		
85. <i>Escallonia</i> /Escalloniaceae				1000100100	0030001001	1000000001
?031a00011	10aa3a0a?3	0000211005	010000a002	010g0100e0	00e1?10120	00????????1
g324121100	10001000?1	0002100?00	001?e?01?1	0???????		
86. <i>Forgesia</i> /Escalloniaceae				1000100100	00000a1101	?000000001
e00aa00011	10003000?3	0001211005	0100000a02	0102010110	0021010120	00?????????
23?40?1?00	10001000?1	0002100?00	0?1?e?01?1	0???????		
87. <i>Quintinia</i> /Escalloniaceae				1000100000	0030011001	10?0000001
?230a00001	10103101?g	000021100w	0100000002	010Hg00020	001?010120	00????????1
eS2402?a10	?01?1?0?01	??2??0?00	0?012?03?0	?q?????		
88. <i>Icacina</i> /Icacinaceae				1000100a0?	0f000a0aa0	00000001a?
?????100?a	00a0r00a?E	0?002?a00E	010000a?02	010Ajc0a20	001?0aa0a0	0??1r0?01
?3?u??????	11000110?1	0a0211a0?0	001?ba0a00	0???????		
89. <i>Sphenostemon</i> /Sphenostemonaceae				1000100a00	00?001a00m	00100aa001
a0?00?0011	00112?01?2	0?00210?0§	0100000202	?10yk00?0?	00e?001000	00??0?????
e3230e110v	1a0?01?0??	??2??????0	0?????????	?t?????		
90. <i>Tribeles</i> /Tribelaceae				100020000?	0?000?0?1	????000?1
?????0001	00103g01?3	0000210?05	0100000100	0103200020	001?010220	00?????????
?????0000	100?1????1	??2??0?00	0?????????	?0?????		
91. <i>Apium</i> /Apiaceae				000b20qaa?	0a000e1001	0000003010
12bba1?0a1	2040301103	0100211005	0100000a02	01021c1010	0011010010	0c0110g2f1
33240?2100	1001100001	0002100?00	010a0a0310	0h00100		

Appendix 3 (continued)

