

**Zeitschrift:** Candollea : journal international de botanique systématique = international journal of systematic botany  
**Herausgeber:** Conservatoire et Jardin botaniques de la Ville de Genève  
**Band:** 52 (1997)  
**Heft:** 2

**Artikel:** Present state of Angiospermae phylogeny  
**Autor:** Spichiger, Rodolphe / Savolainen, Vincent  
**DOI:** <https://doi.org/10.5169/seals-879448>

### **Nutzungsbedingungen**

Die ETH-Bibliothek ist die Anbieterin der digitalisierten Zeitschriften auf E-Periodica. Sie besitzt keine Urheberrechte an den Zeitschriften und ist nicht verantwortlich für deren Inhalte. Die Rechte liegen in der Regel bei den Herausgebern beziehungsweise den externen Rechteinhabern. Das Veröffentlichen von Bildern in Print- und Online-Publikationen sowie auf Social Media-Kanälen oder Webseiten ist nur mit vorheriger Genehmigung der Rechteinhaber erlaubt. [Mehr erfahren](#)

### **Conditions d'utilisation**

L'ETH Library est le fournisseur des revues numérisées. Elle ne détient aucun droit d'auteur sur les revues et n'est pas responsable de leur contenu. En règle générale, les droits sont détenus par les éditeurs ou les détenteurs de droits externes. La reproduction d'images dans des publications imprimées ou en ligne ainsi que sur des canaux de médias sociaux ou des sites web n'est autorisée qu'avec l'accord préalable des détenteurs des droits. [En savoir plus](#)

### **Terms of use**

The ETH Library is the provider of the digitised journals. It does not own any copyrights to the journals and is not responsible for their content. The rights usually lie with the publishers or the external rights holders. Publishing images in print and online publications, as well as on social media channels or websites, is only permitted with the prior consent of the rights holders. [Find out more](#)

**Download PDF:** 01.04.2026

**ETH-Bibliothek Zürich, E-Periodica, <https://www.e-periodica.ch>**

# Present state of Angiospermae phylogeny

RODOLPHE SPICHIGER  
&  
VINCENT SAVOLAINEN

## RÉSUMÉ

SPICHIGER, R. & V. SAVOLAINEN (1997). Etat actuel de la phylogénie des Angiospermes. *Candollea* 52: 435-455. En anglais, résumés anglais et français.

Le but de cet article est de donner une vue générale de la classification des Angiospermes basée sur notre cours de botanique à l'Université de Genève, mis à jour grâce aux résultats de la systématique moléculaire. Les lignées suivantes sont proposées: *Magnoliidae* (lignées nymphéaliennes, pipéraliennes, illiciales, et magnoliales); *Liliidae* (= Monocotylédones) (lignées araliennes, alismatiales, lilielles, et commeliniales); le complexe renonculien (lignées renonculaires, nélumbonales, protéales, trochodendraliennes et buxales); *Caryophyllidae* (lignées caryophyllales et polygonales); *Rosidae* (lignées saxifragales, dilléniales, rosales, santalales, linales, capparales, sapindales, géraniales, célastrales, et myrtales); *Asteridae* (lignées éricales, gentianales, et astérales). La phyllotaxie se trouve avoir une bonne valeur prédictive des affinités évolutives, de même que plusieurs caractères morphologiques et biochimiques utilisés dans les systèmes de Candolle, Engler, Dahlgren et Thorne.

## ABSTRACT

SPICHIGER, R. & V. SAVOLAINEN (1997). Present state of Angiospermae phylogeny *Candollea* 52: 435-455. In English, French and English abstracts.

The aim of this paper is to give a general picture of *Angiospermae* classification based on our formal botanical course at the University of Geneva updated with the results of molecular systematics. The following lineages are presented: *Magnoliidae* (nymphaealian, piperalian, illicialian, magnolialian lineages); *Liliidae* (= *Monocotyledons*) (aralian, alismatalian, lilialian, commelinalian lineages); the ranunculalian grade (ranunculalian, nelumbonalian, protealian, trochodendralian and buxalian lineages); *Caryophyllidae* (caryophyllalian, polygonalian lineages); *Rosidae* (saxifragalian, dillennialian, rosalian, santalalian, linalian, capparalian, sapindalian, geranalian, celastralian and myrtalian lineages); *Asteridae* (ericalian, gentianalian, asterolian lineages). Phyllotaxy appears as having a good predictive value as well as the morphological and biochemical features used by the Candollean, Englerian and Dahlgren-Thorne systems.

**KEYWORDS:** Angiosperms – Molecular phylogeny – Classification of flowering plants.

## Introduction

The application of molecular biology in botany has drastically changed our knowledge in systematics and evolution. The most recent systems of classification proposed by TAKHTAJAN

(1980), DAHLGREN (1983), THORNE (1983, 1992) and CRONQUIST (1981, 1988) are questioned by molecular phylogenetics whereas these results are not yet fully accepted. However, molecular botany is now close to draw the picture of plant phylogeny since large datasets are currently analysed in several institutes. It is consequently a difficult period for the teaching of academic botany where modern results have to be integrated into the conventional classification. This paper is not a new classification of flowering plants as we know that such a work will be published later by many researchers of an angiosperm phylogeny group. The aim of this paper is to give a general picture of the angiosperms as based on our formal botanical course (SPICHLER, multigr.) updated with the results of molecular systematics (mainly CHASE, SOLTIS, OLMSTEAD & al., 1993; and various abstracts in the issue S83 of the American Journal of Botany, 1996). We hope this could become a frame for lectures in botany until a new classification is available.

### How to divide angiosperms: classes, subclasses, and superorders

The angiosperms may have emerged in the Triassic (DOYLE & DONOGHUE, 1993; CRANE, 1993) possibly from tree-like seed-ferns (e.g. *Bennettitales*, *Caytoniales* or *Glossopteridales*) (for the early evolution of flowers, see also the special issue of *Pl. Syst. Evol.* edited by ENDRESS & FRIIS, 1994). According to CRANE (1985) and DOYLE & DONOGHUE (1987), the *Bennettitales* and the flowering plants have a common ancestor. However, ENDRESS (1986), ENDRESS & FRIIS (1994) and DOYLE (1994) discussed the origin of angiosperm flower, which may have originated more than once from larger floral structures (which we will call here "euanthia") to inflorescence of small flowers (which we will call here "pseudanthia" or "pseudoflowers"). Besides, it is then common to consider that the phylum *Angiospermae* diverged in two major classes: the monocotyledons (*Liliopsida*) and the dicotyledons (*Magnoliopsida*). This classical dichotomy has been questioned by modern systematists for a long time (see DAHLGREN, 1983, p. 127) because primitive dicotyledons (*Nymphaeales*, *Piperales*, *Aristolochiales*) share numerous morphological features with archaic monocotyledons (*Arales*, *Alismatales*). Based on molecular data, CHASE, SOLTIS, OLMSTEAD & al. (1993) showed that angiosperms are divided up according to pollen type rather than number of cotyledons: 1) the *Angiospermae* with uniaperturate pollen (or their derived types) containing the monocotyledons and the primitive dicotyledons (paleoherbs: *Aristolochiales*, *Nymphaeales*, *Piperales* and what we would like to call "paleotrees" here, i.e. *Magnoliales*, *Laurales*), 2) the *Angiospermae* with triaperturate pollen (or their derived types) containing all other dicotyledons *eudicotyledons* i.e. true dicotyledons). BURGER (1996) explained that the cotyledons of the monocotyledons and the dicotyledons are not homologous since in the monocotyledons the cotyledon would be a modified leaf.

Apart from the division into the classes monocotyledons and dicotyledons, various authors have divided the angiosperms into different subclasses or superorders. Anyhow these groupings are defined, EHRENDORFER (1977) showed that many similarities exist among these systems. The subclass *Magnoliidae* sensu Takhtajan, Stebbins and Cronquist roughly corresponds to the superorders *Annoniflorae*, *Nymphaeiflorae* and *Rafflesiiflorae* of THORNE (1983) and *Magnoliiflorae*, *Nymphaeiflorae* and *Ranunculiflorae* of DAHLGREN (1983). Cronquist-Takhtajan's *Rosidae* are more or less equivalent to Thorne-Dahlgren *Geraniiflorae*, *Santaliflorae*, *Rutiflorae*, *Proteiflorae*, *Rosiflorae*, *Myrtiflorae*. Similarly the *Dilleniidae* of the former are equivalent to the *Theiflorae*, *Violiflorae*, *Malviflorae* and *Primuliflorae* of the latter. Finally, Cronquist-Takhtajan's *Asteridae* circumscribe *Gentianiflorae*, *Lamiiflorae*, *Solaniflorae* and *Asteriflorae* of the Thorne-Dahlgren's systems. Cronquist's *Hamamelidae* and *Dilleniidae* and Dahlgren's *Corniflorae* have however no counterpart in other systems. Taking into account molecular studies (e.g. CHASE, SOLTIS, OLMSTEAD & al., 1993; SOLTIS & al., 1997; SAVOLAINEN & al., 1996) the *Hamamelidae* and *Dilleniidae* sensu Cronquist are grossly polyphyletic and Thorne-Dahlgren's *Corniflorae* and *Theanae* p.p. belong to *Asteridae*.

