

## Return of the grades: towards objectivity in evolutionary classification

Návrat ke gradům a snaha o objektivitu v evoluční klasifikaci

Wolfgang Willner<sup>1,2</sup>, Karl Hülber<sup>2</sup> & Manfred A. Fischer<sup>2</sup>

<sup>1</sup>Vienna Institute for Nature Conservation and Analyses, Giessergasse 6/7, 1090 Vienna, Austria, e-mail: wolfgang.willner@vinca.at; <sup>2</sup>Department of Botany and Biodiversity Research, University of Vienna, Rennweg 14, 1030 Vienna, Austria, e-mail: karl.huelber@univie.ac.at, manfred.a.fischer@univie.ac.at

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Evolutionary classification, i.e. a biological classification that recognizes paraphyletic groups as formal taxa, is often regarded as highly subjective and therefore unscientific. We argue that clades with evolutionary key innovations are real biological units and that, as a logical consequence, paraphyletic grades are equally real; if a clade with evolutionary key innovations is nested within an older clade, the remainder of the more inclusive clade forms a paraphyletic grade. Therefore, we regard an evolutionary classification, which recognizes grades and gives formal names to them, as a desirable supplement to the purely phylogenetic classifications, which are dominant today. To increase the objectivity of evolutionary classifications, an approach called “patrocladistic classification” was proposed. We adopted this approach using the approximate number of apomorphies separating two clades along the phylogenetic tree as the patristic distance. Based on a cluster analysis of all angiosperm families, we outline an evolutionary classification of the angiosperms, which includes three subclasses (one of them paraphyletic), 12 superorders (four of them paraphyletic) and ~ 74 orders (12 of them paraphyletic). We suggest that well characterized monophyletic taxa can be reproduced by both phylogenetic and evolutionary approaches and used as a cladistic backbone of any classification. For the remaining groups, we advocate a peaceful coexistence of phylogenetic and evolutionary classifications, admitting both narrowly defined clades and broadly defined paraphyletic grades as valid taxa.

**Key words:** *Angiospermae*, key innovations, monophyly, paraphyly, patrocladistic classification

### Introduction

The question whether paraphyletic groups are acceptable as formal taxa continues to split the taxonomic community (e.g. Stuessy 1997, Brummitt 2002, Potter & Freudenstein 2005, Albach 2008, Hörandl & Stuessy 2010, Schmidt-Lebuhn 2012, Stuessy & Hörandl 2014). A strictly phylogenetic classification recognizes only monophyletic groups, which keeps the number of potential classifications of a given phylogenetic tree relatively low. However, the rank given to a clade and the decision which clades should be given formal ranks, still remains the subjective choice of the author (Backlund & Bremer 1998). In evolutionary classification, by contrast, the acceptance of both para- and monophyletic groups strongly increases the number of theoretical possibilities for grouping. Thus, evolutionary classification has been regarded as “the ultimately subjective, i.e. unscientific, preference of the researcher” (Schmidt-Lebuhn 2012).

Classification is a way of describing and interpreting reality (Stuessy 2009: 20). In a process of “logical division”, a class of objects is hierarchically divided into subclasses

based on the diagnostic characters of these objects, which can subsequently be used to assign new objects to these hierarchical units. According to Gower (1974), a classification should seek an optimal balance between the competing aims of minimizing the internal heterogeneity and maximizing the divergence among units of the same rank. Most scientific classifications are solely based on similarity among units (e.g. soil or bedrock classifications) and there are also examples of this kind of classification in the field of botany. The system of life-forms classifies plant species into functional types (e.g. Ellenberg & Müller-Dombois 1967). The system of vegetation types structures plant communities into hierarchical units as in Linnaean taxonomy, based on the similarity of their species compositions (Willner 2006, Jennings et al. 2009). In all these cases, the heterogeneity and average size of units increases with increase in hierarchical level. A phylogenetic classification of species, which recognizes only monophyletic taxa, is quite different in this respect. For instance, Chase & Reveal (2009) divide the angiosperms into 16 superorders of which 12 contain only one order (three of them even a single family). Lewis & McCourt (2004) distinguish 10 classes of green algae while all land plants are grouped within a single class. Obviously, ranks in phylogenetic classification tell us nothing about similarity. The only thing they tell us is when the taxa in question were split.