92. <i>Sanicula</i> /Apiaceae				000b210f1?	0a000e10a1	0000003010
12bba1?0a1	2040301103	0100211005	0100000a02	01021c1010	0011010010	0c0110g2f1
33240?2100	1001100001	0002100??0	010a0a0310	0h00100		
93. <i>Aralia</i> /Araliaceae				a0002eqaa?	0a000e100m	00000030a0
?200a1100a	204ag1aa0g	0a00211005	0100000a02	010xhc10e0	000a00a000	0001e03001
33e40121ao	1a011aa031	0002100?00	0101010310	1(hi)00100		
94. <i>Hydrocotyle</i> /Araliaceae				a00b210a1?	0a000e1001	0000003010
12bba1?0a1	2040301103	0?00211005	0100000a02	01021c10e0	0011011010	0c0110g2f1
g3e40?2100	1001100001	0002100??0	010a0a0310	0h00100		
95. <i>Aralidium</i> /Aralidiaceae				1000204100	0230020003	10??0?000
?2f??11000	20113101?3	000?211005	0100000002	0103000?20	001?001000	00?130??0?
23?40?2110	110?1??02?	??2?00?0	0?10000201	?d0???		
96. <i>Griselinia</i> /Griselinaceae				1000200a00	00000e1011	00??000001
?020a10010	20103101?3	0?002?1005	010000000e	0103130020	000?000000	00?1?02?0?
33?4?2?100	110010?020	0002??0?0	001?000111	0n????		
97. <i>Melanophylla</i> /Melanophyllaceae				1000200000	00?00?0001	?0?0000011
?23??1?011	20103101?3	0000210005	0100000102	010gec0010	000??0a000	00?1?0w?0?
e3?4021100	110?1??02?	00?2?0??0	00??0?????	???????		
98. <i>Pittosporum</i> /Pittosporaceae				1000100a00	01t00a000m	10?00a30a0
?2baa1101a	001a310a?3	0000210a05	010000a002	0102aa0020	0001010220	a001e03101
g324022100	1001000021	0012100??0	0101a10310	0c0????		
99. <i>Toricellia</i> /Toricelliaceae				1000200110	00300?0003	00?0000011
?ae??1?0?0	20403011?3	0000210?05	010000010e	010vg30010	000?001000	00?140120?
23340?1100	1??010002?	0002??0?0	0?10?0?201	?i0????		
100. <i>Ilex</i> /Aquifoliaceae				10a0110f00	00300aa00m	0000000a01
a030a11010	0010C100?C	0?0021000K	0101001102	010w330020	00f10010a0	00??0?0?1?0
g3241b0a?4	1a01111010	000e100??0	0?0a2a?3?0	?(fg)0????		
101. <i>Helwingia</i> /Helwingiaceae				1000110101	00?0000001	0000000001
1030a11000	21??001?h	0?0021100H	010000010e	010vg30020	0010?00000	00?????????
h324??0?1	1?0?1??0?1	??2?00?0	0?0????3??	0o????		
102. <i>Phyllonoma</i> /Phyllonomaceae				1000110a00	0??00000??	?1??00?0?
0??0??1001	20?0g00a?g	0?0021100w	0100000101	0102a10110	000?100020	00??0?0??0
g32u01?101	k00?1??0?0	1??2?000?0	0?????????	???????		
103. <i>Alseuosmia</i> /Alseuosmiaceae				10f0100100	00?0010100	1100000001
e030?1a011	e0d03000?3	0010211005	0100001002	0102100020	001?0000e0	00?12002?1
33e20e2100	1000000???	000e?0??0	00a12003?0	?f0????		
104. <i>Wittsteinia</i> /Alseuosmiaceae				1000100a0a	00?0010100	1100000001
103??1a011	20013000?3	00100?1005	0100001002	0102e00020	001?000020	00?????????
?3?4??????	100??????0	??2??????0	0?0???????	???????		
105. <i>Corokia</i> /Argophyllaceae				1000a00000	00000?0a00	100?0?001
f000a11011	2000v001?v	0?a0001001	010000010?	?102i00?20	001?001000	00?1?0?2f1
g3?4?221?1	1001100050	1102??0?00	0?102?03??	?f????		
106. <i>Carthamus</i> /Asteraceae				010000be00	0??001??0m	aa0aa00010
2200aaa001	2001400003	0000201005	0100001212	0112020021	1010010001	020111?2?1
23340?????	1000100020	0000100?00	010?e00???	1(egi)?0000		
107. <i>Dasyphyllum</i> /Asteraceae				1000a000a0	0??001??0m	aa0aa00010
2200aaa001	2001400003	0000201005	0100001212	0112020020	1010010001	020111?2?1
23040?????	1000100020	0000100?00	010?e00???	1?0000		

Appendix 3 (continued)