### Classification according to affinities and macroscopic features

Since taxonomic names are still confused until a new classification of angiosperms is available, we prefer to present the flowering plants by grouping them according to their macroscopic features and their phyletic relationships, using idiosyncratic terminology. Figures 1 and 2 present the comparisons between the system described below and the classifications of CRONQUIST (1981, 1988) and THORNE (1992), respectively. Our groupings include the following lineages:

Primitive featured *Angiospermae* with trimerous and/or helically arranged or achlamydeous flowers (*Magnoliidae* and *Ranunculidae sensu* Takhtajan, *Monocotyledons sensu auct.*):

M. *Magnoliidae sensu* Takhtajan (= paleodicotyledons)

M1. (Paleoherbs)

Nymphaealian lineage

Piperalian lineage

Illicialian lineage

M.2. (Paleotrees)

Magnolialian lineage

L. *Liliidae sensu* Dahlgren (= *Monocotyledons auct.*)

L.1. (*Protomonocotyledons*)

Aralian lineage

Alismatalian lineage

L.2. (Homoiochlamydeous monocotyledons mainly euanthial)

Lilialian lineage

L.3. (Heterochlamydeous monocotyledons mainly pseudanthial)

Commelinalian lineage

R.G. Ranunculalian grade (archaic eudicotyledons, *Ranunculidae sensu* Takhtajan)

R.G.1. (Mainly euanthial lineages)

Ranunculalian lineage

Nelumbonalian lineage

Protealian lineage

R.G.2. (Mainly pseudanthial lineages)

Trochodendralian lineage

Buxalian lineage

Homoio- or haplochlamydeous polypetalous *Angiospermae* (*Caryophyllidae s.l.*):

C. *Caryophyllidae*

C.1. (Caryophyllids with curved embryo and perisperm)

Caryophyllalian lineage

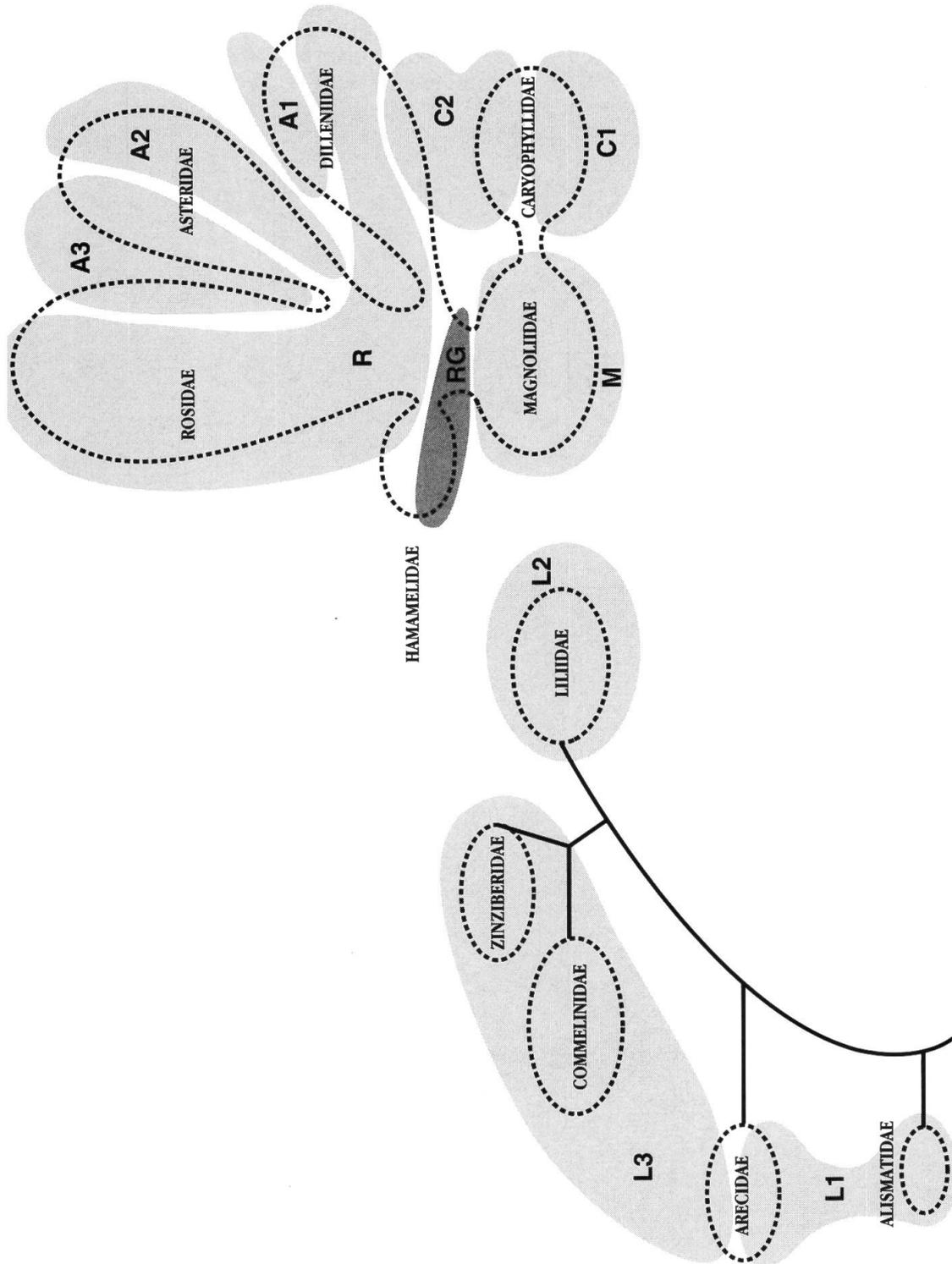


Fig. 1. – Comparison between the classification of CRONQUIST (1981, 1988; dotted areas) and the groupings presented in this paper (grey areas). **A** = Asteridae; **C** = Caryophyllidae; **L** = Liliidae; **M** = Monocotyledons; **R** = Rosidae; **RG** = ranunculalian grade; see text.

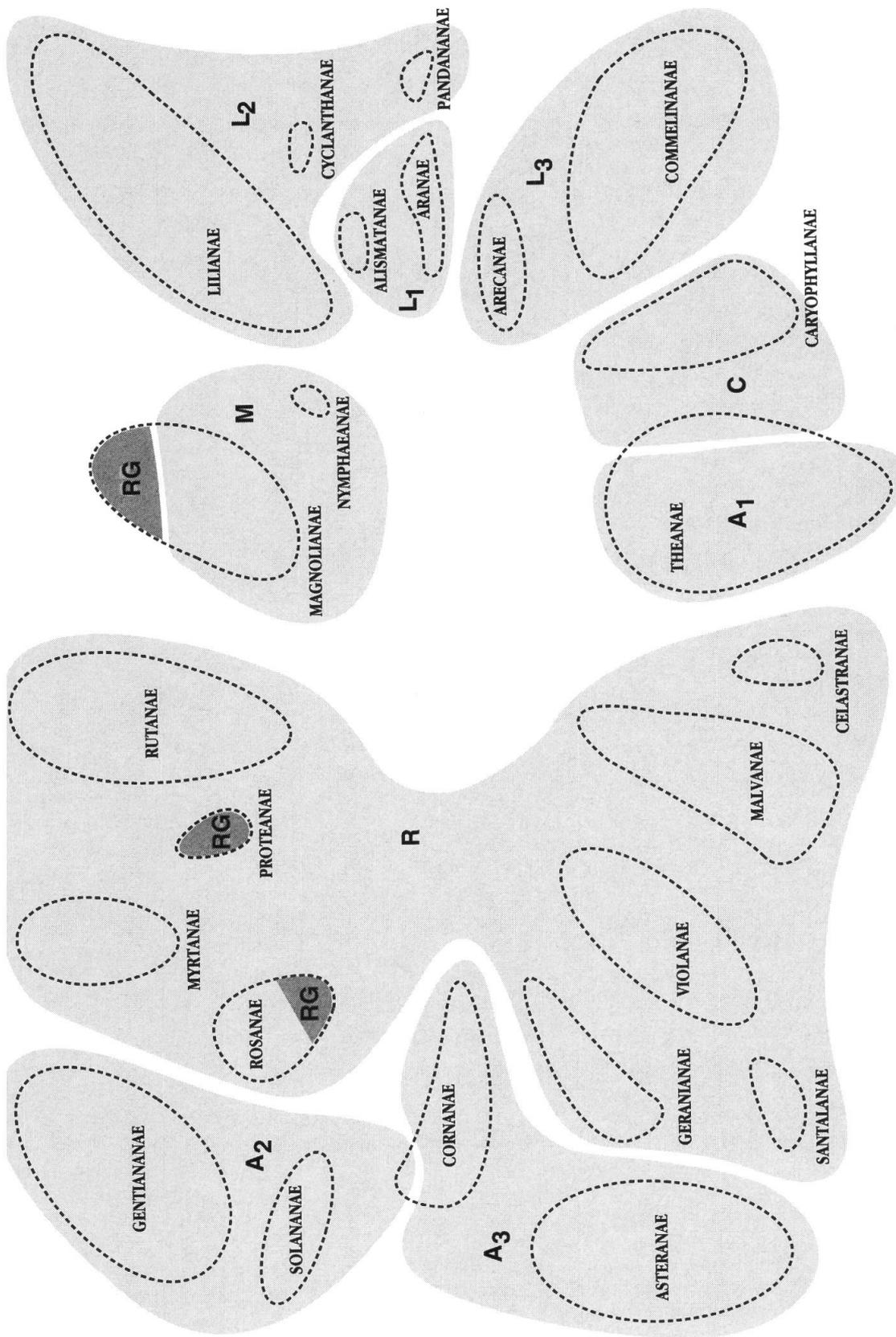


Fig. 2. – Comparison between the classification of THORNE (1992; dotted areas) and the groupings presented in this paper (grey areas). **A** = *Asteridae*; **C** = *Caryophyllidae*; **L** = *Liliidae*; **M** = *Monocotyledons*; **R** = *Rosidae*; **RG** = *ranunculian grade*; see text.