Most biologists will agree that evolution is more than just genealogy. Key innovations are an important factor for diversification of lineages (Vamosi & Vamosi 2011). Clades with key innovations represent biological units, which have been optimized by natural selection (Chase et al. 2000). These units initially typically undergo rapid diversification, which slows through time due to ecological limitations until new adaptive traits are acquired leading to a new burst of diversification (Rabosky 2009). If a clade with entirely new evolutionary features is nested within an older clade, the remainder of the latter becomes a grade. Huxley (1959) defined grades as units “which have undergone improvement for some particular mode of life, become successful, spread, split up into numerous forms, and maintained their new form of organization under the different conditions which these forms have met”. In the past, the term “grade” was applied to all kinds of groups with common organizational features, even polyphyletic ones. We propose to restrict the term to mono- and paraphyletic groups, which are separated from each other by evolutionary key innovations. For polyphyletic units the designation as a “functional type” or “structural type” seems more appropriate. In phylogenetic classifications, grades are not recognized as formal taxa. Their traditional name may be maintained if their extant members by chance form a monophyletic group, which is not unlikely for very old grades (Hörandl & Stuessy 2010). Proponents of phylogenetic classifications often argue that paraphyletic groups do not represent “groups in any meaningful sense” (Schmidt-Lebuhn 2012). However, if there are any clades that are real biological units and not just artificial boxes on a tree, then grades are equally real. They are the remains of older clades from which new clades have evolved.

In phylogenetic systems, grades are usually split into many narrow or even monotypic taxa, which often barely differ from each other. To keep the number of taxa in a reasonable range, branches immediately below a well characterized clade (i.e. a clade having several key innovations) are commonly united with the latter, resulting in a broader and less recognizable taxon, e.g. as in the case of the *Urticales*, which are included in the *Rosales* in APG III (2009). In contrast, evolutionary classification unites basal grades to larger, paraphyletic taxa. Accordingly, the paraphyletic superkingdom *Prokaryota* can be placed alongside

the monophyletic *Eukaryota*, the paraphyletic kingdom *Protista* alongside the monophyletic *Plantae*, *Chromista*, *Fungi* and *Animalia* (see Cavalier-Smith 2010), the paraphyletic superphylum *Chlorophyta* (green algae) alongside the *Embryophyta*, the paraphyletic phylum *Bryophyta* alongside the *Tracheophyta*, the paraphyletic subphylum *Pteridophytina* alongside the *Spermatophytina* and the paraphyletic class *Gymnospermae* alongside the *Angiospermae*. These examples suggest that the number of meaningful alternatives for an evolutionary classification is in fact not much greater than for a purely phylogenetic classification.

The main aim of evolutionary taxonomy, as we understand it, is the study of character evolution and the identification of important evolutionary steps in the tree of life. Admittedly this can be done without bothering about paraphyletic taxa. However, we regard an evolutionary classification, which recognizes grades and gives formal names to them, as a desirable supplement to the purely phylogenetic classifications, which currently dominate. To increase the objectivity of taxonomic decisions, statistical methods such as ordination and cluster analysis based on patristic distance (Stuessy & König 2008) or quantitative measures evaluating the information content of alternative classifications should be used (e.g. Gower 1974). Paraphyletic grades may also be separated from well characterized clades using a total evidence approach (Hörandl & Emadzade 2012). To make paraphyletic taxa immediately obvious, we suggest the insertion of the Greek  $\Pi$  before the scientific taxon name.

In this paper, we present a patrocladistic classification of the angiosperms using the approach proposed by Stuessy & König (2008). On this basis, we outline a revised evolutionary classification of orders, superorders and subclasses of flowering plants. Finally, we present some ideas on how evolutionary and phylogenetic classifications could be combined into a synthetic double system.

## Material and methods

We used the families of the APG III system (APG III 2009) as the basic units for our analysis. Phylogenetic relationships and apomorphies were obtained from Stevens (2012) with minor modifications (see Electronic Appendix 1 for a complete list of all clades and their apomorphies). Deviating from Stuessy & König (2008), we used a combined “patrocladistic branch length” to obtain the distance matrix instead of calculating the patristic and cladistic distance separately. Patristic distance was defined as the number of apomorphies separating two families on the phylogenetic tree. Families were arbitrarily given the value 1, disregarding differences in the number of autapomorphies. As an exception, orders containing only a single family in the APG III system were given the full number of apomorphies (at least 1). Branch length was obtained by adding the value 0.1 to the number of apomorphies of the respective node. This was done to avoid branches with zero length. Thus, the resulting phylogram and distance matrix reflected almost exclusively the patristic distances (Electronic Appendix 2).

