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REVIEW

Recent developments in angiosperm phylogeny and classification in the light of molecular data and cladistics

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Abstract: The recent developments in molecular biology and methods of analyses have revolutionized the area of plant systematics and have shed new light on our understanding of the angiosperm phylogeny. The angiosperms, or flowering plants, are one of the major groups of extant seed plants. The angiosperms are recognized as a monophyletic group with good support. Three major groups can be identified, "phylogenetically basal groups", monocots and eudicots. The dicots are paraphyletic and are no longer recognized. The monotypic *Amborella* has come up as the sister to all other extant angiosperms in most analyses. Majority of the dicots were recovered as a well supported monophyletic group which are now recognized as the eudicots. The rest are included under the "phylogenetically basal group".

Several terminologies have been used to recognize the "phylogenetically basal group", and presently they are termed nonmonocot, nontricolpate angiosperms. Their phylogenetic relationships are gradually being resolved with the incoming data. This group lacks the specialization of the monocots and the eudicots. The eudicot clade is characterized primarily by the triaperturate pollen grains. Eudicots consist of a grade of eudicot families, and groups of families, successively branching off the main lineage, followed by the core eudicots which include two major groups, rosids and asterids. The monocots are well established as a monophyletic group, supported by several morphological advanced characters. Although the phylogenetic placement of the monocots in relation to eudicots, magnoliids, and Chloranthaceae is unclear, the monocots represent one of the oldest lineages of angiosperms.

Key words: Angiosperm phylogeny, basal angiosperms, eudicots, molecular data, monocots

The angiosperms, or flowering plants, are the major group of extant seed plants, totalling up to about 260,000 living species classified in 453 families.[1-3] Further, the angiosperms are the most diverse major extant plant group on land, and occupy every habitat on Earth except extreme environments such as the highest mountain-tops, the regions immediately surrounding the poles, and the deepest oceans.[3] The size ranges from species of *Eucalyptus* trees over 100 m tall with trunks nearly 20 m in girth to some duckweeds, which are simple, floating plants often scarcely 1mm in length. They occur as free floating, rooted aquatics in both freshwater and marine habitats and as terrestrial plant, and also vary tremendously in longevity, and overall form. Furthermore, angiosperms are crucial for human existence; the vast majority of the world's crops are angiosperms, as are most natural clothing fibres. Angiosperms are also sources for other important resources such as medicine and timber.[3]

For the past 250 – 300 years, from the time of Linnaeus, taxonomists have been trying to improve the way in which plants are classified. Starting with artificial systems of classification through natural to phylogenetic systems and phenetics to cladistics, taxonomists have come a long way to unveil the phylogenetic relationships and to build up a solid system of classification. Despite the number of different classification systems developed, it is evident that the taxonomists have failed to construct one universally accepted classification system. Considering the past 30 years, there have been three major classifications of angiosperms. In 1981, the angiosperms were divided into 321 families and 64 orders[4]; next, in 1992 they were divided into 440 families and 69 orders[5]; and in 1997 they were divided into no less than 589 families in 232 orders.[6] All these systems and past systems have employed morphological and anatomical features.

More recently, new categories of data have become available as the basis for classification. Even so, morphology has long been the mainstay of taxonomy, and during recent years with the development of the molecular biological techniques and new methods of building phylogenetic estimates such as cladistics, angiosperm relationships have been disclosed stepwise. Novel techniques in molecular biology such as polymerase chain reaction (PCR) and automated sequencing facilities that became available in the past decade have permitted extraction, amplification and sequencing of genes and gene regions in plants and utilizing them for determining phylogenetic relationships. All plant genomes have been utilized to obtain data for taxonomic studies, based on their properties and level of utilization. Currently molecular data are becoming popular over other data especially morphological, due to the difficulties encountered in coding morphological features for phylogenetic studies. Similarities among plants in various characters are inferred to reflect genetic similarities. Therefore, the character states are the direct reflection of genetic differences, and consequently the genetic material itself provides the most basic or fundamental characters that can be employed in estimating phylogenetic trees and constructing classifications. Furthermore, the genetic material is passed from generation to generation, and changes in organisms through time are the result, ultimately, of the transmission of genetic differences to subsequent generations. This forms the basic rationale for the use of genes and DNA data in studies of plant phylogeny.[7]