## C.2. (Caryophyllids with straight embryo and endosperm)

Polygonalian lineage

Higher polypetalous *Angiospermae* with cyclic, heterochlamydeous and dialypetalous flowers (*Rosidae sensu* Chase, Soltis, Olmstead & al.):

R. *Rosidae*

## R.1. (Hypogynous dialycarpellate rosids)

Saxifragalian lineage

Dillennialian lineage

Rosalian lineage

## R.2. (Hypogynous gamocarpellate rosids, mainly with alternate simple leaves)

Santalalian lineage

Linalian lineage

## R.3. (Hypogynous gamocarpellate rosids, mainly with compound leaves)

(Glucosinolate-bearing lineage)

Capparalian lineage

(Non glucosinolate-bearing lineages)

Malvalian lineage

Sapindalian lineage

Geranialian lineage

## R.4. (Peri- and epigynous rosids, mainly with opposite simple leaves)

Celastralian lineage

Myrtalian lineage

Higher sympetalous *Angiospermae* with cyclic, heterochlamydeous and gamopetalous flowers (*Asteridae sensu* Chase, Soltis, Olmstead & al.):

A. *Asteridae*

## A.1. (Hypogynous asterids with polystemonous or obhaplostemonous flowers)

Ericalian lineage

## A.2. (Hypogynous asterids with haplo- or oligostemonous flowers)

Gentianalian lineage

## A.3. (Epigynous, mainly pseudanthial asterids)

Asteralian lineage

**Primitive featured Angiospermae with trimerous, homoïo- or achlamydeous, mainly with helically arranged flowers (*Magnoliidae* and *Ranunculidae sensu Takhtajan, Monocotyledons auct.*)**

*Magnoliidae* are at the basis of the ranalian concept: since Arber & Parkin and Bailey, the strobiloid flower is considered as primitive. Although criticized by various recent authors the *Magnoliaceae*-centered derivation of the angiospermian flower is still a commonly used hypothesis. Dilcher's and other neo-Englerian theories favour simply constructed flowers as ancestor of the dicotyledons (e.g. see DAHLGREN, 1983; for discussion on the early flower evolution see ENDRESS & FRIIS, 1994; FRIIS & al., 1994). The two former floral types are however present in the following magnoliidian lineages. The monocotyledons have to be considered as a clade derived from the *Magnoliidae*.

***MAGNOLIIDAE (sensu Takhtajan) (= paleodicotyledons)***

They correspond to Cronquist's *Magnoliidae* without his *Ranunculales* and *Papaverales*. They are also Chase, Soltis, Olmstead & al.'s paleodicots (paleoherbs and paleotrees, see also QIU & al., 1993). They share many features with the monocots and especially with the most archaic ones, *i.e.* Dahlgren's *Ariflorae* and *Alismatiflorae*. They retain many plesiomorphies, among others: inaperturate or uniaperturate pollen (or derived types), vesselless stem and root (or imperfect vessels), homoiochlamydeous, haplo- or achlamydeous flower, often helically arranged and/or trimerous.

According to the pollen types and the habit, the following lineages can be recognized which are supported by molecular data and by more traditional views.

**M.1. Paleoherbs**

***Nymphaealian lineage*** (*Nymphaeanae p.p. sensu Takhtajan, paleoherbs sensu Chase, Soltis, Olmstead & al.*)

- *Nymphaeales* (without *Nelumbonaceae*): *Nymphaeaceae, Cabombaceae, Ceratophyllaceae*

Characteristic features are: aquatic herbaceous habit, absence of vessels or vessels present only in roots and rhizomes (CARLQUIST & SCHNEIDER, 1996), lamellar and simple stamens (without a distinct filament), homoiochlamydeous flowers, lack of ethereal oil cells.

***Piperalian lineage*** (paleoherbs *sensu Chase, Soltis, Olmstead & al.*)

- *Piperiales*: *Saururaceae, Piperaceae*
- *Aristolochiales*: *Aristolochiaceae*

This clade circumscribes Chase, Soltis, Olmstead & al.'s remaining paleoherbs, *i.e.* paleoherbs with uniaperturate pollen (or derived types). According to the neo-Englerian hypothesis, the angiospermian progenitor could have looked like a piperalian taxon. The main features shared by the piperalian taxa are: terrestrial or viny herbaceous habit, imperfect or absent vessels, achlamydeous or haplochlamydeous flowers.

***Illicialian lineage***

- *Illiciales: Illiciaceae, Schisandraceae*
- *Austrobaileyaceae (Magnoliales), Amborellaceae (Laurales)*

According to SOLTIS & al. (1997) these small woody magnoliid families appear as sister to all other angiosperms. They are sometimes woody vines (*Austrobaileyaceae, Schisandraceae*) vesselless plants (*Amborellaceae*), with tri- or sexaperturate pollen grains, ethereal oil cells (*Illiciales*) and imperfect stamens (*Austrobaileyaceae*).

**M.2. Paleotrees**

***Magnolialian lineage*** (*Magnoliana* p.p. *sensu* Takhtajan, paleotrees *sensu* Chase, Soltis, Olmstead & al.)

- *Magnoliales: Magnoliaceae, Annonaceae, Myristicaceae, Winteraceae, Canellaceae, Degeneriaceae*
- *Laurales p.p.: Lauraceae, Monimiaceae*

Trees or shrubs with imperfect vessels and uniaperturate pollen (or derived types), with hypogynous, homiochlamydeous or haplochlamydeous, trimerous and/or helically arranged flowers. Arber & Parkin's *Wielandiella* would be the progenitor of the modern *Magnoliales*.

***LILIIDAE sensu Dahlgren (Monocotyledons auct.)***

According to CHASE, SOLTIS, OLMSTEAD & al. (1993), CHASE & al. (1995) and DUVALL & al. (1993), monocotyledons are sisters to paleoherbs and paleotrees. The main features of the monocotyledons are: herbaceous habit (absence of cambium), absence of primary root, trimerous flowers, parallelnerved leaves, uniaperturate pollen or derived types. The monocotyledons would have appeared in the Cretaceous from a protomagnoliid bulk of ligneous plants with imperfect vessels and trimerous flowers. The herbaceous habit and the absence of cambium would be secondary reductions. BURGER (1981) considers monocotyledons as the progenitor of the angiosperms, the angiospermian archetype being an herbaceous protomonocotyledonian plant with small trimerous flowers. Molecular results are generally congruent with Dahlgren and Thorne classifications.

**L.1. Protomonocotyledons: mainly with broad reticulate leaves and simple flowers**

***Aralian lineage*** (*Ariflorae sensu* Dahlgren)

- *Arales: Acoraceae sensu Cronquist, Araceae*

*Acorus* is considered as the basalmost group of the *Liliidae*, as it shows some dicotyledonian features such as ethereal oils and dicot-type anther walls (CHASE & al. 1995; DUVALL & al., 1993, SOLTIS & al., 1997). The genus is not close to *Arales* and should consequently be considered at family level as proposed by Cronquist. The placement of *Araceae* as basal among *Liliidae* could be in agreement with the hypothesis of an archaic angiospermian complex being derived from *Arales* and *Piperales* (paleoherbs) (EMBERGER & CHADEFAUD, 1960; DAHLGREN & al., 1985). According to Dahlgren and Thorne, *Arales* are related to *Alismatales* and not to *Arecales*. Consequently, *Arecidae* *sensu* Cronquist, Takhtajan and Stebbins have to be rejected. The aralian reticulate-nerved leaves and small achlamydeous flowers are considered by various authors as plesiomorphic characters although *Acorus*, the basalmost liliidian genus, is

parallel-nerved. The reticulate leaf venation is a feature shared with paleoherbs (*Aristolochiales*, *Nymphaeales*, *Piperales*) and more advanced liliid lineages (*Dioscoreales*), and consequently it could also be considered as an homoplasy among *Liliidae*. The aralian lineage is sister to alismatids and shares with them the following features: vesselless root, trinucleate pollen, seeds lacking albumen, reticulate-veined leaves and, sometimes small imperfect flowers. The plesiomorphic achlamydeous and imperfect flower is another challenge to the magnoliid angiospermian archetype, enhancing the pseudo-flower theory.

**Alismatalian lineage** (*Alismatiflorae sensu* Dahlgren, *Alismatidae sensu* Cronquist and Takhtajan)

- *Alismatales: Alismataceae*
- *Hydrocharitales: Hydrocharitaceae*
- *Zosteriales: Zosteraceae*

Cronquist and Takhtajan consider *Alismatidae* as the most archaic monocotyledons. According to Dahlgren, the androecial and gynoecial polymeries have to be considered as derived states from the typical trimerous liliacean model. Molecular results enhance the hypothesis of a common protoangiospermian bulk built up by paleoherbs and the protomonocotyledons.