In the next step, the patrocladistic distance matrix was used as input for a cluster analysis. We used average-linkage as a cluster algorithm because it also reflects the internal heterogeneity of a group and not only the size of the gap between groups as in the case of single-linkage. Moreover, average-linkage is less sensitive to the number of apomorphies,

which is inevitably a very rough approximation of the evolutionary divergence of a clade. The resulting dendrogram was simplified in the following way: first, we identified all monophyletic clusters that were characterized by at least one apomorphy, then we completed the classification with the lowest possible number of paraphyletic clusters without violating the hierarchy.

## Results

The cluster analysis resulted in four main groups (Table 1; Electronic Appendix 3): cluster I represented the monocots, which is the clade with the greatest number of apomorphies (18); cluster II consisted of only four families representing the core of the *Apiales*; cluster III included the basal dicots up to the *Gunnerales* and cluster IV comprised all core eudicots except *Gunnerales* and core *Apiales*.

Cluster I was further divided into group Ia corresponding to the *Alismatales* excl. the two most basal families *Araceae* and *Tofieldiaceae* and group Ib including all other monocots. Within group Ia, the clade comprising *Posidoniaceae*, *Ruppiaceae*, *Cymodoceaceae*, *Zosteraceae* and *Potamogetonaceae* (*Zosterales*) was separated from the rest, which formed a paraphyletic grade. Within group Ib, the *Zingiberales*, *Arecales* and *Acorales* were reproduced to the same extent as in APG III, while the *Poales*, *Pandanales* and *Dioscoreales* were more narrowly circumscribed excluding some basal families. There were also two paraphyletic clusters in group Ib. One included the *Commelinales* plus some basal families of the *Poales* (i.e. a basal commelinids grade), and the other one included the *Liliales*, *Asparagales*, *Petrosaviales* and some basal families of the *Dioscoreales*, *Pandanales* and *Alismatales*.

Cluster III was divided into eight subunits: group IIIa included the *Nymphaeales*, group IIIb the *Laurales* (excl. *Calycanthaceae*), group IIIc the *Magnoliales* (excl. *Myristicaceae*), group IIId a paraphyletic cluster including *Calycanthaceae*, *Myristicaceae*, *Piperales* and *Canellales*, group IIIe the *Ceratophyllales*, group IIIf a paraphyletic cluster comprising *Amborellales* and *Austrobaileyales*, group IIIg the *Chloranthales* and group IIIh a paraphyletic cluster including the basal eudicots plus *Gunnerales*. Most of the APG III orders within the last group were reproduced except for one paraphyletic group comprising the *Eupteleaceae*, *Sabiaceae* and *Nelumbonaceae*.

Cluster IV was further divided into four subunits: group IVa included the Core *Caryophyllales*, group IVb the Core *Brassicales*, group IVc the second major clade of the *Caryophyllales* including *Droseraceae*, *Polygonaceae* and others, group IVd the asterids (except for the Core *Apiales*) and group IVe all other *Pentapetales*. Twelve orders were reproduced to the same extent as in APG III while several orders appeared in a similar, although somewhat reduced circumscription (Table 1). The *Malpighiales* sensu APG III were placed in 10 monophyletic clusters, which were scattered throughout the group IVe. There were also several paraphyletic clusters that could not be further divided into monophyletic units because of the lack of apomorphies: a basal *Apiales* grade; two grades at the base of the campanulids and lamiids, respectively; a paraphyletic *Rosales* excluding the *Urticales*; a basal *Caryophyllales* grade; and finally a very large grade at the base of the *Pentapetales*, which included the *Berberidopsidales*, *Geraniales*, *Huertales*, *Zygophyllales*, *Celastrales* and basal families of the *Saxifragales*, *Malvales*, *Oxalidales* and *Malpighiales*.

Table 1. – Cluster analysis (average linkage) of the angiosperms based on the patrocadistic distances between families.  $\Pi$  paraphyletic cluster, = same circumscription as in APG III, < narrower than in APG III, << much narrower than in APG III, ! not recognized in APG III. Proposed classifications deviating from the cluster hierarchy are given in square brackets (see Discussion for details). The full dendrogram is provided in the Electronic Appendix 3.