108. <i>Schlechtendalia</i> /Asteraceae				0012000020	0??001??0m	aa0aa00010
2200aaa001	2001400003	0000201005	0100001112	0112020020	1010010001	020111??2?1
23040?????	1000100020	0000100?00	010?e00???	1e?0000		
109. <i>Acicarpa</i> /Calyceraceae				0102002100	00?000000q	0000000010
??2??011	20d1g0000g	0000211005	0100101112	0102030020	1021010001	0211?0???
33040121?0	1000100000	00021?0???	0?1?0???	1(eknp)00000		
110. <i>Boopis</i> /Calyceraceae				0002002000	00?000000q	0000000010
??2??011	20d1g0000g	0000211005	0100101112	0102030020	1021010001	0211?0???
33240121?0	1000100000	00021?0???	0?1?0???	1(eknp)00000		
111. <i>Campanula</i> /Campanulaceae				0a0f100a0?	00j110a101	1100ag0010
22c21aa001	20a0300003	a000210105	01000aae02	0103200121	001a010420	00?110?1a1
e32300e1?4	1000100000	1102100000	0100010c00	?m00000		
112. <i>Codonopsis</i> /Campanulaceae				00a0100a0?	005110a101	1100ag0010
22c21aa001	e0a0300003	0?00210105	01000aae02	010??00121	001a010420	00?110?1a0
e72202e1?4	1000100000	1102100000	0100010c00	?e00000		
113. <i>Cyananthus</i> /Campanulaceae				000000aa0?	00?110a101	1100ag0010
22c21aa001	00a0300003	0?00210105	01000aae02	010??00121	001a010420	00?110?1a?
27220ee104	1000100000	1102100000	0100010c00	?d00000		
114. <i>Cyphia</i> /Campanulaceae				0a0f100a0?	00?110a101	1100ag0010
22c21aa001	e0a0300003	2100210105	0100010e02	0103200121	001a010420	00?110?1a?
33240?e10?	1000100000	1102100000	0100010c00	?f00000		
115. <i>Cyphocarpus</i> /Campanulaceae				010000010?	00?110a101	1100ag0010
22c21aa001	20a0300003	b10a210105	01000a1e02	0103200121	001a010420	00?110?1a?
?P?C??????	1000100000	1102100000	0100010c00	??00000		
116. <i>Lobelia</i> /Campanulaceae				aa0fa00a0?	0030100100	10000g0010
22c211a001	20a0300003	2100210115	01001?0e12	0103200121	001a010420	00?110?1aa
332401e1?0	1000100000	1102100000	0100010c00	?d00000		
117. <i>Nemacladus</i> /Campanulaceae				0101000a0?	00?110a101	1100ag0010
22c21aa001	e0a0300003	b100210125	01000aae02	0103200121	001a010420	00?110?1a?
g3240?e1??	1000100000	1102100000	0100010c00	?f00000		
118. <i>Abrophyllum</i> /Carpodetaceae				1000100100	00?0010100	000??100??
f0caa1?0?1	00013001?3	0?01211005	0??00?0102	?105300???	00??000020	00????????
?????????	?????????	??21?????	0?????????	???????		
119. <i>Donatia</i> /Donatiaceae				0000a0000?	0a?0000?10	1100101000
?23????001	20m0v1010v	f?0?2?200g	0100000000	010ge00010	002?010020	00????????
23241011?1	1000100000	11121?0???	0?0???????	1(ce)0????		
120. <i>Brunonia</i> /Goodeniaceae				0000100a0?	01?00e0011	0000000011
?0cbaa0011	0040300003	0000200105	0100001012	1102020021	10??010000	0?0110?2?0
g3240111?0	1000100000	a0121?0???	001?000000	0f?0000		
121. <i>Lechenaultia</i> /Goodeniaceae				a00000ba0?	00?00e001m	0000a00011
?0jbaa0011	e001300003	101021a005	010000a112	0102ab0021	10e0010520	000110?2a0
2W?301a1?0	1001100000	00021001?0	0?1?0a?0?0	1(def)00000		
122. <i>Velleia</i> /Goodeniaceae				0a0a00ba0?	00?00e001m	0000a00011
?0jbaa0011	0001300003	101021a005	010000a102	01020b0021	1020010520	000110?2a0
?3?4??????	1001100000	00021001?0	0?1?0a?0?0	1(def)00000		
123. <i>Menyanthes</i> /Menyanthaceae				0001203a10	00?00e11a0	10000000a?
?????????01	a00a300003	0a1?f11005	0100001202	1102010?20	0011????20	0001e0?2?0
332402e1?0	1001100020	0002a?0???	0?110?????	1f01000		

Appendix 3 (continued)