In addition to the features which are shared with the aralian lineage, the alismatids are characterized by the aquatic habit, the frequently trimerous and heterochlamydeous euanthium, the polymerous androecium, the dialycarpellate ovary, frequent occurrence of perfect flowers. The pseudanthium made up of small imperfect flowers is however also a common feature.

## L.2. Homoiochlamydeous Monocotyledons: mainly euanthial, with narrow leaves and imperfect vessels

**Lilialian lineage** (*Liliiflorae sensu* Dahlgren)

- *Liliales: Liliaceae, Smilacaceae, Melanthiaceae, Colchicaceae, etc.*
- *Asparagales: Asparagaceae, Agavaceae, Iridaceae, Dracaenaceae, Amaryllidaceae, Orchidaceae, etc.*
- *Dioscoreales: Dioscoreaceae, Burmanniaceae, Pandanaceae, Cyclanthaceae, Taccaceae, Velloziaceae, etc.*

According to Dahlgren, the following features are common among his *Liliiflorae*: vesselless stems or stems with imperfect vessels (scalariform perforations), homoiochlamydeous flowers, presence of nectaries, binucleate pollen, axile placentation, pluriovulate locules, capsular or bacciform fruits, absence of cell-wall-bound ferulic acid, and presence of calcium oxalate raphides. Contrarily to Cronquist's classification, Dahlgren considers *Cyclanthaceae* and *Pandanaceae* as not being close to *Arecaceae* and far from *Araceae*. *Taccaceae* are not related to *Arales*, contrarily to Dahlgren's proposal. *Dioscoreales* have reticulate-veined leaves like *Smilacaceae* which belong however to another order. *Orchidaceae* and *Burmanniaceae* are not closely related.

## L.3. Heterochlamydeous Monocotyledons: mainly pseudanthial, with perfect vessels

**Commelinian lineage** (*Bromeliiflorae, Zingiberiflorae, Commeliniflorae, Areciflorae sensu* Dahlgren, *Commelinidae* and *Zingiberidae sensu* Cronquist)

- *Poales: Poaceae*
- *Juncals (incl. Cyperales): Juncaceae, Cyperaceae*

- *Bromeliales: Bromeliaceae, Rapateaceae*
- *Commelinales: Commelinaceae, Pontederiaceae*
- *Zingiberales: Zingiberaceae, Musaceae, Strelitziaceae, Heliconiaceae*
- *Typhales: Typhaceae*
- *Arecales: Arecaceae*

According to Dahlgren, the following features ought to be considered as derived from the ancestral liliid lineage: stems with vessels, heterochlamydeous flowers, absence of nectaries, trinucleate pollen, apical or basal placentation, uniovulate locule, nutlet, cell-wall-bound ferulic acid, and presence of calcium oxalate raphides. Considering the relationships within the clade, the use of “*commelinalian*” should be replaced by “*poalian*” (the most advanced) or “*arecalian*” (the basalmost).

### **R.G. RANUNCULALIAN GRADE (*Ranunculidae sensu Takhtajan*) (archaic eudicotyledons)**

These lineages (“grade” is used because they are paraphyletic groups) correspond to Takhtajan’s *Ranunculidae* and *Hamamelidae p.p.* and to Chase, Soltis, Olmstead & al.’s ranunculids and hamamelids I and II. It is paraphyletic to the rest of the eudicotyledons and contains most plesiomorphies among all eudicotyledonian lineages. It is characterized by triaperturate pollen (or derived types), generally perfect vessels, trimerous, spiral and cyclic, dialycarpellate, homoio- or haplochlamydeous flowers with trends to heterochlamydy, dialycarpelly. Apomorphies such as gamocarpelly and (tetra-) pentamery are observed among the more advanced taxa.

#### **R.G.1. Mainly euanthial lineages**

##### ***Ranunculalian lineage* (*Ranunculanae sensu Takhtajan*)**

- *Ranunculales: Ranunculaceae, Berberidaceae, Menispermaceae, Lardizabalaceae*
- *Papaverales: Papaveraceae, Fumariaceae*

The main features of this clade are choripetaly, homoio- or haplochlamydeousy, tri-, tetra- or pentamery, dialycarpelly. HOOT & CRANE (1996) recognize the monophyly of the ranunculalian families based on 18S ribosomal DNA. *Eupteleales* also appear as closely related to *Ranunculales*.

##### ***Nelumbonalian lineage* (*Nelumbonanae sensu Takhtajan*)**

- *Nelumbonales: Nelumbonaceae*

With the exception of Cronquist’s system, all recent ones separate *Nelumbonaceae* from *Nymphaeales*. The fruit and the triaperturate pollen as well as the vessels in root metaxylem of *Nelumbo* are not nymphaealian features (SCHNEIDER & CARLQUIST, 1996).

##### ***Protealian lineage***

- *Proteales (sensu Cronquist, i.e. without Elaeagnaceae), Proteaceae, etc.*

The flowers are symtepalous, apocarpellate, tetramerous. *Proteaceae* are placed in the lower hamamelids close to *Platanaceae* by CHASE, SOLTIS, OLMSTEAD & al. (1993). SYTSMA & al. (1996a) exclude *Elaeagnaceae* from *Proteales* and relate them to *Rosaceae/Rhamnaceae*.

**R.G.2. Mainly pseudanthial lineages**

The following lineages correspond more or less to Chase, Soltis, Olmstead & al.'s lower hamamelids.

***Trochodendralian lineage* (sensu Takhtajan, without *Cercidiphyllales*)**

- *Trochodendrales*: *Trochodendraceae*, *Tetracentraceae*
- *Eupteleales*: *Eupteleaceae*

The superorder *Trochodendraneae* is used by Takhtajan to circumscribe the two above-mentioned orders. Contrarily to Takhtajan's hypothesis, *Cercidiphyllum* is not related to *Trochodendrales* but to *Hamamelidales* (HOOT & CRANE, 1996). Based on molecular data *Euptelea* appears closer to *Ranunculales* than to *Trochodendrales* which is different from Thorne's and Melchior's placements. Based on molecular data *Platanus* is related to various lower hamamelidian taxa but not to *Hamamelidales* (CHASE, SOLTIS, OLMSTEAD & al., 1993; SOLTIS & al., 1997).

***Buxalian lineage* (*Hamamelidanae p.p.* sensu Takhtajan)**

- *Buxales* (sensu Dahlgren): *Buxaceae*, *Didymelaceae*

The small family *Didymelaceae* is considered as belonging to a separate hamamelidian order by Cronquist and Takhtajan or related to rosids by Thorne and Dahlgren. Based on molecular data *Didymeles* is related to *Buxaceae* (SOLTIS & al., 1997).

**Homoio- or haplochlamydeous polypetalous Dicotyledons: mainly with cyclic flowers  
(= *Caryophyllidae s.l.*)****C. CARYOPHYLLIDAE**

This grouping corresponds to Cronquist's and Takhtajan's *Caryophyllidae*, Thorne's *Caryophyllanae* and Dahlgren's *Caryophylliflorae*, *Plumbaginiflorae* and *Polygoniflorae*. According to molecular data (CHASE, SOLTIS, OLMSTEAD & al. (1993), SOLTIS & al., 1997) two insectivorous families (*Droseraceae*, *Nepenthaceae*) as well as *Frankeniaceae*, *Tamaricaceae*, *Rhabdodendron* and *Simmondsia* are included in *Caryophyllidae*. The morphological cladistics study of ALBERT & STEVENSON (1996) corroborates the caryophyllidian alliance *sensu lato*, *i.e.* by including *Nepenthales* (without *Sarraceniaceae*), *Tamaricales*, *Rhabdodendraceae* and *Simmondsiaceae*. In this lineage plesiomorphic features such as homoiochlamydy and trimery are concomitant with apomorphies such as gamocarpely, heterochlamydy and pentamery. Several unusual features, *i.e.* insectivorous habit, campylotropous or amphitropous ovules, perisperm and occurrence of betalain, are common.

**C. 1. Caryophyllids with curved embryo and perisperm*****Caryophyllalian lineage* (*Caryophyllanae sensu* Takhtajan & Thorne)**

- *Caryophyllales sensu* Cronquist: *Caryophyllaceae*, etc.

This lineage is characterized by campylotropous or amphitropous ovules, a curved embryo bordering the perisperm, sieve-tubes with P-type plastids, and production of betalain.

## C. 2. Caryophyllids with straight embryo and endosperm

### *Polygonalian lineage*

- *Polygonales*: *Polygonaceae*
- *Plumbaginales*: *Plumbaginaceae*
- *Nepenthales* (without *Sarraceniaceae*): *Nepenthaceae*, *Droseraceae*, and probably *Ancistrocladaceae* and *Dioncophyllaceae*
- *Tamaricales* (*sensu* Dahlgren): *Frankeniaceae*, *Tamaricaceae*

*Polygonales* and *Plumbaginales* belong to Cronquist's *Caryophyllidae* but differ from *Caryophyllales* by anatropous or orthotropous ovules, a straight embryo, absence of perisperm, presence of sieve-tubes with S-type plastids, and production of proanthocyanin. *Nepenthales* and *Tamaricales* are stress-tolerant orders. According to ALBERT & STEVENSON (1996), *Ancistrocladaceae* and *Dioncophyllaceae* are related to *Nepenthales*.

### Higher polypetalous Angiospermae: mainly with cyclic, heterochlamydeous and dialypetalous flowers (= *Rosidae sensu* Chase, Soltis, Olmstead & al.)