The initial landmark study was a work carried out by Prof. Mark Chase and his co-workers [8], who analyzed seed plants using 499 *rbcL* sequences. *rbcL* is the gene encoding the large subunit of the photosynthetic enzyme RuBisCO, ribulose 1-5 – biphospate carboxylase, the main carbon accepter in all photosynthetic plants and is an important gene present in all photosynthetic plants. The tale told by the results was exciting, but at the same time several doubts were expressed. Could the computers and software available then deal with the complexity of such an enormous data set. Did gene sequences still contain evolutionary information in spite of their functional constraints ?, and would the patterns found with this first gene be repeated with other genes? As the first data set took approximately 12 years to assemble, and no one was sure how long it would take to produce the second gene-based data set, this time a gene with completely different constraints. It was clear that a gene with a completely different function should be used as the next candidate to build up the phylogeny. About this time, the automated sequencers were developed, allowing a rapid increase in gene sequencing and as a result in 1997, the second large dataset for angiosperms, based on 18S nuclear ribosomal DNA, and the resulting tree was published.[10-11] The results indicated similar patterns in the evolution. Furthermore in the same year, a second plastid gene *atpB* encoding the β subunit of ATP Synthase, the third large gene based data set, was published.[12,13] The evolution rate of *atpB* is similar to that of *rbcL*, and further the two genes also share various other properties. Therefore, the sequences of *atpB* have provided additional sequence data to resolve angiosperm relationships further in turn an alternative gene to test *rbcL* based results. As the previous analyses, the same tree topologies were recovered by *atpB* based trees.

As all genes related the same story it became evident that reconstruction of the phylogeny and reclassification of angiosperms was necessary. Further, as important as the similarity of these studies was the fact that combining these data resulted in clear patterns of relationships.[9] The most exciting breakthrough of all these analyses was the traditional division of angiosperms into monocotyledones and dicotyledons was not supported.[8,14,15,16,17] In all published analyses the dicots or dicotyledons are paraphyletic (dicots were not recovered as a single clade originating from a single ancestor). Based on the data, "An ordinal classification for the families of flowering plants" was published in 1998 by a group of taxonomists under the acronym APG standing for the Angiosperm Phylogeny Group. The Angiosperm Phylogeny Group is an international group of systematic botanists who have come together to try to establish a consensus view of the taxonomy of flowering plants in the light of the rapid rise of molecular systematics.[18] The first APG system recognized 462 families placed in 40 putatively monophyletic orders and few monophyletic higher groups. The aim of the APG authors was to concentrate on orders and, in general orders were broadly circumscribed.[3] Several formal clades above the level of orders were also recognized, using informal names rather than Linnaean ranks; monocots, eudicots, core eudicots, rosids and asterids. Further, two major subclades within rosids (eurosid I (fabids) and eurosid II (malvids); asterids (euasterids I (lamiids) and euasterids II (campanulids) were also recognized. All these clades that were recognized received moderate to strong support in molecular phylogenetic analyses.[19] In addition several families were not placed in orders due to lack of support being unavoidable for DNA analysis.

In addition to molecular data, several non-DNA based cladistic analyses were performed, and the first large phylogenetic analysis of morphological, anatomical and phytochemical data was published by Nandi *et al.*[20] This too gave highly similar patterns regarding phylogentic patterns. Even so, the basic assumption however has remained that traits useful for identifying plants were also the best basis for classification,[9] but recently it has been argued that all data should be integrated; it was not a matter of one category of information versus the others, but rather it was important to combine all data into one system.

With the compilation of new data a revised version of the APG 1998 classification system has also been published recently, APG II[2] where several newly adopted orders including Austrobaileyales, Canellales and Celastrales and several additional families have been placed within the scheme. Many additional families are now placed in the phylogenetic scheme. Among these are Triuridaceae (Pandanales), Hanguanaceae (Commelinales), Bromeliaceae, Zygophyllaceae (unplaced to order, but included in eurosids I), Elatinaceae and Podostemaceae (Malpighiales).[2] Several major families are recircumscribed. Salicaceae are expanded to include a large part of Flacourtiaceae, including the type genus of that family; another portion of former Flacourtiaceae is assigned to an expanded circumscription of Achariaceae. Euphorbiaceae are restricted to the uniovulate subfamilies; Phyllanthoideae are recognized as Phyllanthaceae and Oldfieldioideae as Picrodendraceae. Scrophulariaceae are recircumscribed to include Buddlejaceae and Myoporaceae, and several former members have been excluded; these are assigned to Calceolariaceae, Orobanchaceae and Plantaginaceae. Further few families have been recognized as could be included optionally in broader circumscriptions with other related families; these include Agapanthaceae and Amaryllidaceae in Alliaceae *s.l.*, Agavaceae, Hyacinthaceae and Ruscaceae (among many other Asparagales) in Asparagaceae *s.l.*, Dichapetalaceae in Chrysobalanaceae, Turneraceae in Passifloraceae, Erythroxylaceae in Rhizophoraceae, and Diervillaceae, Dipsacaceae, Linnaeaceae, Morinaceae and Valerianaceae in Caprifoliaceae *s.l.*[2] Based on detailed studies, several major families have been recircumscribed.