124. <i>Villarsia</i> /Menyanthaceae				0001200aa0	00?00e11a0	10000000a?
??????001	a00a300003	0?1?f11005	0100001202	1102010?20	0011????20	0001e0?2??
?U?u?????	1001100020	0002a?0??0	0?110????0	1f01000		
125. <i>Pentaphragma</i> /Pentaphragmataceae				0000100a0?	00?00?0000	11000?0001
?23??0011	f01a300a?3	0?1?211005	0100001102	010ge00120	00e?000020	000120?1b?
1g3401h1?0	1000100000	1a020?00?0	0????0??0	??0????		
126. <i>Phelline</i> /Phellinaceae				1000100001	0030010000	00??00000?
a000a?0000	0040C001?C	0?0021???J	0100000?02	010xhc000?	001?001000	00????????
332410111c	g?0?0????	???2????0	0????1????	???????		
127. <i>Roussea</i> /Rousseaceae				1010100100	00?001110m	0000000001
02001?00?1	00003000?3	0?012?1005	0100000100	0?0w300?20	001??00020	00????????
?3?N??1100	?????????	??1??????	????0?????	???????		
128. <i>Stylidium</i> /Stylidiaceae				aa0eb000b?	0000000aa0	01?110a?11
?23??00001	2010F10003	1000012022	0110100000	0102a00020	0000010z20	00?110?100
hE2200a1?4	1000100000	11121?00?0	0?1ae0?3?0	1??????		
129. <i>Lonicera</i> /Caprifoliaceae				1010100000	00j0010?01	a000000a11
20b0a00011	2010310003	100a2001a5	01000a1b02	010Ah00020	00e0a0a010	00?1111e01
2324022104	1000100020	0002100??0	00110a0310	?(ef)00110		
130. <i>Triosteum</i> /Caprifoliaceae				101010b000	0030000?01	a000000a00
20b0a00011	2010310003	100a2001a5	a100011b02	0104g00020	00e0a01010	00?1112e01
2324022110	1000100020	0002100??0	00110a0010	?f00110		
131. <i>Diervilla</i> /Diervillaceae				1010a00100	0020010?01	1000000a01
20b0a00011	2010310003	100a2001a5	01000a1b02	010210002a	00e0010120	00?1112e01
2v25021104	1000100020	0002100??0	00110a0110	?f00110		
132. <i>Dipsacus</i> /Dipsacaceae				001210bf00	0000020001	1000000011
?0j0a00131	2000210002	100a200104	0100001002	01030c0020	00e0010000	02?11ah201
232N02211v	1001100040	0002110?01	0?1a010000	1f00110		
133. <i>Knautia</i> /Dipsacaceae				0a1b10ba00	0000010001	10000000a1
?0j0a10131	2000210002	100a200104	0100011002	01030c0020	0010010000	02?11ah201
232N02311v	1001100040	0002110?01	0?1a0100?0	1(eg)00110		
134. <i>Ptercephalus</i> /Dipsacaceae				aa1b10ba00	0000010001	1000000001
?0j0a00131	200021000g	100a200104	0100001002	01030c0020	0020010000	01?11ah201
g32202311v	1001100040	0002110?01	0?1a0100?0	1f00110		
135. <i>Succisa</i> /Dipsacaceae				001210ba00	0000010001	1000000011
?0j0a00131	2000g12002	100a200104	0100001002	01030c0020	00e0010000	02?11ah201
232202311v	1001100040	0002110?01	0?1a010010	1(eg)00110		
136. <i>Kolkwitzia</i> /Linnaeaceae				1010100100	0030010?01	a000000001
2000a00021	2010310003	1000200114	1100001002	0103300020	0020010010	00?1112e01
2324022114	1000100020	0002100??0	00112a0110	?e00110		
137. <i>Morina</i> /Morinaceae				0012100201	0b200e0004	1000000001
?23??0?131	2010210003	1001201014	1101011a02	0103000020	002?010000	00012131a1
3325011112	1001100040	0002100?00	0?0?000110	?m00000		
138. <i>Centranthus</i> /Valerianaceae				aa1b10b000	0000010000	1000000010
22b2100111	2010310003	1000200101	0100001102	0103000020	0010010000	0n01113201
232202310C	1000100020	000a110??0	0?10010300	0(de)00110		
139. <i>Nardostachys</i> /Valerianaceae				0012a000b?	0000010004	1000000010
?2b2100121	2010310003	1000200105	0100001102	0103200020	0020010000	0101113201
232202310C	1000100020	000a110??0	0?11010300	0j00110		

Appendix 3 (continued)