I. *Liliidae* (monocots)

- a. *Alismatales*! (Alismatales excl. *Araceae* & *Tofieldiaceae*)
  - $\Pi$  *Alismatales* << (excl. *Araceae*, *Tofieldiaceae*, *Zosterales*)
  - *Zosterales*! (*Alismatales* p.p.)
- b.  $\Pi$  *Lilianaes* < [commelinids may be classified as *Commelinanae*]
  - *Poales* < (excl. basal families) [*Commelinanae* p.p.]
  - *Zingiberales* = [*Commelinanae* p.p.]
  - *Pandanales* < (excl. basal families)
  - *Arecales* = [*Commelinanae* p.p.]
  - $\Pi$  *Commelinales* s. lat.<sup>1</sup> [*Commelinanae* p.p.]
  - *Acorales* =
  - *Dioscoreales* < (excl. *Nartheciaceae*)
  - $\Pi$  *Liliales* s. lat.<sup>2</sup> [*Araceae* and *Orchidaceae* may be treated as separate orders]

II. *Apiales* << (*Pittosporaceae* + *Araliaceae* + *Myodocarpaceae* + *Apiaceae*) [to *Asteranae*]

III.  $\Pi$  *Magnoliidae* (basal dicots)

- a. *Nymphaeanae*/*Nymphaeales* =
- b. *Laurales* < (excl. *Calycanthaceae*) [*Magnolianaes* p.p.]
- c. *Magnoliales* < (excl. *Myristicaceae*) [*Magnolianaes* p.p.]
- d.  $\Pi$  *Magnoliids* p.p. [*Magnolianaes* p.p.]
  - *Piperales* =
  - *Canellales* =
  - $\Pi$  Basal magnoliids (*Calycanthaceae*, *Myristicaceae*)
- e. *Ceratophyllanae*/*Ceratophyllales* =
- f.  $\Pi$  *Austrobaileyanae* s. lat. (ANITA grade excl. *Nymphaeales*)
  - *Amborellales* =
  - *Austrobaileyales* =
- g. *Chloranthanae*/*Chloranthales* =
- h.  $\Pi$  *Ranunculanae* s. lat. (basal eudicots)
  - *Ranunculales* < (excl. *Eupteleaceae*)
  - *Proteales* < (excl. *Nelumbonaceae*)
  - *Gunnerales* =
  - *Trochodendrales* =
  - *Buxales* =
  - $\Pi$  Basal *Ranunculanae* (*Eupteleaceae*, *Sabiaceae*, *Nelumbonaceae*)

IV. *Rosidae* (Pentapetalae)

- a. *Caryophyllales* < (Core *Caryophyllales*) [*Caryophyllanae* p.p.]
- b. *Brassicales* < (excl. *Tropaeolales*, *Caricales*, *Limnanthaceae*, *Setchellanthaceae*) [to *Rosanae*]
- c. *Polygonales* et al. [*Caryophyllanae* p.p.]
  - *Nepenthales*! (*Caryophyllales* p.p.)
  - *Tamaricales*! (*Caryophyllales* p.p.)
  - *Polygonales*! (*Caryophyllales* p.p.)
- d. *Asteranae* = (asterids)
  - *Asterales* << (*Calyceraceae* + *Asteraceae*)
  - *Balsaminales*! (*Ericales* p.p.: *Marcgraviaceae* + *Balsaminaceae* + *Tetrameristaceae*)
  - *Lamiales* < (Core *Lamiales*)
  - *Cornales* =
  - *Aquifoliales* =
  - $\Pi$  *Griseliniales*! (*Apiales* p.p.: *Pennantiaceae*, *Toricelliaceae*, *Griselinaceae*)
  - *Dipsacales* =
  - $\Pi$  *Campanulales*! (*Escalloniales*, *Bruniales*, *Paracryphiales*, basal *Asterales*)
  - $\Pi$ ? *Garryales* s. lat. (*Icacinaceae*, *Garryales*)