During the next few paragraphs, the current understanding of the phylogeny of angiosperms will be discussed under three major groups "phylogenetically basal groups", monocots and eudicots [including basal groups such as buttercups (Ranunculaceae), rosids, and asterids], stressing important discoveries, commenting on ambiguities and also highlighting major changes in circumscriptions of families and orders that occur in Sri Lanka (Figure 1).

As mentioned above, the majority of the dicots were recovered as a well-supported monophyletic group which was recognized as the eudicots. The rest of the members that broke away from the dicots were collectively known as "phylogenetically basal angiosperms", meaning only that branch leading to the group attached at a basal position in the phylogeny, and it does not mean that the group itself is basal or ancestral to other groups. There have been several terminologies used to recognize the group, and presently they are termed nonmonocot, nontricolpate angiosperms.[17,21] Their phylogenetic relationships are gradually being resolved with the incoming data. This group lacks the specialization of the monocots and the eudicots.

Starting from the base of the tree, in most analyses the monotypic *Amborella* has come up as the sister to all other extant angiosperms.[22-29] Certain other analyses suggest *Amborella* together with water lilies (Nymphaeaceae) may occupy this key position.[30,31] *Amborella trichopoda* is an endemic genus in cloud forests of New Caledonia and was described in the mid-nineteenth century.[32] Since then it has been classified with various groups of basal angiosperms, most often with Laurales under subclass Magnoliidae.[4] *Amborella* lacks features considered to be advanced for Laurales.[33] Further, several recent morphological studies also support the new position. [1,3,33-36] Features that unite all extant angiosperms except *Amborella* include vessels [33,1,3] and pollen grains with a reticulate tectum.[3,33] Synapomorphies for all extant angiosperms except *Amborella* and Nymphaeaceae [2,3] include ethereal oil cells–common throughout basal angiosperms–and columellate pollen grains.[3,33]

In contrast to this view, few studies have found alternative rootings, using either different genes or different methods of analysis. For example, *Amborella*+Nymphaeaceae [23,31] or Nymphaeaceae alone [37] have occasionally been reported as sister to all other angiosperms. Therefore, APG II [2] refrains from proposing a formal name; either one order with both families or two separate orders, where both possibilities are available.

Although there has been strong support for *Amborella* and Nymphaeales (water lilies) as branching from basal-most nodes in the angiosperm phylogeny, this hypothesis has recently been challenged by recent phylogenetic analyses of 61 protein-coding genes extracted from the chloroplast genome sequences of *Amborella*, *Nymphaea*, and 12 other available land plant plastid genomes. The results placed the monocots, represented by three grasses (Poaceae), as sister to all other extant angiosperm lineages.[38] This study has been widely criticized and refuted.

The phylogenetically basal group lacks the specializations of the monocots and the eudicots. They have various types of flowers often tri-merous or with spirally inserted free sepals, stamens and carpels; the flowers are often protogynous. Differentiation into sepals and petals, various connations and zygomorphic flowers are rare. Pollen is usually monosulcate (not triaperturate as in eudicots) or inapertuate; furthermore, ethereal oil cells and benzylisoquinoline alkaloids are common.

The basal angiosperms represent a grade that includes the following groups: Amborellaceae, Nymphaeaceae (sensu APG II [2]), Austrobaileyales, Ceratophyllaceae, Chloranthaceae and magnoliids (includes Magnoliales, Laurales, Piperales and Canellales). In few analyses (with five genes, [22,23]; six genes, [39] and large multigene datasets, [28]) following Austrobaileyales, Ceratophyllaceae + monocots form a clade that is sister to all remaining angiosperms. This is followed by Chloranthaceae. The remaining basal angiosperms form a well supported magnoliid clade, which in turn is sister to the eudicots. However, support received for these placements is low even with combining many genes. [19]

Nymphaeaceae are aquatic rhizomatous herbs with floating leaves, scattered vascular bundles, without ethereal oil cells and usually producing mucilage (slime). They have some features in common with the monocots, for example scattered vascular bundles, but these are parallelisms. The present APG system suggests in recognizing Cabombaceae under a broadly circumscribed Nymphaeaceae.