140. <i>Patrinia</i> /Valerianaceae				f01210ba00	0000010001	100000000a
22b2a0?121	2010310003	a00020010X	0100001102	0103200020	0020010000	0301113201
232202210C	1000100020	000a110??0	0?11010300	0h00110		
141. <i>Triplostegia</i> /Valerianaceae				0012102100	000001000m	1000000010
?2b2100131	2010210003	1000200104	0100001102	0103200020	0010010000	0101113201
232202310v	1000100020	000a110??0	0?11010300	0f00110		
142. <i>Valeriana</i> /Valerianaceae				f01f10oa00	0000010a00	1000000010
22221a0111	2010310003	1000200103	0100001a02	0a03000020	0010010000	0n01113201
232202310C	1000100020	000a110??0	0110010300	0d00110		

References

- Albert V. A., Chase M. W., Mishler B. D. (1993) Character-state weighting for cladistic analysis of protein-coding DNA sequences. *Ann. Missouri Bot. Gard.* 80: 752–766.
- Anderberg A. A. (1992) The circumscription of the Ericales, and their cladistic relationships to other families of “higher” dicotyledons. *Syst. Bot.* 17: 660–675.
- Anderberg A. A. (1993) Cladistic interrelationships and major clades of the Ericales. *Plant Syst. Evol.* 184: 207–231.
- Anderberg A. A., Ståhl B. (1995) Phylogenetic interrelationships in the order Primulales with special emphasis on the family circumscriptions. *Canad. J. Bot.* 73: 1699–1730.
- Angiosperm Phylogeny Group (APG) (1998) An ordinal classification for the families of flowering plants. *Ann. Missouri Bot. Gard.* 85: 531–553.
- Backlund A. (1996) Phylogeny of the Dipsacales. Ph.D. thesis, Uppsala University.
- Backlund A., Bremer B. (1997) Phylogeny of the Asteridae s.str. based on *rbcL* sequences, with particular reference to the Dipsacales. *Plant Syst. Evol.* 207: 225–254.
- Backlund M., Oxelman B., Bremer B. (2000) Phylogenetic relationships within the Gentianales based on *ndhF* and *rbcL* sequences, with particular reference to the Loganiaceae. *Amer. J. Bot.* 87: 1029–1043.
- Bailey I. W. (1933) The cambium and its derivative tissues 8. Structure, distribution and diagnostic significance of vestured pits in dicotyledons. *J. Arnold Arb.* 14: 259–273.
- Barrett M., Donoghue M. J., Sober E. (1991) Against consensus. *Syst. Zool.* 40: 486–493.
- Benko-Iseppon A. M., Morawetz W. (1993) Cold-induced chromosome regions and karyosystematics in *Sambucus* and *Viburnum*. *Bot. Acta* 106: 183–191.
- Benko-Iseppon A. M., Morawetz W. (2000) Viburnales: cytological features and a new circumscription. *Taxon* 49: 5–16.
- Bremer K., Bremer B., Thulin M. (2000) Introduction to phylogeny and systematics of flowering plants. Compendium, Uppsala University.
- Bremer B., Jansen R. K., Oxelman B., Backlund M., Lantz H., Kim K.-J. (1999) More characters or more taxa for a robust phylogeny – case study from the Coffee family (Rubiaceae). *Syst. Biol.* 48: 413–435.
- Chase M. W., Soltis D. E., Olmstead R. G., Morgan D., Les D. H., Mishler B. D., Duvall M. R., Price R. A., Hills H. G., Qiu Y.-L., Kron K. A., Rettig J. H., Conti E., Palmer J. D., Manhart J. R., Sytsma K. J., Michaels H. J., Kress W. J., Karol K. G., Clark W. D., Hedrén M., Gaut B. S., Jansen R. K., Kim K.-J., Wimpee C. F., Furnier G. R., Strauss S. H., Xiang Q.-Y., Plunkett G. M., Soltis P. S., Swensen S. M., Williams S. E., Gadek P. A., Quinn C. J., Eguiarte L. E., Golenberg E., Learn G. H. Jr., Graham S. W., Barrett S. C. H., Dayanandan S., Albert V. A. (1993) Phylogenetics of seed plants: an analysis of nucleotide sequences from the plastid gene *rbcL*. *Ann. Missouri Bot. Gard.* 80: 528–580.
- Corner E. H. G. (1976) The seeds of dicotyledons, 1 and 2. Cambridge University Press.
- Cronquist A. (1981) An integrated system of classification of flowering plants. Columbia University Press, New York.
- Cubas P., Vincent C., Coen E. (1999) An epigenetic mutation responsible for natural variation in floral symmetry. *Nature* 401: 157–161.
- Dahlgren G. (1989). The last dahlgrenogram. System of classification of the dicotyledons. In: Tan K. (ed.) *The Davis and Hedge Festschrift*. Edinburgh University Press, pp. 249–260.