## R. ROSIDAE

This lineage corresponds to *Rosidae* and *Dilleniidae p.p.* according to Takhtajan, Cronquist and Stebbins, and approximately to Thorne-Dahlgren's *Rosiflorae*, *Santaliflorae*, *Violiflorae*, *Myrtiflorae*, *Malviflorae* and *Theiflorae p.p.* (Thorne uses the suffix *-anae* in his 1992 realignment, *viz* *Theanae*). *Rosidae* are characterized by polypetaly, heterochlamydy, (tetra-) pentamery, bitegmic and crassinucellate ovules. Floral reductions due to wind pollination are common.

### R. 1. Hypogynous dialycarpellate rosids, often with floral reductions and pseudanthia

#### *Saxifragalian lineage* (Rosid III and IV *sensu* Chase, Soltis, Olmstead & al.)

- *Saxifragales sensu* Morgan & Soltis: *Saxifragaceae s.str.* (*Saxifragoideae*), *Crassulaceae*, *Grossulariaceae*
- *Haloragales*: *Haloragaceae* (excl. *Gunneraceae*)
- *Hamamelidales p.p.*: *Cercidiphyllaceae*, *Hamamelidaceae*
- *Daphniphyllales*: *Daphniphyllaceae*
- *Paeoniales*: *Paeoniaceae*

As stressed by MORGAN & SOLTIS (1993), SOLTIS & al. (1996) and HIBSCH-JETTER & SOLTIS (1996) the saxifragalian alliance includes the above-mentioned taxa. The main features are close to those of the ranunculids: dialycarpelly or imperfect syncarpelly, high floral variability, hypogyny. Saxifragalian representatives "provide" a lot of plesiomorphies which make them basal to most other rosids. Cronquist's *Hamamelidae* appear at least as triphyletic: the lower hamamelids related to the *Ranunculidae* (Trochodendralian lineage), the *Hamamelidales* and *Daphniphyllales* placed close to *Saxifragales*, and the higher hamamelids which belong to a rosalian lineage (see below). The placement of *Euptelea* among *Ranunculidae* and separated from *Hamamelidales* is supported by molecular data

***Dillennialian lineage***

- *Dilleniales*: *Dilleniaceae*
- *Vitales*: *Vitaceae*, *Leeaceae*

According to CHASE, SOLTIS, OLMSTEAD & al. (1993) *Dilleniaceae* and *Vitaceae* are closely related and placed among their “asterid V” or “rosid III” near the caryophyllids. *Vitis* and *Leea* have definitively no relationship with *Rhamnaceae*, the oppositipetalous stamens being an homoplasy shared by *Rhamnales* and *Vitales*. The relationship between *Dillenia* and *Leea* is also supported by common consumers (SPICHIGER & al., 1997). The obvious feature shared by several of these taxa is the viny habit.

***Rosalian lineage*** (Nitrogen-fixing clade *sensu* Chase, Soltis, Olmstead & al.)

- *Urticales sensu* Cronquist: *Urticaceae*, *Moraceae*
- *Leguminosae sensu* Cronquist (*Fabales*): *Fabaceae*, etc.
- *Rhamnales sensu* Thorne: *Rhamnaceae*, *Elaeagnaceae*
- *Polygalales p.p.*: *Polygalaceae*
- *Rosales*: *Rosaceae*
- *Cucurbitales*: *Corynocarpaceae*, *Begoniaceae*, *Datisceae*, *Coriariaceae*, *Cucurbitaceae* (*sensu* Stevenson & al.)
- *Fagales*: *Fagaceae*
- *Juglandales*: *Juglandaceae*
- *Myricales*: *Myricaceae*
- *Casuarinales*: *Casuarinaceae*
- *Violales pp.*: *Cucurbitaceae*, *Datisceae*

The main features are: heterochlamydeous and zygomorphic insect-pollinated flowers (*Leguminosae*, *Polygalaceae*) ranging to simply constructed flowers or pseudo-flowers which are wind-pollinated (*Urticales*); hypogyny, dialycarpelly or apocarpelly, monomerous or pseudomerous gynoecium (with exception of the epigynous gamocarpellate *Rhamnaceae*). Most rosalian representatives are nitrogen-fixing. *Rhamnales sensu* Cronquist appear as diphyletic, *Leeaceae* and *Vitaceae* being close to *Dilleniales*. *Rhamnaceae* are sister to *Urticales*, sharing with them the typically palmatinerved basis of the leaves.

The relationship between the rosalian *Urticales* and the fagalian representatives supports Takhtajan's and Cronquist's placement in the same subclass. Dahlgren's placement of *Urticales* close to *Malvales* and *Euphorbiaceae* is not supported by molecular data. EHRENDORFER (1977) considers amentifers as rather ancestral unlike DAHLGREN (1983) who considers the petaliferous and insect-pollinated groups as customarily plesiomorphic. According to SYTSMA & al. (1996a) *Urticales* are derived from a rosoid lineage including *Rhamnaceae*, *Elaeagnaceae*, *Barbeyaceae* and *Rosaceae*; *Ulmaceae* is sister to other urticalian families. The placement of *Leguminosae* close to *Rosales* supports Takhtajan-Cronquist's classification. It is noteworthy that the two zygomorphic-flowered orders (*Polygalales p.p.* and *Leguminosae*) appear as sisters.

The amentiferous lineages (fagalian, juglandalian lineages) are well supported by various molecular sequences (CHASE, SOLTIS, OLMSTEAD & al., 1993; MANOS & STEELE, 1996; SAVOLAINEN, unpubl.). It shares many features with the haplochlamydeous rosalian taxa (*Urticales*): wind-pollinated simply constructed flowers, pseudanthia, nitrogen-fixing roots. Unlike the representatives of the rosalian sister-group, the achenes are frequently surrounded or even imbedded in bracts or cupules, the male flowers are aments, the calyx is reduced or none, and the ovary 2-3 carpellate. Epigynous taxa classically considered as violalian (*Cucurbitaceae*, *Datis-*

*caceae*) appear amazingly as a sister-group of *Fagales*; the features shared between them are: scanty or no endosperm, unisexual flowers, monoecious plants, occurrence of p-coumarin, linol- acid and ferulic acid.

## R. 2. Hypogynous gamocarpellate rosids, mainly with simple alternate leaves

### *Santalalian lineage*

- *Santalales*: *Santalaceae*, *Viscaceae*, *Olacaceae*, *Loranthaceae*, *Opiliaceae*

The main features are the imperfectly or ategumented ovules which are immersed into the placenta and the tendency to parasitism. Gamopetaly occurs frequently. The common sympeta- lous flowers in the santalalian taxa would make logical a placement close to asterids. NICKRENT (1996) considers *Olacaceae* the most primitive family in the order and *Viscaceae* the most advanced.

### *Linalian lineage* (Rosid I *p.p.* *sensu* Chase, Soltis, Olmstead & al.)

- *Linales*: *Erythroxylaceae*, *Linaceae*, *Humiriaceae*
- *Theales p.p.*: *Ochnaceae*, *Medusagynaceae*, *Clusiaceae*, *Quiinaceae*, etc.
- *Chrysobalanales*: *Chrysobalanaceae* and probably *Dichapetalaceae* and *Trigonia- ceae*
- *Euphorbiales*: *Euphorbiaceae* (without *Drypetes*)
- *Violales*: *Violaceae*, *Turneraceae*, *Passifloraceae*, *Flacourtiaceae*
- *Malpighiales* as an order not related to *Polygales*: *Malpighiaceae*
- *Salicales* (*sensu* Takhtajan): *Salicaceae*

The main features which appear within this heterogenous alliance are: stipulate, simple and alternate leaves, flowers with a tricarpellate and trilocular ovary with free styles, obdiplostemo- nous or isostemonous anthers, frequent occurrence of glands on various organs.

*Euphorbiales* appear as the closest to *Passifloraceae* and *Malpighiaceae* and related to *Geraniales p.p. sensu* Engler (*Linaceae*, *Erythroxylaceae*, *Zygophyllaceae*) and hypogynous *Vio- lales*. (CHASE, SOLTIS, OLMSTEAD & al., 1993) It is noteworthy that, based on molecular data, *Geraniaceae* are excluded from the linalian lineage which is for all the other families in agreement with Engler's geranianian concept. *Malpighiaceae*, *Passifloraceae* and *Euphorbiaceae* share the presence of glands on various organs, tricarpellate and trilocular ovaries, partially free styles. Besides, *Chrysobalanaceae* appear as the closest to *Dichapetalaceae* and *Trigoniaceae* (CHASE & SAVOLAINEN, unpublished); these three families present the typically linalian tri- carpellate ovary (often reduced to two or a single fertile carpel in *Chrysobalanaceae*), zygomor- phy and floral reduction. The conventional concept of proximity between *Chrysobalanaceae*, *Euphorbiales* and *Malvales* (for instance in Thorne's, Dahlgren's and Takhtajan's systems) is not congruent with molecular data (e.g. CHASE, SOLTIS, OLMSTEAD & al., 1996) which rather support the Englerian classification.