In recent classification systems such Cronquist [4,40]; Takhtajan [6,41] and Thorne [42,43], most of these taxa have been placed in the subclass Magnoliidae, which also included Ranunculales. Even though Ranunculales, especially Ranunculaceae, share many features in common with the basal angiosperms, still they share derived features with the eudicot group and hence are now placed with eudicots.

Although the phylogenetic placement of the monocots in relation to eudicots, magnoliids, and Chloranthaceae is unclear, the monocots represent one of the oldest lineages of angiosperms. [19] The group is well established as a monophyletic group, supported by several morphological advanced characters, such as monocotyledonous seedlings, presence of calcium oxalate raphides, absence of vessels in the leaves, parietal placentation and persistent radicle etc;.[44-46] The monocot tree has been gradually built up with various major studies; three-genes analyses [27,47] and from the International monocot symposia held consecutively in 1993, 1998 and 2003 (Royal Botanic Gardens, Kew; Royal Botanic Garden, Sydney, and Rancho Santa Ana Botanical Garden).[19]

Phylogeny of monocots begins with several families of aquatic and semi-aquatic plants (Alismatales), followed by many familiar large-flowered families such as lilies and orchids and ending with a large group of families collectively known as the commelinoids.[21] *Acorus* stands as the sister to the whole monocot group. This peculiar genus that includes '*wada kaha*' or 'sweet flag' is now placed in Acoraceae in its own order Acorales. This position is supported by many analyses. Alismatales comprise of 14 families according to the circumscription of APG II [2], Araceae being the largest. The smallest angiosperms, Lemnaceae, are all embedded within the Araceae and therefore have been included under the family. Lilialels (*sensu* APG II [2]) occupy a position that is sister to Asparagales and the large commelinoid clade. Asparagales is the other major lilioid monocot and has also gained much attention regarding its circumscription. The Asparagales was first suggested by Huber [48] and later adopted by Dahlgren *et al.*[49] As currently circumscribed the order comprise of 14 families, including Alliaceae, (including Agapanthaceae and Amaryllidaceae), Asparagaceae (including Agavaceae, Hyacinthaceae and few other families), Hypoxidaceae, Iridaceae and Orchidaceae. In the recent past, new families were recognized to accommodate genera that fell as sister taxa to clades composed of several families, but this process has led to both a rearrangement of family limits and an increased recognition of monogeneric and small families. [19] Due to various problems encountered in these circumscriptions and also in trying to define the groups based on morphology, specialists in these families have considered to take a broader view of family limits in Asparagales, which is now possible because the patterns are relatively clear.[2] Further, work on Asparagales by Fay and his co-workers [50] has contributed to clarifying relationships within the order. Therefore, the APG II system[2] proposed to simplify the higher Asparagales by optionally reducing the number of families to two, Alliaceae and Asparagaceae. The two families can easily be identified by the umbellate inflorescences of Alliaceae (optionally including both Agapanthaceae and Amaryllidaceae) vs. the racemes of Asparagaceae, (except for Themidaceae with umbels), but these have many subtending and internal bracts, whereas those of Alliaceae typically have just two (or if there are more they are not internal in the umbel).[51] It is accepted that some researchers may be perturbed by this further re-organization of family line within Asparagales, but this modification would provide a much-needed simplification of the familial taxonomy in this order.[2] The commelinids are a clade that had long been suspected, due to the number of unique characters that were exhibited by the members included in the group: cell walls with ultraviolet-fluorescent ferulic and coumaric acids, silica bodies in leaves etc.[19] However the arrangements within the commelinoid orders have not been stable. The commelinids comprise about half the species of monocots and according to the present studies, the group includes Zingiberales, Poales, Commelinales and Arecaceae.[52] An isolated entity within the commelinid clade is the palms, Arecaceae, recognized in its own order Arecales. The inclusion of the palms with the clade is well supported [21,19] and in order to convey the relationship, the palms are now included in commelnids, although it should be noted that in the former classifications, the palms were recognized as a subclass of their own with another subclass Commelinidae restricted to the remaining complex of families. [19] Some molecular data indicate that the palms may be the sister to the group of this complex, but recently it has been placed as the sister to the monophyletic group containing Zingiberales and Commelinales.[21]