- Π *Boraginales*! (*Boraginaceae*, basal *Lamiales*, basal *Solanales*)
- *Ericales* < (excl. *Balsaminales*)
- *Solanales* << (*Convolvulaceae* + *Solanaceae*)
- *Gentianales* =
- e. Π *Rosanae* s. lat. (rosids and basal *Pentapetalae*)
  - *Urticales*! (*Rosales* p.p.)
  - *Fagales* =
  - *Cucurbitales* =
  - *Clusiales*! (*Malpighiales* p.p.: *Ochnaceae* + clusioids)
  - *Myrtales* =
  - *Rhizophorales*! (*Malpighiales* p.p.: *Erythroxylaceae* + *Rhizophoraceae*)
  - *Burserales*! (*Sapindales* p.p.: *Anacardiaceae* + *Burseraceae*) [better to *Sapindales*?]
  - *Santalales* =
  - *Tropaeolales*! (*Brassicales* p.p.: *Akaniaceae* + *Tropaeolaceae*)
  - Π *Rosales* < (excl. *Urticales*)
  - Π *Physenales*! (basal *Caryophyllales*) [better to *Caryophyllanae*?]
  - *Caricales*! (*Brassicales* p.p.: *Moringaceae* + *Caricaceae*)
  - *Oxalidales* << (*Connaraceae* + *Oxalidaceae*)
  - *Violales*! (*Malpighiales* p.p.<sup>3</sup>)
  - *Chrysobalanales*! (*Malpighiales* p.p.<sup>4</sup>)
  - *Saxifragales* < (excl. *Peridiscaceae*, *Hamamelidales*)
  - *Malpighiales* << (*Elatinaceae* + *Malpighiaceae*)
  - *Vitales* =
  - *Hamamelidales*! (*Saxifragales* p.p.<sup>5</sup>)
  - *Crossosomatales* =
  - *Elaeocarpales* (*Oxalidales* p.p.<sup>6</sup>)
  - *Malvales* < (excl. *Neuradaceae*)
  - *Putranjivoids* (*Malpighiales* p.p.: *Lophopyxidaceae* + *Putranjivaceae*) [doubtful group]
  - Π [*Limnanthaceae*, *Setchellanthaceae*] (*Brassicales* p.p.) [doubtful group]
  - *Fabales* =
  - [*Irvingiaceae* + *Pandaceae*] (*Malpighiales* p.p.) [doubtful group]
  - *Ctenolophonaceae* (*Malpighiales* p.p.) [to *Rhizophorales*]
  - *Picramniales* =
  - Π *Sapindales* < (excl. *Burserales*) [may be combined with *Burserales*]
  - [*Phyllanthaceae* + *Picrodendraceae*] [doubtful group]
  - *Euphorbiales*! (*Malpighiales* p.p.: *Peraceae* + *Rafflesiaceae* + *Euphorbiaceae*)
  - Π *Dilleniales* s. latiss.<sup>7</sup>

<sup>1</sup>(incl. *Poales* p.p. [*Typhaceae*, *Bromeliaceae*, *Rapateaceae*])

<sup>2</sup>(incl. *Asparagales*, *Petrosaviales*, *Dioscoreales* p.p. [*Nartheciaceae*], *Pandanales* p.p. [*Triuridaceae*, *Stemonaceae*, *Velloziaceae*], *Alismatales* p.p. [*Araceae*, *Tofieldiaceae*])

<sup>3</sup>(*Goupiaceae*, *Violaceae*, *Passifloraceae*, *Lacistemataceae*, *Salicaceae*)

<sup>4</sup>(*Trigoniaceae*, *Dichapetalaceae*, *Euphroniaceae*, *Chrysobalanaceae*)

<sup>5</sup>(*Paeoniaceae*, *Altingiaceae*, *Hamamelidaceae*, *Cercidiphyllaceae*, *Daphniphyllaceae*)

<sup>6</sup>(*Cunoniaceae*, *Elaeocarpaceae*, *Brunelliaceae*, *Cephalotaceae*)

<sup>7</sup>(incl. *Berberidopsidales*, *Geraniales*, *Huerteales*, *Zygophyllales*, *Celastrales*, *Saxifragales* p.p. [*Peridiscaceae*], *Malvales* p.p. [*Neuradaceae*], *Oxalidales* p.p. [*Huaceae*], *Malpighiales* p.p. [*Caryocaraceae*, *Centroplacaceae*, *Balanopaceae*])

## Discussion

### *Transforming the tree into a classification*

The list of apomorphies used in our analysis is only a very rough approximation, which should be improved by future studies on character evolution. Nevertheless we believe that our results are a reasonable step towards achieving objectivity in the evolutionary classification



of the angiosperms. We suggest that both phylogenetic and evolutionary classifications should start with the assignment of formal ranks to the best characterized clades. We propose the term “cladistic backbone” for this stage of the classification. The most recognizable clades among the principal angiosperm lineages are the monocots (cluster I) and the *Pentapetalae* (cluster IV), both characterized by major changes in floral organization (Stevens 2012). The *Pentapetalae* are, of course, only monophyletic if the Core *Apiales* (cluster II) are included. We regard their isolated position in the cluster analysis as an artefact caused by the large number of secondary metabolites, which were all counted as individual apomorphies. Obviously, the relative weighting of phytochemical and morphological apomorphies is a critical issue that needs further investigation.