DAHLGREN's *Violiflorae* (1983) include *Violales*, *Capparales*, *Salicales*, *Cucurbitales* and *Tamaricales*. According to Dahlgren, the dominant features are: unilocular ovary with parietal placentation, androecial trend to polystemony or rarely haplostemony, and frequent occur- rence of a gynophore or androgynophore. THORNE's *Violanae* (1992) correspond to Dahlgren's concept as well as to the "*Parietales*" of the classical authors. The alliance of *Violales sensu lato* with *Capparales* is questioned by molecular studies (CHASE, SOLTIS, OLMSTEAD & al., 1993), Dahlgren's and Thorne's *Violiflorae* being divided at least into three clades: *Violales* with hypogynous flowers, *Violales* with epigynous flowers and a *Capparales-Tropaeolales* clade. The

segregation between hypogynous and epigynous *Violales* has already been suggested by serological studies (Kolbe & John, 1979 cited by DAHLGREN, 1983). The thealian affinity of *Ochnaceae*, *Medusagynaceae*, *Quiinaceae* and *Clusiaceae* is demonstrated by molecular data (CHASE & al., 1996; FAY & CHASE, 1996).

### R. 3. Hypogynous gamocarpellate rosids, mainly with compound leaves

#### Glucosinolate-producing lineage

**Capparalian lineage** (*sensu* Rodman & al., *Parietales p.p. sensu auct.*)

- *Capparales*: *Capparaceae*, *Brassicaceae*
- *Tropaeolales*: *Tropaeolaceae*, *Limnanthaceae*
- *Violales p.p.*: *Caricaceae*

The main features are: leaves often compound, tetramery, parietal placentation, presence of glucosinolates. The occurrence of mustard oil is the most important characteristic of the lineage (RODMAN & al., 1995). The placement of *Tropaeolales* (*Tropaeolaceae* and *Limnanthaceae*) close to *Capparales* is congruent with DAHLGREN's proposal of 1975. *Capparales* are clearly separated from *Violales* which belong to the linalian lineage. The parietal placentation is consequently to be considered as a homoplasy shared by the two lineages.

#### Non glucosinolate-producing lineages

**Malvalian lineage**

- *Malvales sensu* Dahlgren (without *Elaeocarpaceae*): *Malvaceae*, *Sterculiaceae*, *Tiliaceae*, *Bombacaceae*, *Bixaceae*, *Cistaceae*, *Dipterocarpaceae*

Main features are: multistaminate flowers, sometimes with a monadelphous or polyadelphous androecium and with contorted aestivation of the petals, leaves often compound, stellate hairs. *Rhamnales*, *Urticales* and *Juglandales* are placed by Thorne and Dahlgren in *Malviflorae*, whereas they are related to the rosalian lineage based on molecular data (CHASE, SOLTIS, OLMSTEAD & al., 1993). *Euphorbiales*, another malvifloralian order *sensu* Thorne and Dahlgren, belongs to the linalian clade according to Chase, Soltis, Olmstead & al. *Malvales* contain at least *Malvaceae*, *Bombacaceae*, *Sterculiaceae*, *Cistaceae*, *Dipterocarpaceae*, and *Bixaceae*, but not *Elaeocarpaceae*. Dahlgren's *Malviflorae* are clearly polyphyletic and divided into at least four lineages: 1) *Malvales sensu* Dahlgren (without *Elaeocarpaceae*); 2) *Elaeocarpaceae* (clearly related to *Cunoniaceae*, *Oxalidaceae*, *Connaraceae*); 3) *Rhamnales* (without *Vitaceae* and *Leeaceae*) and *Urticales* related to the rosalian clade; 4) *Euphorbiales* related to the linalian clade.

**Sapindalian lineage** (*Rutanae sensu* Takhtajan)

- *Sapindales sensu* Cronquist: *Sapindaceae*, etc.

The compound leaves, the mainly disciferous, (ob-)diplostemonous or haplostemonous flowers are common features within this lineage. *Fabales* are not related to a sapindalian lineage but to the rosalian lineages contrarily to Thorne's *Rutanae* concept.

A synapomorphy of the sapindalian, capparalian and malvalian lineage is the compound leaves, a character more common among the sapindalian representatives.

**Geranialian lineage** (sensu PRICE & PALMER, 1993)

- *Geraniales s. str.: Geraniaceae*
- *Melanthaceae, Stachyuraceae, Staphyleaceae, Greyiaceae, Geissolomataceae*

*Geraniales* sensu Engler and Cronquist are split into various lineages, most of the classically considered geranialian taxa being related to the linalian clade. The placement of the geranialian phylum is not yet clear. Some features include compound or dissected leaves, obdiplostemony, floral glands. The mericarpic fruit appears as a predictive character for the geranialian lineage.

**R. 4. Peri- or epigynous rosids, mainly with simple opposite leaves****Celastralian lineage**

- *Celastrales p.p.: Celastraceae, Hippocrateaceae, Stackhousiaceae* and various small taxa generally considered as saxifragalian (*Brexia, Lepuropetalon, Parnassia*), excl. *Icacinaceae, Dichapetalaceae, Aquifoliaceae, Corynocarpaceae*, etc.

The main features are: simple, exstipulate, sometimes opposite leaves, haplostemonous and disciferous, sometimes perigynous, flowers. According to KOONTZ & SOLTIS (1996), several members of Engler and Prantl's *Saxifragaceae* are to be placed among *Celastrales*. This order is still being worked on with different genes (SPICHTER & al., 1993; SAVOLAINEN & al., 1994, SAVOLAINEN & al., 1997; SAVOLAINEN & CHASE, in prep.). It appears as distant from *Santalales* and *Vitales*, which is not congruent with Dahlgren's placement. The Englerian placement of *Aquifoliaceae* among *Celastrales* has to be rejected, *Ilex* being a member of the asteridian clade based on molecular data.

**Myrtalian lineage** (sensu SYTSMA & al., 1996b; CONTI & al., 1996)

- *Myrtales sensu Cronquist: Myrtaceae*, etc.
- *Polygalales p.p.: Vochysiaceae*

The main features are: internal phloem, vestured pits in phloem cells, frequent extra-floral myrmecophilous organs, simple opposite exstipulate leaves, a frequently occurring well developed hypanthium, peri- or epigyny, polymerous or diplostemonous androecium. The unexpected placement of *Vochysiaceae* among *Myrtales* pinpoints the predictive value of the opposite exstipulate simple leaves for this lineage. Furthermore, the extra-floral myrmecophilous organs are characteristics shared by some melastoms and *Qualea*, as well as the floral reduction which occurs frequently in *Vochysiaceae*. *Polygalales sensu Cronquist* appear consequently as polyphyletic since they are divided into at least three lineages: 1) *Polygalaceae* close to *Rosales*; 2) *Malpighiaceae* close to *Euphorbiaceae* (linalian clade); 3) *Vochysiaceae*.

**Higher sympetalous dicotyledons: mainly cyclic, heterochlamydeous and gamopetalous flowers (= Asteridae sensu Chase, Soltis, Olmstead & al.)****A. ASTERIDAE**

This grouping contains the gamopetalous taxa together with a few dialypetalous exceptions. It corresponds to Engler's *Sympetalae*, to Cronquist-Stebbins-Takhtajan's *Asteridae* with the sympetalous dilleniids (*Ericales, Primulales, Ebenales*). DAHLGREN (1983) proposed to define six gamopetalous superorders: *Solaniflorae, Gentianiflorae, Lamiiflorae, Primuliflorae, Asteri-*

*florae* and *Corniflorae*. THORNE (1992) had more or less the same concept except for his inclusion of Dahlgren's *Lamiiflorae* into his *Gentiananae* and the placement of Dahlgren's *Primuliflorae* and *Corniflorae p.p.* among his *Theanae*. Based on molecular studies CHASE, SOLTIS, OLMSTEAD & al. (1993) and OLMSTEAD & al. (1993) defined an asteridian clade containing the eudicotyledons with sympetalous corolla, unitegmic and tenuinucellate ovules plus some dialypetalous taxa such as *Cornales*, *Araliales*, *Theales p.p.* etc. The occurrence of iridoid compounds is another common feature, however with some noticeable exceptions (inulin in *Asterales* and *Campanulales*).

### A. 1. Asterids with hypogynous polystemonous or obhaplostemonous flowers

**Ericalian lineage** (Thorne's *Theanae* sensu lato)

- *Cornales p.p. sensu* Thorne (crassinucellate and bitegmic ovulate representatives): *Cornaceae*, *Alangiaceae*, *Nyssaceae*
- *Theales p.p. sensu* Thorne: *Marcgraviaceae*, *Tetrameristaceae*, *Theaceae*, *Sarracenaceae*, *Lecythidaceae*, *Pelliciearaceae*
- *Primulales sensu* Thorne: *Primulaceae*, *Myrsinaceae*, etc.
- *Ericales sensu* Cronquist (incl. *Clethraceae* and *Cyrillaceae*): *Ericaceae*, etc.
- *Fouquieriales sensu* Thorne: *Fouquieriaceae*, etc.
- *Ebenales sensu* Thorne: *Ebenaceae*, etc.
- *Balsaminaceae*, *Polemoniaceae p.p.* (*Polemonium*, *Cobaea*)

With the exception of *Impatiens* (*Geranianae*) and *Cobaea* (*Solananae*) this lineage circumscribes Thorne's *Theanae*. It also corresponds to Cronquist's sympetalous dilleniids plus some of his dialypetalous dilleniidian orders, as well as to Chase, Soltis, Olmstead & al.'s asterids.