Zingiberales comprise eight, closely related families, forming a well-supported monophyletic group. The largest is Zingiberaceae. A familiar member of Zingiberales is banana (*Musa* spp.) in the Musaceae. Some spectacular ornamentals include the bird of paradise (*Strelitzia reginae*) in Strelitziaceae, *Heliconia* (Heliconiaceae) and canna-lilies (*Canna indica*) in Cannaceae whereas several foliage plants come under Marantaceae. These families have been long considered as closely linked due to their morphological similarities.[53-55] These families are well known for their androecial modifications, such that what often appears to be the perianth are petaloid stamens.[19]

Commelinales including Commelinaceae and Pontederiaceae is well supported with molecular data and also with few non-molecular data.[19]

The Poales (*sensu* APG II [2]) are a large order comprising of 17 families, most of them small. The two most important are Cyperaceae and Poaceae. Most Poales, excluding Bromeliaceae, Xyridaceae, Juncaceae and some Eriocaulaceae, are wind pollinated with much reduced, inconspicuous flowers in complex inflorescences. In Juncaceae there are flowers with common monocot organization, but in the other families there are many reductions of various floral parts. Cyperaceae and Poaceae both have flowers arranged in spikelets and an ovary with a single ovule. They are not sister groups, where Poaceae comes under the core Poales, but they represent independently modified groups within the order. The origin of the Poaceae can be dated by the appearance of grass pollen, which is distinctive in the fossil record; the earliest unequivocal records are from the Paleocene of South America and Africa, dating 60-55 million years ago.[56]

The eudicots represent about 75% of all angiosperm species and the clade is characterised primarily by the triaperturate pollen. [8,10,15,17,44] Analysis of molecular data of three or more genes has provided good support. [12,17,19,22,23,26,27] Eudicots consist of a grade of eudicot families and groups of families successively branching off the main lineage, followed by the core eudicots, which include two major groups, rosids and asterids.

As the triaperturate pollen grain is so distinctive, the estimated age of the eudicots is perhaps the firmest date in the paleobotanical record, where they are placed at early Cretaceous.[57,58,19] Further, based on the fossil record, the uneven distribution of the species diversity across the major clades of the eudicots, with the most species-rich groups known only from the relatively recent fossils, suggests a relatively recent radiation.[58] The 'early-diverging eudicots' are the Ranunculales, Proteales, Buxaceae and few other smaller groups. The placement of certain 'early-diverging eudicots' has attracted lot of attention as members such as Ranunculales were typically placed in Magnoliidae in recent classifications as they were thought to possess primitive or ancestral floral characters. [4,5,19,40,42,43,59,60] Takhtajan [6], in contrast, recognized a separate subclass to Ranunculidae that he considered to be closely related to Magnoliidae. Even though these members share several features (ethereal oil cells, chloranthoid leaf teeth, absence of vessels, and valvate anther dehiscence) common with the basal angiosperms, molecular as well as morphological analyses have placed them as the sister to the eudicots. [3,61] Further, Ranunculales have always appeared as the sister in all molecular analyses.[8,12,13,19,29,62-66,] The relationships among the other 'early-diverging eudicots' are yet to be resolved.

'Early-diverging eudicots' are sister to a strongly supported core eudicot clade, which include most of the angiosperms. [13,26,27,66] The most interesting situation is that the circumscription of the core eudicot clade is only based on DNA data. There has not been support from non-molecular data, but nevertheless, strong internal support for the relationships has been gained with addition of molecular data.

The core eudicot clade comprises the caryophyllid clade, Santalales, Saxifragales, rosids, and asterids. [2,27,65,19] Even though the clades are strongly supported by multigene analyses, their inter-relationships are yet to be resolved. [19]

The Saxifragales are now circumscribed mainly following investigations of molecular data; this circumscription was one of the major surprises of molecular phylogenetic analyses of angiosperms as these families have never been classified together before. [8,12,13,19,27,62,63,66-68]

The present circumscription of Santalales is in a smaller scale, which includes families from Santalales *s.l.* [19] The members of the Santalales are considered hemiparasites.[19]

The Caryophyllales are now expanded to encompass the whole of the former subclass Caryophyllidae and is circumscribed in a broader sense including 29 families.[2,18,19] The clade gained strong support from multigene analyses.[27] The most notable of the added families are the carnivorous plants, Droseraceae (sun-dews, *Drosera* and Venus flytrap) and Nepenthaceae (pitcher-plants, *Nepenthes*).[8,69] The most important families of the traditional Caryophyllales *sensu stricto* are Caryophyllaceae, Amaranthaceae, Cactaceae and Aizoaceae. Many Aizoaceae are south African and consist of leaf succulents, many of peculiar shapes, such as living stones (*Lithops*).