- Downie S. R., Palmer J. D. (1992) Restriction site mapping of the chloroplast DNA inverted repeat: a molecular phylogeny of the Asteridae. *Ann. Missouri Bot. Gard.* 79: 266–283.
- Erbar C. (1991) Sympetaly – a systematic character? *Bot. Jahrb.* 112: 417–451.
- Erbar C., Leins P. (1996) Distribution of the character states “early sympetaly” and “late sympetaly” within the “Sympetalae Tetracyclidae” and presumably allied groups. *Bot. Acta* 109: 427–440.
- Erdtman G. (1952) Pollen morphology and plant taxonomy. *Almqvist & Wiksell*, Stockholm.
- Gustafsson M. H. G. (1995) Petal venation in the Asterales and related orders. *Bot. J. Linn. Soc.* 118: 1–18.
- Gustafsson M. H. G., Backlund A., Bremer B. (1996) Phylogeny of the Asterales sensu lato based on *rbcL* sequences with particular reference to the Goodeniaceae. *Plant Syst. Evol.* 199: 217–242.
- Gustafsson M. H. G., Bremer K. (1995) Morphology and phylogenetic interrelationships of the Asteraceae, Calyceraceae, Campanulaceae, Goodeniaceae, and related families (Asterales). *Amer. J. Bot.* 82: 250–265.
- Gustafsson M. H. G., Bremer K. (1997) The circumscription and systematic position of Carpodetaceae. *Austr. Syst. Bot.* 10: 855–862.
- Hegnauer R. (1964–1989) *Chemotaxonomie der Pflanzen*, 3-8. Birkhäuser Verlag, Basel.
- Hempel A. L., Reeves P. A., Olmstead R. G., Jansen R. K. (1995) Implications of *rbcL* sequence data for higher order relationships of the Loasaceae and the anomalous aquatic plant *Hydrostachys* (Hydrostachyaceae). *Plant Syst. Evol.* 194: 25–37.
- Hickey L. J., Wolfe J. A. (1975) The bases of angiosperm phylogeny: vegetative morphology. *Ann. Missouri Bot. Gard.* 62: 538–589.
- Hufford L. (1992) Rosidae and their relationships to other nonmagnoliid dicotyledons: a phylogenetic analysis using morphological and chemical data. *Ann. Missouri Bot. Gard.* 79: 218–248.
- Johri B. M. (1984) *Embryology of angiosperms*, Springer, Berlin.
- Jussieu A. L. de (1789) *Genera plantarum secundum ordines naturales disposita*. Herissant & Barrois, Paris.
- Källersjö M., Farris J. S., Chase M. W., Bremer B., Fay M. F., Humphries C. J., Petersen G., Seberg O., Bremer K. (1998) Simultaneous parsimony jackknife analysis of 2538 *rbcL* DNA sequences reveals support for major clades of green plants, land plants, seed plants, and flowering plants. *Plant Syst. Evol.* 213: 259–287.
- Kårehed J., Lundberg J., Bremer B., Bremer K. (2000) Evolution of the Australasian families Alseuosmiaceae, Argophyllaceae, and Phellinaceae. *Syst. Bot.* 24: 660–682.
- Leins P., Erbar C. (1990) On the mechanisms of secondary pollen presentation in the Campanulales-Asterales-complex. *Bot. Acta* 103: 87–90.
- Metcalf C. R., Chalk L. (1979–1983) *Anatomy of the dicotyledons, 1 and 2*. Edition 2. Clarendon Press, Oxford.
- Morton C. M., Chase M. W., Kron K. A., Swensen S. M. (1996) A molecular evaluation of the monophyly of the order Ebenales based upon *rbcL* sequence data. *Syst. Bot.* 21: 567–586.
- Nandi O. I., Chase M. W., Endress P. K. (1998) A combined cladistic analysis of angiosperms using *rbcL* and non-molecular data sets. *Ann. Missouri Bot. Gard.* 85: 137–212.
- Olmstead R. G., Bremer B., Scott K. M., Palmer J. D. (1993) A parsimony analysis of the Asteridae sensu lato based on *rbcL* sequences. *Ann. Missouri Bot. Gard.* 80: 700–722.
- Olmstead R. G., Michaels H. J., Scott K. M., Palmer J. D. (1992) Monophyly of the Asteridae and identification of their major lineages inferred from DNA sequences of *rbcL*. *Ann. Missouri Bot. Gard.* 79: 249–265.
- Olmstead R. G., Reeves P. A. (1995) Evidence for the polyphyly of the Scrophulariaceae based on chloroplast *rbcL* and *ndhF* sequences. *Ann. Missouri Bot. Gard.* 82: 176–193.
- Olmstead R. G., Kim K.-J., Jansen R. K., Wagstaff S. J. (2000) The phylogeny of the Asteridae sensu lato based on chloroplast *ndhF* gene sequences. *Mol. Phylogenet. Evol.* 16: 96–112.
- Oxelman B., Backlund M., Bremer B. (1999) Relationships of the Buddlejaceae s.l. investigated using parsimony jackknife and branch support analysis of chloroplast *ndhF* and *rbcL* sequence data. *Syst. Bot.* 24: 164–182.
- Pleijel F. (1995) On character coding for phylogeny reconstruction. *Cladistics* 11: 309–315.
- Plunkett G. M., Soltis D. E., Soltis P. S. (1996) Higher level relationships of Apiales (Apiaceae and Araliaceae) based on phylogenetic analysis of *rbcL* sequences. *Amer. J. Bot.* 83: 399–415.