The *Pentapetalae* are phylogenetically nested within the eudicots, which have significantly fewer apomorphies and did not form a cluster in our analysis. Therefore, we divide the angiosperms into three subclasses, which are slightly different from the three classes proposed by Stuessy (2010):  $\Pi$  *Magnoliidae* (basal angiosperms including basal eudicots), *Liliidae* (monocots) and *Rosidae* (*Pentapetalae*) (Fig. 1). In accordance with the evolutionary ladder outlined in the introduction, we suggest that the angiosperms as a whole be given the rank of a class.

The further division of the monocots was somewhat unexpected as the Core *Alismatales* were separated from the rest of the monocots at the highest level. However, the number of apomorphies of this clade is indeed large and of ecological significance (adaptation to aquatic conditions). The commelinids, on the other hand, did not form a compact cluster. Nevertheless we suggest that both the *Alismatanae* and *Commelinanae* are accepted as monophyletic superorders, while the rest of the monocots are classified in the basal superorder  $\Pi$  *Lilianae* (Table 1). An alternative would be to include all monocots in a single superorder, as proposed by Chase & Reveal (2009). However, this solution would not be very informative.

The three orders basic to the angiosperms (*Amborellales*, *Nymphaeales* and *Austrobaileyales*) are often placed in the “ANITA grade”. However, our results suggest that only the *Amborellales* and *Austrobaileyales* are really part of this grade (group IIIf) while the *Nymphaeales* (group IIIa) is a highly derived clade having the second largest number of apomorphies after the monocots. The magnoliids did not form a cluster in our analysis but we think that combining groups IIIb–d into a monophyletic superorder results in a more informative classification than raising each of these groups to superorder level. The basal eudicots (group IIIh) form a compact grade without any obvious apomorphies along the branch leading to the *Pentapetalae*. Therefore, we combine them into a single paraphyletic superorder, which comprises five superorders of Chase & Reveal (2009). The *Chloranthanae* and *Ceratophyllanae* were confirmed by our analysis.

The *Pentapetalae* were divided into four major subgroups: groups IVa and IVc include the two major clades of the *Caryophyllales*, group IVd the asterids and group IVe the paraphyletic remainder. The Core *Brassicales* (group IVb) should be included in the last group; they were separated at this very high level for similar reasons as the Core *Apiales* (see above). Thus, our results suggest four superorders within the subclass *Rosidae*: the *Asteranae* following the same circumscription as in Chase & Reveal (2009), the  $\Pi$  *Rosanae* including the *Dilleniaceae*, *Saxifragaceae*, *Berberidopsidaceae* and *Santalaceae*, and two superorders representing the two main branches of the *Caryophyllales* sensu APG III. However, we advocate keeping the *Caryophyllanae* in the circumscription of Chase & Reveal (2009),