The rosid clade encompasses approximately 140 families, which is about one third of all angiosperm species and roughly 39% of eudicot species diversity.[19,58] In older systems the subclass was differently circumscribed; it included several families now in asterids, and excluded several families then classified in now abolished subclasses (Hamamelidae and Dilleniidae). For example, Casuarinaceae, Fagaceae, Moraceae, and Ulmaceae are members of the former subclass Hamamelidae whereas Brassicaceae, Dipterocarpaceae, Malvaceae, Ochnaceae and Passifloraceae are members of the former subclass Dilleniidae that are now recognized under rosids based on molecular support. Inter-relationships of the orders and families of the rosids are now gradually being resolved by analysis of molecular data. The relationships of Vitales, Geraniales, and Myrtales are unresolved within the rosids. The eurosid I (fabids) and eurosid II (malvids) are two other major clades that have been recognized within the rosids. Within the eurosid I the Rosales, Fabales, Cucurbitales and Fagales constitute a monophyletic group containing all flowering plants known to form symbiotic associations with nitrogen-fixing bacteria.[2,18] The most important of the nitrogen- fixing plant families is Fabaceae. The monophyly of Fabaceae is supported by several morphological features and DNA data.[8,70,71] In most classifications the subgroups within the family have been recognized as subfamilies,[1,18] whereas there have been occasions where they have been treated as separate families. [4,72] How ever certain studies have indicated that the subfamily Caesalpinioideae are paraphyletic and some members show a closer relationship with Mimosoideae and Faboideae.[8,70,71]

In recent morphological based classifications[4,5,6,40-43], eurosid I families have been considered as distantly related, and were distributed in several subclasses. This clade containing the 10 nitrogen-fixing families has been referred to as the nitrogen-fixing clade, but many families within the clade do not fix nitrogen and furthermore, many genera and species with these families also lack the ability of fixing nitrogen. Celastrales, Malpighiales and Oxalidales are few other members of the eurosid I.[19] Within, Malpighiales, Euphorbiaceae *s.l.* are now considered to be polyphyletic. [27,66] APG II recognizes a more narrowly circumscribed Euphorbiaceae, and they are divided into four families; Euphorbiaceae s.s., Phyllanthaceae, Picrodendraceae, and Putranjivaceae. Another significant finding is the placement Podostemaceae in the Malpighiales as sister *Hypericum* (Hypericaceae) with strong support.[19,27,73] Podostemaceae are a highly modified family with submerged aquatics; the family has been variously associated with Piperaceae, Nepenthaceae and Scrophulariaceae etc.[73,74] Relationships among these clades including Clusiaceae are unclear.[19]

Eurosid II (malvids) are another major clade nested within the rosids that gained strong support. The clade includes Brassicales, Malvales, Sapindales, and Tapisciaceae.[2,19,27] The clade is not supported by non-DNA data, and also the relationships within the clade needs further work. Brassicales are well supported and include 15 families, including Brassicaceae (including Capparaceae), Caricaceae and Moringaceae. The present circumscription of Brassicales includes all the families that produce mustard-oil glucosides, except for Putranjivaceae.[19] This character is a non-DNA synapomorphy for the clade and is a feature that evolved two times in the angiosperms. Members of Brassicaceae have served as model systems for studies of floral development and genome evolution (e.g., *Arabidopsis* and *Brassica*). The correct phylogenetic placement of these taxa will allow the extension of these models into other related taxa.