- Porembski S., Kochi M. (1999) Inulin occurrence in *Sphenoclea* (Sphenocleaceae). *Plant Biol.* 1: 288–289.
- Reveal J. L., Judd W. S., Olmstead R. (1999) Proposal to conserve the name Antirrhinaceae against Plantaginaceae (Magnoliophyta). *Taxon* 48: 182.
- Roels P., Smets E. (1994) A comparative floral ontogenetical study between *Adoxa moschatellina* and *Sambucus ebulus*. *Belg. J. Bot.* 127: 157–170.
- Roels P., Smets E. (1996) A floral ontogenetic study in the Dipsacales. *Int. J. Plant Sci.* 157: 203–218.
- Savolainen V., Amnan J. F., Douzery E., Spichiger R. (1994) Molecular phylogeny of families related to Celastrales based on *rbcL* 5' flanking sequences. *Mol. Phyl. Evol.* 3: 27–37.
- Savolainen V., Chase M. W., Hoot S. B., Morton C. M., Soltis D. E., Bayer C., Fay M. F., De Bruijn A. Y., Sullivan S., Qiu Y. L. (2000a) Phylogenetics of flowering plants based on combined analysis of plastid *atpB* and *rbcL* gene sequences. *Syst. Biol.* 49: 306–362.
- Savolainen V., Fay M. F., Albach D. C., Backlund A., van der Bank M., Cameron K. M., Johnson S. A., Lledo M. D., Pintaud J.-C., Powell M., Sheahan M. C., Soltis D. E., Soltis P. S., Weston P., Whitten W. M., Wurdack K. J., Chase M. W. (2000b) Phylogeny of the eudicots: a nearly complete familial analysis based on *rbcL* gene sequences. *Kew Bull.* 55: 357–309.
- Sennblad B., Bremer B. (2000). Is there a justification for differential a priori weighting in coding sequences? – a case study from *rbcL* and Apocynaceae s.l. *Syst. Biol.* 49: 101–113.
- Soltis D. E., Soltis P. S. (1997) Phylogenetic relationships in Saxifragaceae sensu lato: a comparison of topologies based on 18S rDNA and *rbcL* sequences. *Amer. J. Bot.* 84: 504–522.
- Soltis D. E., Soltis P. S., Mort M. E., Chase M. W., Savolainen V., Hoot S. B., Morton C. M. (1998) Inferring complex phylogenies using parsimony: an empirical approach using three large DNA data sets for angiosperms. *Syst. Biol.* 47: 32–42.
- Soltis D. E., Soltis P. S., Nickrent D. L., Johnson L. A., Hahn W. J., Hoot S. B., Sweere J. A., Kuzoff R. K., Kron K. A., Chase M. W., Swensen S. M., Zimmer E. A., Chaw S.-M., Gillespie L. J., Kress W. J., Sytsma K. J. (1997) Angiosperm phylogeny inferred from 18S ribosomal DNA sequences. *Ann. Missouri Bot. Gard.* 84: 1–49.