Dahlgren's *Corniflorae* are built up around three core orders: *Ericales*, *Cornales* and *Dipsacales*. Thorne's *Cornanae* are in agreement with the placement of *Cornales* and *Dipsacales* but do not contain *Ericales* which are placed among his *Theanae*. Based on molecular data (CHASE, SOLTIS, OLMSTEAD & al., 1993) *Ericales* are members of a thealian lineage, *Dipsacales* belong to "asterids II", i.e. close to *Asterales*, and *Cornales* are split into three asteridian lineages (i.e. Thorne's *Theanae*, *Asteranae* and *Gentiananae*). It is noteworthy that the cornalian basal-most lineage of *Theanae* is characterized by crassinucellate and bitegmic ovules (*Alangium*, *Nyssa*), whereas those of *Asteranae* (*Helwingia*) and *Gentiananae* (*Garrya*, *Aucuba*) possess tenuinucellate and unitegmic ovules. Plesiomorphies are: regular flower, often tetramerous, dialypetaly, isomerous or dimerous androecium, anthers with valvar dehiscence, ligneous habit, vessels with scalariform perforations, presence of iridoids, bitegmic and crassinucellate ovules in pluricarpellate and plurilocular ovaries. The multiplication of stamens is an apomorphy occurring in several thealian families (*Lecythidaceae*, *Theaceae*), as well as the gamopetaly which is a more common feature than the choripetaly. The main thealian apomorphies are: cyclic flowers, gamopetaly, obdiplostemony, or polystemony, stamens sometimes more or less fused, anthers with pericidal dehiscence, tenuinucellate and unitegmic ovule, perfect vessels, simple leaves, distichous (*Ebenaceae*) or clustered at the extremity of the twigs (*Sapotaceae*, *Theaceae*). A developed laticiferous system can be found among *Ebenales* and *Theales*. The placement of *Impatiens* (*Balsaminaceae*) and *Cobaea* (*Polemoniaceae*) among this thealian lineage is surprising.

## A. 2. Asterids with hypogynous, haplostemonous or oligostemonous flowers

### *Gentianalian lineage* (Thorne's *Gentiananae* sensu lato)

- *Cornales p.p. sensu* Thorne: *Aucuba*, *Garrya*, *Eucommia*
- *Boraginales sensu* Dahlgren: *Boraginaceae* and *Hydrophyllaceae*
- *Scrophulariales sensu* Thorne: *Scrophulariaceae*, *Lamiaceae*, etc.
- *Gentianales sensu* Thorne: *Gentianaceae*, *Rubiaceae*, etc.
- *Solanales sensu* Thorne (without *Boraginaceae* and *Hydrophyllaceae*)

This lineage corresponds to Thorne's *Gentiananae* and *Solananae*, to Dahlgren's *Gentianiflorae*, *Lamiiflorae* and *Solaniflorae*, and to Chase, Soltis, Olmstead & al.'s asterid I.

The main features of the gentianalian lineage are: presence of iridoids or alkaloids, sympetalous sometimes zygomorphic corolla, isostemony or paucistemony, bicarpellate and bilocular ovary with 2-n unitegmic and tenuinucellate ovules in each locule, hypo- or epigyny, opposite or alternate leaves. *Solanales* and *Scrophulariales* show many features considered as advanced: presence of alkaloids, paucistemony, multiovulate locules, alternate leaves. ERBAR & LEINS (1996) pinpoint 'late' sympetaly in the lineage, with the exception of *Rubiales* and *Oleales*.

## A. 3. Epigynous asterids, frequently pseudanthial

### *Asteralian lineage* (Thorne's *Asteranae* sensu lato)

- *Theales p.p. sensu* THORNE 1983: *Aquifoliaceae*, *Icacinaceae*
- *Cornanae p.p. sensu* Thorne: *Cornales p.p.* (*Helwingia*), *Hydrangeales p.p.*, *Pittosporales* (*Pittosporaceae*), *Araliales* (*Araliaceae*, *Apiaceae*), *Dipsacales* (*Dipsacaceae*)
- *Asteranae sensu* Thorne: *Campanulales* (*Campanulaceae*, *Menyanthaceae*), *Asterales* (*Asteraceae*)

This lineage corresponds to Cronquist's dipsacalian- asteralian- campanulalian circumscription, to Dahlgren's *Araliiflorae-Asteriflorae* and *Corniflorae p.p.* and to Chase, Soltis, Olmstead & al.'s asterid II clade. The main features are: gamopetaly, epigyny, unilocular ovary (trilocular in some *Campanulales*), unitegmic and tenuinucellate ovules, isostemony, sometimes zygomorphy and synanthery, pseudanthia, absence of iridoid compounds but occurrence of inulin, herbaceous habit. 'Early' sympetaly is a feature shared by all the asteralian taxa (ERBAR & LEINS, 1996).

## Conclusion

The above-proposed classification emphasizes various morphological features. Several have been acknowledged for a long time as being significant for segregating the higher level lineages, e.g. the free-parted, helically arranged and homoiochlamydeous flowers of *Magnoliidae* which are commonly considered as ancestral in contrast to the cyclic and heterochlamydeous flowers of *Rosidae* and *Asteridae*. Other features, such as sympetaly in *Asteridae*, are recovering their major weight that was already proposed by the Candollean and Englerian classifications, whereas it has been reduced in the recent post-Besseyan systems. Bentham and Hooker's *Disciflorae* correspond to the lineages which a common presence of glands and discs (sapindalian, celastralian and geranialian lineages). Likewise, even if their relationships are more accurately described when based upon molecular data, it was always well accepted that the imperfect flo-

wers of *Piperaceae*, the flowers without perianth of *Araceae* and the strobiloid flowers of *Magnoliaceae* and *Nymphaeaceae* are primitive. The idea of the root of the monocotyledons to be found among *Magnoliidae*, as well as the paraphyly of the conventional dicotyledons, were also already suggested in the past, but the monocotyledons-dicotyledons dichotomy has probably been maintained by convenience. Thus, the skeleton of the *Angiospermae* classification, although losing its classical dichotomy, keeps its major bones, i.e. the magnoliidian, liliidian (= monocotyledons), caryophyllidian, rosidian and asteridian concepts.

Some amazing phylogenetical clues are not easily explained by morphological features and numerous new affinities are highlighted by molecular studies: e.g. the relationship between caryophyllids and insectivorous orders, the placement of caryophyllids as possibly sister to asterids, or the occurrence of some polypetalous and spirally-arranged thealian taxa among *Asteridae*. Molecular analyses make several conventional groupings artificial, questioning some well-admitted features. For example, the parietal placentation has to be considered as an homoplasy since the traditionally associated *Capparales* and *Violales* appear as belonging to different major lineages. Since the failure of the Dahlgren-Thorne's malviflorian grouping (*Euphorbiales*, *Malvales s.l.*, *Rhamnales*, *Urticales*), palmateveined leaves are no more a phylogenetically informative character at this level. Some other evident characteristics such as the form of vegetative organs gain some interest for their predictive phylogenetic value: e.g. the compound leaves for three rosidian lineages (*Capparales s.l.*, *Sapindales s.l.*, *Geraniales*), the exstipulate opposite simple leaves for the myrtalian (viz. *Vochysiaceae*) and celastralian lineages, the stipulate alternate simple leaves among the linalian and santalalian lineages.

Thus, plant evolution is now being intensively studied and every day new data are published on this matter. Despite the fact that a new classification will be published soon, we wanted to update here our formal botanical course, in order to give to our students some basis of modern plant systematics.

#### ACKNOWLEDGMENTS

We are very grateful to Prof. P. K. Endress, Drs. M. W. Chase and A. L. Stork for their critical reading of different versions of the manuscript, and to Maryse Kolakowski who made the figures.

#### REFERENCES

- ALBERT, V. A. & D. W. STEVENSON (1996). Morphological cladistics of the Nepenthales. *Amer. J. Bot.* S83 Abstract 380.
- BURGER, W. C. (1981). Heresy revived: the monocot theory of angiosperm origin. *Evol. Theory* 5: 189-225.
- BURGER, W. C. (1996). The real difference between Monocots and Dicots. *Amer. J. Bot.* S83 Abstract 402.
- CARLQUIST S. & E. L. SCHNEIDER (1996). Vessels in *Brasenia* and *Cabomba* (Cabombaceae). *Amer. J. Bot.* S83 Abstract 407.
- CHASE, M.W., D. E. SOLTIS, R. G. OLMSTEAD, D. MORGAN, D. H. LES, B. D. MISHLER, M. R. DUVALL, R. A. PRICE, H. G. HILLS, Y.-L. QIU, K. A. KRÖN, J. H. RETTIG, E. CONTI, J. D. PALMER, J. R. MANHART, K. J. SYTSMA, H. J. MICHAELS, W. J. KRESS, K. G. KAROL, W. D. CLARK, M. HEDREN, B. S. GAUT, R. K. JANSEN, K.-J. KIM, C. F. WIMPEE, J. F. SMITH, G. R. FURNIER, S. H. STRAUSS, Q.-Y. XIANG, G. M. PLUNKETT, P. S. SOLTIS, S. M. SWENSON, S. E. WILLIAMS, P. A. GADEK, C. J. QUINN, L. E. EGUIARTE, E. GOLENBERG, G. H. JR. LEARN, S. W. GRAHAM, S. C. BARRETT, S. DAYANANDAN & V. A. ALBERT (1993). Phylogenetics of seed plants: an analysis of nucleotide sequences from the plastid gene *rbcL*. *Ann. Missouri Bot. Gard.* 80: 528-580.
- CHASE, M. W., STEVENSON, D. W., WILKIN, P. & P. J. RUDALL (1995). Monocot systematics: a combined analysis. In: RUDALL, P. J., P. J. CRIBB, D. F. CUTLER & C. J. HUMPHRIES (ed.), *Monocotyledons: systematics and evolution*. Royal Botanic Gardens, Kew.
- CHASE, M. W., M. D. LLEDO, M. B. CRESPO, & S. M. SWENSON. (1996). "When in doubt, put in Flacourtiaceae": molecular systematics of Flacourtiaceae. *Amer. J. Bot.* S83 Abstract 411.