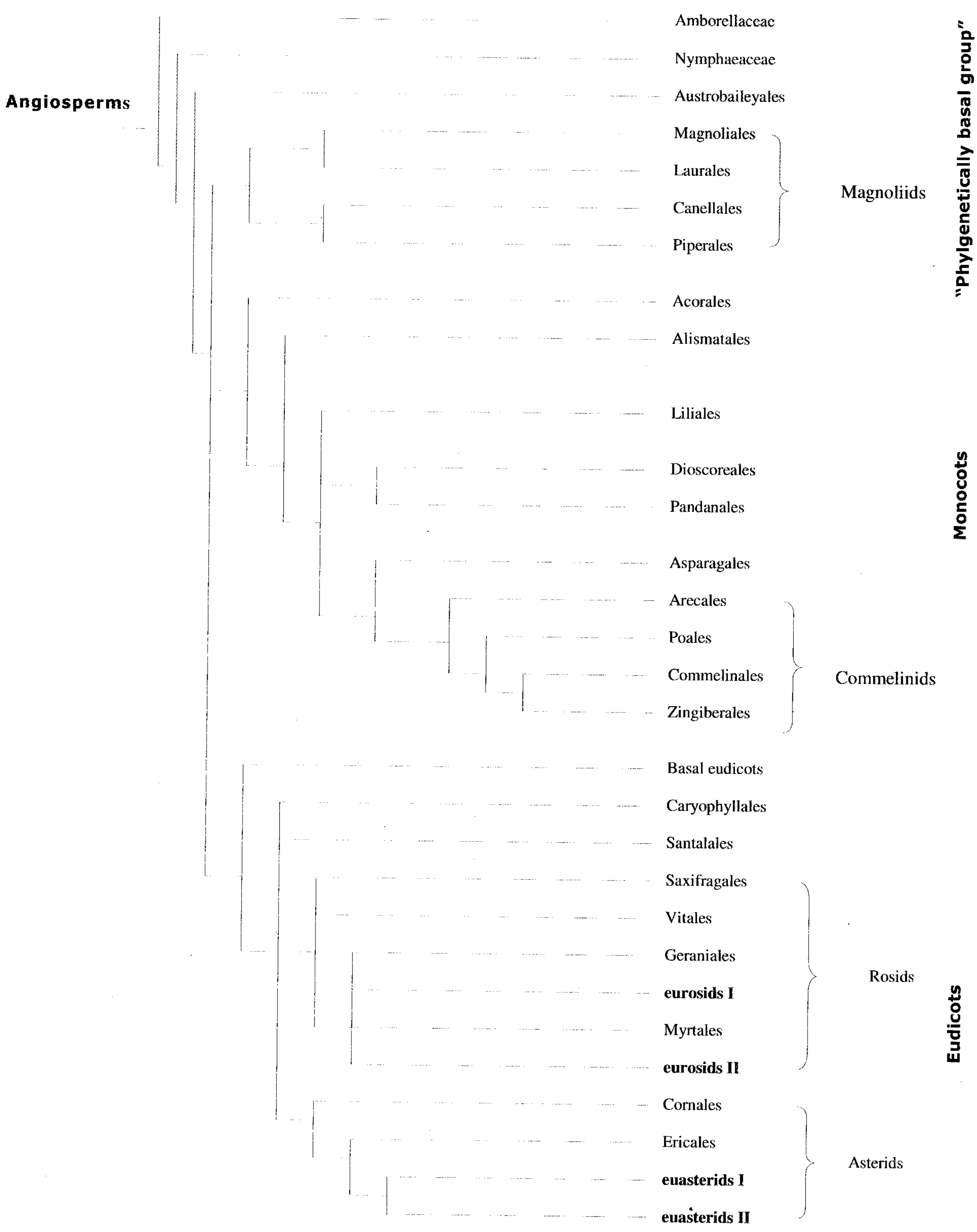

Figure 1: Major Angiosperm clades based on Angiosperm Phylogeny Group (APG) and other recent phylogenetic analyses. [1,2,18,21,23,27,33]

The Sapindales clade consists of nine families include Anacardiaceae, Burseraceae, Meliaceae, Rutaceae, Sapindaceae and a few others. Malvales consist of nine families including Bixaceae (including Cochlospermaceae and Diegodendraceae), Cistaceae, Dipterocarpaceae, Malvaceae (including Bombacaceae, Tiliaceae, and Sterculiaceae), Muntingiaceae and few others. [2,19] Malvales were narrowly circumscribed by Cronquist [4] whereas others circumscribed the order in a larger sense.[5,6,42,72,75] There have been various developments regarding monophyly of certain families such as Dipterocarpaceae[66,76], where it is suggested to combine Cistaceae and Sarcolaenaceae with Dipterocarapaceae where the oldest conserved name is Cistaceae. [19] Malvaceae are also broadly circumscribed under Malvales and have received strong support from molecular analyses.[13,27,66,77-79] In addition to the traditionally recognized Malvaceae, the present circumscription includes former members of Bombacaceae, Tiliaceae, and Sterculiaceae.[1,19,79,80] A close relationship among these taxa has been speculated time to time from the time of Linnaeus, even though the relationships among them were problematic.[19] Likely synapomorphies for this broad Malvaceae include distinctive nectaries composed of tightly packed multicellular hairs, normally found on the adaxial surface of the sepals [80,81] and the distinctive up-right 'tile' cells in wood rays.[19,82] Myrtales consist of 13 families including Lythraceae (including Punicaceae and Trapaceae), Melastomataceae, Myrtaceae, Onagraceae and Combretaceae and are one of the best-studied orders.[19]