- Soltis P. S., Soltis D. E., Chase M. W. (1999) Angiosperm phylogeny inferred from multiple genes as a tool for comparative biology. *Nature* 402: 402–404.
- Soltis D. E., Soltis P. S., Chase M. W., Mort M. E., Albach D. C., Zanis M., Savolainen V., Hahn W. H., Hoot S. B., Fay M. F., Axtell M., Swensen S. M., Prince L. M., Kress W. J., Nixon K. C., Farris J. S. (2000) Angiosperm phylogeny inferred from 18S rDNA, *rbcL* and *atpB* sequences. *Bot. J. Linn. Soc.* 133: 381–461.
- Struwe L., Albert V. A., Bremer B. (1994) Cladistics and family level classification of the Gentianales. *Cladistics* 10: 175–206.
- Swofford D. L. (1999) PAUP*: Phylogenetic Analysis using Parsimony. Version 4.0. Sinauer Associates, Sunderland, Massachusetts.
- Takhtajan A. (1964) The taxa of the higher plants above the rank of order. *Taxon* 13: 160–164.
- Takhtajan A. (1969) Flowering plants, origin and dispersal. Oliver & Boyd. Edinburgh.
- Takhtajan A. (1987) *Systema magnoliophytorum*. Nauka, Leningrad.
- Takhtajan A. (1997) Diversity and classification of flowering plants. Columbia University Press, New York.
- Thorne R. F. (1992) An updated phylogenetic classification of flowering plants. *Aliso* 13: 365–389.
- Wagenitz G. (1992) The Asteridae: evolution of a concept and its present status. *Ann. Missouri Bot. Gard.* 79: 209–217.
- Wagstaff S. J., Hickerson L., Spangler R., Reeves P. A., Olmstead R. G. (1998) Phylogeny in Labiatae s.l., inferred from cpDNA sequences. *Plant Syst. Evol.* 209: 265–274.
- Wagstaff S. J., Olmstead R. G. (1997) Phylogeny of Labiatae and Verbenaceae inferred from *rbcL* sequences. *Syst. Bot.* 22: 165–179.
- Wilkinson M. (1995) A comparison of two methods of character construction. *Cladistics* 11: 297–308.

Addresses of the authors: K. Bremer, M. Hjertson, J. Lundberg, M. Backlund, B. Bremer, Department of Systematic Botany, Evolutionary Biology Centre, Uppsala University, Norbyvägen 18D, SE-752 36 Uppsala, Sweden. A. Backlund, Department of Medicinal Chemistry, Uppsala

University, P. O. Box 574, SE-751 23 Uppsala, Sweden. B. Sennblad, Stockholm Bioinformatics Center, Stockholm University, SE-10691 Stockholm, Sweden. U. Swenson, Department of Botany,

University of Stockholm, SE-106 91 Stockholm, Sweden. K. Andreasen, Molecular Systematics Laboratory, Swedish Museum of Natural History, P. O. Box 50007, SE-104 05 Stockholm, Sweden.