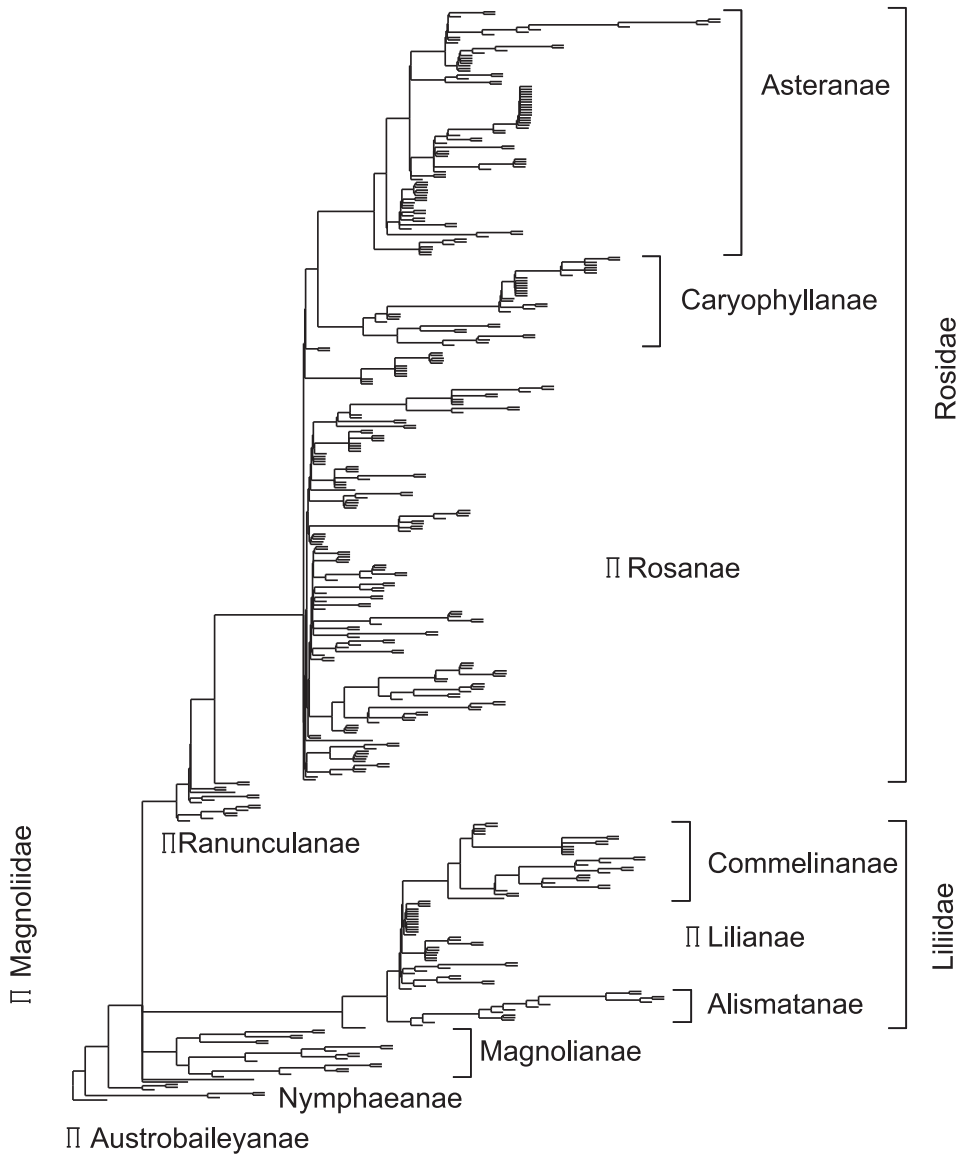


Fig. 1. – Phylogram of the APG III families and proposed supraordinal taxa of the angiosperms including the paraphyletic ones (the latter are indicated by Π). Branch lengths represent the number of synapomorphies between nodes. Phylogeny and apomorphies follow Stevens (2012) with minor modifications. *Chloranthanae* and *Ceratophyllanae* are not labelled. A larger version of this phylogram, with all families labelled, is available in the Electronic Appendix 2.

which would also include the paraphyletic cluster comprising *Rhabdodendraceae*, *Simmondsiaceae*, *Asteropiaceae* and *Physenaceae* (Π *Physenales*). The latter cluster was included in group IVE in our analysis (Table 1). Future studies on the character evolution within the bigger *Caryophyllanae* will help to clarify which of these two alternatives is the more informative.



It is noteworthy that neither the rosids nor their subclades, fabids and malvids, seem to have any apomorphies. In the phylogram (Fig. 1), the APG III orders *Saxifragales*, *Geraniales*, *Huertales*, *Malvales*, *Zygophyllales*, *Oxalidales* and *Malpighiales* are all “sessile” clades, sitting directly at the base of the *Pentapetales*. Accordingly, they were not reproduced by the patrocadistic analysis (Table 1). In contrast, the *Fagales*, *Myrtales*, *Santalales* and some other orders “with a long stalk” were perfectly reproduced. The basal grade of the *Pentapetales*, for which we propose the name  $\Pi$  *Dilleniales*, probably reflects an explosive speciation phase at the onset of their evolution. The optimal delimitation between this grade and the monophyletic orders rooting in it remains a task for future studies.

The evolutionary classification of the asterids is difficult because of uncertainties about the phylogenetic relationships and the position of some key innovations such as sympetaly (e.g. Schönenberger et al. 2005, Endress 2011). It is clear, however, that there should be at least two paraphyletic orders at the basis of the lamiids and campanuliids, respectively (Table 1). Another grade would be expected at the basis of asterids, but no such unit was identified by our analysis. Potential candidates are parts of the *Cornales*, *Ericales* as well as the *Garryales* and *Icacinaceae*. However, our current knowledge of the character evolution within the asterids is insufficient to propose any such grade.