The asterids are usually recognized formally as subclass Asteridae. [4,6] In a different circumscription they have been long known as Sympetalae because of their frequently fused petals. [21] The asterids (sensu APG [2,18)]) comprise of one-third of all flowering plants, with almost 80,000 species in nearly 4,700 genera and 144 families.[19] Further, the clade received support from non-DNA characters as well; the clade includes nearly all species of angiosperms that produce iridoids [83] and tropane alkaloids [84] and most angiosperms that produce caffeic acid. [19,85] Four major clades have been identified within the asterids. [8,13,26,27,62,86,87] Cornales, Ericales, and the euasterids clade contain two sister groups referred as euasterids I (lamiids) and euasterids II (campanulids).[2] Several studies have identified some possible morphological synapomorphies to define the clades.[19]

Few strongly supported subclades Garryales, Gentianales, Lamiales and Solanales can be identified with the euasterids I clade.[2,18] The order Lamiales have 21 families with strong support.[2] The clade includes Acanthaceae (including Avicenniaceae), Bignoniaceae, Gesneriaceae, Lentibulariceae, Oleaceae, Lamiaceae, Scrophulariceae, Verbenaceae and several others. Most of the members of the clade possess several non-DNA characters that are not found outside the group giving additional support.[19,83,88-90] Circumscription of several families such as Scrophulariceae, Avicenniaceae, Verbenaceae and Lamiaceae has been changed in the light of molecular data.[2] Lamiaceae are broadly circumscribed to include members of Verbenaceae (*Clerodendrum, Tectona, Vitex*) whereas Verbenaceae are circumscribed to include only the former subfamily Verbenoideae (with the exclusion of tribe Monochileae). [19,91,92,93]

Gentianales constitute a well-supported clade of five families: Rubiaceae, Loganiaceae, Gentianaceae, Apocynaceae (including Asclepiadaceae) and Gelsemiaceae. [19] Rubiaceae are the sister to the rest of the clade. Phylogenetic analyses of both molecular and non-molecular characters support combining Asclepiadaceae with Apocynaceae to form single family. [19,94] Apocynaceae *s.l.* is united by a number of non-molecular characters, including tissues with lacticifers and usually milky sap; carpels united by style and/ or stigmas with ovaries usually distinct; and apical portion of the style expanded and modified to form a secretory head. [95] Solanales include three small families and two larger families, Solanaceae and Convolvulaceae.[2,18]

The euasterids II or campanulids include four major subclades Dipsacales, Aquifoliales, Apiales and Asterales and few other taxa.[21,19] The clade had gained support from molecular studies [8,13,63,96-98] and also non-molecular studies.[19] Aquifoliales are the sister to the rest of the clade, which is well supported. [10] Apiales comprise the large families Apiaceae and Araliaceae, as well as a number of small obscure families. Asterales are strongly supported and consist of 12 families including Asteraceae, Campanulaceae (including Lobeliaceae), Goodeniaceae, and Menyanthaceae. Asterales have also been supported by possible non-molecular synapomorphies.[99] Despite much work carried on the order, internal relationships are still to be resolved.[19]

Going through the phylogeny it is apparent that many clades have not received support from non-molecular data especially from morphology. This was one of the major concerns at the XVII International Botanical Congress[100], urging the necessity of concentrating on detailed studies on other characters. It is optimistic that angiosperm phylogeny will be completely resolved in the near future with the rapid progress on its present course. Uncovering the phylogeny will answer several unresolved questions in many fields; comparative biology requires a solid phylogenetic foundation to reveal and understand patterns of diversification and to evaluate hypotheses of the process responsible for these patterns. Relationships of model organisms will be very vital in extrapolating inferences. Although the new system does not "turn the botanical world on its head" as once stated, it will bring in new surprises. As Prof. Mark Chase once stated in a popular newspaper, "a rose is still a rose, but everything else has indeed changed".

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