- CONTI, E., A. LITT & K. J. SYTSMA (1996). Circumscription of Myrtales and their relationships to other rosids: evidence from rbcL sequence data. *Amer. J. Bot.* 83: 221-233.
- CRANE, P. R. (1985). Phylogenetic analysis of seed plants and the origin of angiosperms. *Ann. Missouri Bot. Gard.* 72: 716-793.
- CRANE, P. R. (1993). Time for the angiosperms. *Nature* 366: 631-632.
- CRONQUIST, A. (1981). *An integrated system of classification of flowering plants*. Columbia University Press, New-York.
- CRONQUIST, A. (1988). *The evolution and classification of flowering plants*. Allen Press, Lawrence, Kansas.
- DAHLGREN, R. M. T. (1975). The distribution of characters within an angiosperm system. *Bot. Notiser* 128: 181-197.
- DAHLGREN, R. M. T. (1983). General aspects of angiosperm evolution and macrosystematics. *Nordic J. Bot* 3: 119-149.
- DAHLGREN, R. M. T., H. T. CLIFFORD & P. F. YEO (1985). *The families of the monocotyledons: structure, evolution, and taxonomy*. Springer, Berlin.
- DOYLE, J. A. (1994). Origin of the angiosperm flower: a phylogenetic perspective. *Pl. Syst. Evol.* S8: 7-29.
- DOYLE, J. A. & M. J. DONOGHUE (1987). The importance of fossils in elucidating seed plant phylogeny and macroevolution. *Rev. Paleobot. Palynol.* 50: 63-95.
- DOYLE, J. A. & M. J. DONOGHUE (1993). Phylogenies and angiosperm diversification. *Paleobiol.* 19: 141-167.
- DOYLE, J. A., M. J. DONOGHUE & E. A. ZIMMER. (1994). Integration of morphological and ribosomal RNA data on the origin of angiosperms. *Ann. Missouri Bot. Gard.* 81: 419-450.
- DUVALL, M. R., M. T. CLEGG, M. W. CHASE, W. D. CLARK, W. J. KRESS, H. G. HILLS, L. E. EGUIARTE, J. F. SMITH, B. S. GAUT, E. A. ZIMMER & J. H. Jr. LEARN (1993). Phylogenetic hypothesis for the monocotyledons constructed from rbcL data. *Ann. Missouri Bot. Gard.* 80: 607-619.
- EHRENDORFER, F. (1977). New ideas about early differentiation of angiosperms. *Pl. Syst. Evol.* S1: 227-234.
- EMBERGER L. & M. CHADEFAUD (1960). *Traité de botanique*. Masson & cie (ed).
- ENDRESS, P. K. (1986). Reproductive structures and phylogenetic significance of extant primitive angiosperms. *Pl. Syst. Evol.* 152: 1-28.
- ENDRESS, P. K. & E. M. FRIIS (1994). Introduction: Major trends in the study of early flower evolution. *Pl. Syst. Evol.* S8: 1-6.
- ERBAR, C. & P. LEINS (1996). Distribution of the character states "early sympetaly" and "late sympetaly" within "Sympetalae Tetracyclae" and presumably allied groups. *Bot. Acta* 109: 427-440.
- FAY, M. F. & M. W. CHASE (1996). Molecular phylogeny of Ochnaceae and related families. *Amer. J. Bot.* S83 Abstract 438.
- FRIIS, E. M., K. R. PEDERSON & P. R. CRANE (1994). Angiosperm floral structures from the Early Cretaceous of Portugal. *Pl. Syst. Evol.* S8: 31-49.
- HIBSCH-JETTER, C. & D. E. SOLTIS (1996). Phylogenetic analysis of 'Saxifragales' based on nrDNA and cpDNA sequence data (18S, rbcL, and matK). *Amer. J. Bot.* S83 Abstract 462.
- HOOT, S. B., & P. R. CRANE (1996). A comparison of results from 18S nuclear ribosomal DNA sequences with two chloroplast genes (atpB and rbcL) within "lower"Hamamelidae and Ranunculidae. *Amer. J. Bot.* S83 Abstract 604.
- KOONTZ, J. A. & D. E. SOLTIS (1996). Molecular phylogenetics of Brexiaceae. *Amer. J. Bot.* S83 Abstract 479.
- MANOS, P. S. & K. P. STEELE (1996). A phylogenetic analysis of "higher"Hamamelidae based on sequences from nuclear ribosomal DNA. *Amer. J. Bot.* S83 Abstract 503.
- MORGAN, D. R. & D. E. SOLTIS (1993). Phylogenetic relationships among members of Saxifragaceae sensu lato based on rbcL sequence data. *Ann. Missouri Bot. Gard.* 80: 631-660.
- NICKRENT, D. L. (1996). Phylogenetic relationships of parasitic Santalales and Rafflesiales inferred from 18S rRNA sequences. *Amer. J. Bot.* S83 Abstract 605.
- OLMSTEAD, R.G., B. BREMER, K. M. SCOTT & J. D. PALMER (1993). A parsimony analysis of the Asteridae sensu lato based on rbcL sequences. *Ann. Missouri Bot. Gard* 80: 700-722.
- PRICE, R. A. & J. D. PALMER (1993). Phylogenetic relationships of the Geraniaceae and Geraniales from rbcL sequence comparisons. *Ann. Missouri Bot. Gard.* 80: 661-671.
- QIU, Y.-L., M. W. CHASE, D. H. LES, & C. R. PARKS (1993). Molecular phylogenetics of the Magnoliidae: cladistic analyses of nucleotide sequences of the plastid gene rbcL. *Ann. Missouri Bot. Gard.* 80: 587-606.
- RODMAN, J. E., K. KAROL, R. PRICE & V. SAVOLAINEN (1995). Salvadoraceae are Capparalean, all but one of the mustard oil taxa form a monophyletic clade and Dahlgren was right. *Amer. J. Bot.* S82 Abstract 459.

- SAVOLAINEN, V., J.-F. MANEN, E. DOUZERY & R. SPICHIGER (1994). Molecular phylogeny of families related to Celastrales based on *rbcL* 5' flanking sequences. *Mol. Phyl. Evol.* 3: 27-37.
- SAVOLAINEN, V., C. M. MORTON, S. B. HOOT, & M. W. CHASE (1996). An examination of phylogenetic patterns of plastid *atpB* gene sequences among eudicots. *Amer. J. Bot.* S83 Abstract 541.
- SAVOLAINEN, V., J.-F. MANEN & R. SPICHIGER (1997). Polyphyletism of Celastrales deduced from a chloroplast noncoding DNA region. *Mol. Phylogenet. Evol.* 7: 145-157.
- SCHNEIDER, E. L. & S. CARLQUIST (1996). Vessels in *Nelumbo* (Nelumbonaceae). *Amer. J. Bot.* S83 Abstract 543.
- SOLTIS, D. E., P. S. SOLTIS, D. L. NICKRENT, L. A. JOHNSON, W. J. HAHN, S. B. HOOT, J. A. SWEERE, R. K. KUZOFF, K. A. KRON, M. W. CHASE, S. M. SWENSON, E. A. ZIMMER, S.-M. CHAW, L. J. GILLESPIE, W. J. KRESS & K. J. SYTSMA (1997). Angiosperm phylogeny inferred from 18S ribosomal DNA sequences. *Ann. Missouri Bot. Gard.* 84: 1-49.
- SPICHIGER, R., V. SAVOLAINEN & J.-F. MANEN (1993). Systematic affinities of Aquifoliaceae and Icacinaceae from molecular data analysis. *Candollea* 48: 459-464.
- SYTSMA, K. J., E. CONTI, M. NEPOKROEFF, J. C. PIRES & Y.-L. QIU (1996a). Urticales: *rbcL* sequences clarify placement in Rosidae, composition, and familial relationships. *Amer. J. Bot.* S83 Abstract 562.
- SYTSMA, K. J., M. NEPOKROEFF & J. C. PIRES (1996b). The utility of *ndhF* sequence analysis in Myrtales, with emphasis on the relationships within Myrtaceae and Melastomataceae clade. *Amer. J. Bot.* S83 Abstract 563.
- TAKHTAJAN, A. (1980). Outline of the classification of flowering plants. *Bot. Rev.* 46: 225-359.
- THORNE, R. F. (1983). Proposed new realignments in the Angiosperms. *Nordic J. Bot.* 3: 85-117.
- THORNE, R. F. (1992). Classification and geography of the flowering plants. *Bot. Rev.* 58: 225-348.

---

Addresses of the authors: R. S.: Conservatoire et Jardin botaniques de la Ville de Genève, Case postale 60, CH-1292 Chambésy/Genève, Suisse.

V. S.: Conservatoire et Jardin botaniques de la Ville de Genève, Case postale 60, CH-1292 Chambésy/Genève, Suisse and IBSG, Université de Lausanne, CH-1015 Lausanne, Suisse.