#### *Schism or new synthesis?*

One criterion of a natural classification that has received little attention in recent years is that its divisions and groupings made on the basis of characteristics of one kind should be exactly the same as those made on the basis of characteristics of another kind (Ruse 1979). According to this principle, the monocots, asterids or *Fagales* are more natural groups than the malvids, *Malpighiales* (sensu APG III) or  $\Pi$  *Ranunculanae* (in our sense) because the first were identified by both the cladistic and evolutionary methods, whereas the latter were only identified by one of these methods. It was not our aim to condemn phylogenetic classifications such as the APG III system. Rather, we argue for a harmonious coexistence of phylogenetic and evolutionary classifications. We suggest the use of well characterized monophyletic taxa, which are accepted by both phylogenetic and evolutionary taxonomists as the cladistic backbone. However, we also appreciate that this proposal causes practical problems; if all the monophyletic clades identified by our analysis are adopted in a phylogenetic classification, the necessary splitting of the paraphyletic grades (such as the  $\Pi$  *Dilleniales*) would considerably increase the number of orders of angiosperms. In our opinion, the most logical solution for a purely phylogenetic system is not to assign members of the basal grades to certain ranks. A consequence of this would be that some species are not assigned to a genus, some genera to a family and so on (van Welzen 1998, Schmidt-Lebuhn 2012). On the other hand, extensive splitting of basal grades might not be too high a price to pay if we seek for a natural system including both cladistic and evolutionary aspects. As neither the paraphyletic grades nor their constituent clades are identified by both approaches, we probably need a double system that admits the simultaneous assignment of a taxon to two units of the same rank: clade and grade. Researchers could use either the phylogenetic or the evolutionary units, or both, according to their needs (and taste). In our opinion, the combination of a phylogenetic tree and a classification recognizing grades would be the most informative approach since it displays both aspects of evolution: genealogy and innovation.

Although in this paper we focused on the higher taxonomic levels, our considerations are, of course, also applicable to the lower ranks. Within the *Urticales*, the *Cannabaceae* are a clade with hardly any apomorphies. The monophyletic *Cannabaceae* s. str. (= *Cannabis* L. and *Humulus* L.) are nested within this clade, and given the morphological hiatus separating them from their next living relatives, they could probably be considered as a good family. The rest of the *Cannabaceae* sensu APG III are a problem group for any phylogenetic classification, but following our approach they could be united as  $\Pi$  *Celtidaceae*. Likewise, the traditional  $\Pi$  *Scrophulariaceae*, which was fragmented by phylogenetic classification, might be seen as a grade and maintained in a broader sense (but excluding the *Pedicularieae*, which are more derived and fit well in the *Orobanchaceae*). A taxon  $\Pi$  *Caprifoliaceae* could be viewed as a grade from which the *Dipsacaceae* and *Valerianaceae* emerged. An evolutionary system for the angiosperms will also include a considerable number of paraphyletic genera, located at the bases of the families, subfamilies and tribes. For example, a broadly defined  $\Pi$  *Senecio* L. could be interpreted as the paraphyletic base of the tribe *Senecioneae*, and taxonomists may admit that *Senecio jacobaea* L. and *Jacobaea vulgaris* Gaertn. are equally valid labels for the same species and use both as none of the alternative classifications represent the full “truth”.

See [www.preslia.cz](http://www.preslia.cz) for Electronic Appendices 1–3

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## Souhrn

Evoluční klasifikace je biologická klasifikace, která jako platné taxony přijímá i parafyletické skupiny. Kvůli tomu je často považována za vysoce subjektivní a proto nevědeckou. Pokud se klad s novými evolučními znaky nachází uvnitř staršího kladu, pak zbývající taxony nezahrnuté do mladšího kladu vytvářejí parafyletický grad. Jestliže však klady charakterizované klíčovou evoluční novinkou představují reálné biologické jednotky, pak obdobně reálné jsou i parafyletické grady. Evoluční klasifikaci, která uznává a pojmenovává i grady, proto považujeme za vhodný doplněk k nyní široce přijímané ryze fylogenetické klasifikaci. Pro zvýšení objektivity v evoluční klasifikaci byl navržen přístup zvaný „patrokladistická klasifikace“, který je založen na zhodnocení patristické vzdálenosti přibližného počtu apomorfí (odvozených znaků) odlišujících dva klady ve fylogenetickém stromu. Na základě klastrovací analýzy všech čeledí představujeme návrh evoluční klasifikace krytosemenných rostlin, zahrnující 3 podtřídy (z nichž jedna je parafyletická), 12 nadřádů (z nichž čtyři jsou parafyletické) a přibližně 74 řádů (z nichž 12 je parafyletických). Navrhujeme, aby dobře definované monofyletické taxony, podpořené jak fylogenetickými, tak evolučními přístupy, tvořily páteř každé klasifikace. Podporujeme harmonickou koexistenci fylogenetické a evoluční klasifikace, která umožňuje přijímat jak úzce definované klady, tak široce definované grady jako platné taxony.

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