ISSN 0975-6299 Vol 2/Issue 1/ Jan-Mar 2011

International Journal of Pharma and Bio Sciences

RESEARCH ARTICLE BOTANY

MAGNOLIOPHYTA (FLOWERING PLANTS): A LOGICAL AND PHYLOGENETIC CLASSIFICATION

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ABSTRACT

All recent phylogenetic classifications of flowering plants are never field-oriented and thus the teacher and the taught find them difficult to understand and practise. Therefore a new student-friendly, yet phylogenetic system is proposed here. Since the spectacular diversification and related dominance of the flowering plants are primarily due to the flowers, especially to the petals, the apetalous taxa are grouped separate emerging parallel to the petaliferous taxa. In the present system, the Magnoliophyta (Angiosperms) are divided to two classes Magnoliopsida (Dicotyledonous plants) and Liliopsida Monocotyledonous plants). At the base of Magnoliopsida are the primitive subclasses Magnoliidae and apetalous Hamamelidae. The Caryophyllidae evolved from the latter subclass while the former gave rise to the subclasses Malvidae, Rutidae, Rosidae, and Ebenidae. The highly evolved subclasses, Lamiidae and Asteridae are derived from Ebenidae. The Liliopsida contain five subclasses with Alismatidae at the base from which evolved Cyperidae and Arecidae on one side and Zingiberidae and Liliidae on the other side. The evolutionary strategies and phylogeny of all these classes are also explained.

KEY WORDS

Magnoliophyta, Magnoliidae, Liliidae, Phylogenetic classification, Adaptations, Survival strategies.

INTRODUCTION

The sudden appearance of Angiosperms in fossil history is termed as an "abominable mystery" by Charles Darwin. These plants appeared in the scene by about 130 million years ago, gradually achieving dominance by about 90 million years ago within a short span of 40 million years. The spectacular diversification and related dominance of these plants, despite of their late appearance in the fossil record is attributed mainly to the flowers and their pollinators [1].

Flowers are the organs meant for reproduction and therefore the variations in flowers, floral parts and inflorescences observed in nature are mind-boggling. The flower is especially designed for insect pollination, and insect specificity being crucial for the success of cross-pollination, every conceivable option or "tricks of the trade" has been in operation to attract the specific insect and to facilitate pollination. Attraction is accomplished by bedecking the flower in the form of an insect. This mimicking is done by assuming the same color, fragrance (with pheromones) and shape. Insects are also being attracted by providing some food materials such as honey, pollen etc.

Many modern Angiosperms are pollinated mainly by beetles, others by flies which are attracted by the odours. Bees are the most important group visiting flowering plants. Both male and female bees live on nectar, and the females also collect pollen to feed the larvae. Bees have mouthparts, body hairs and other appendages with special adaptations for collecting and carrying nectar and pollen. That portion of spectrum that is most "visible" for bees is ultraviolet as a distinct colour and other colors of VIBGYOR each color separately but not red. Bee flowers possess showy brightly colored petals that are usually blue or yellow. Even the patterns of these colours are easily recognizable by bees. Such patterns indicate position of nectar and act as "honey guides". Nocturnal insects normally pollinate white or pale coloured flowers which often have a sweet penetrating scent that is emitted only after sunset. Bird-pollinated flowers produce large amounts of nectar and are often red and odorless. Birds have a keen sense of colour. Bat-pollinated flowers are dull and open at night.

1. Color

Since the insects (butterflies) are highly adorned by colors and patterns, the same colors and patterns are adapted by the flower, mostly in the petals. It is the petal which is highly colored and the color includes all possible shades seen in the world. And that is why it is correctly said that it is the Angiosperms which "colored" the world. Since the pollinator has to be specific to each plant, no two flowers will have the same color just like no two insects possess the same color and pattern. This specificity in color is produced by an admixture of anthocyanins, flavonoids, carotenoids and at times betalains. Colours are "advertisements" for peculiar kinds of pollinators. In some plants like *Gossypium, Quisqualis* etc. flowers change color to red after pollination so that they are less conspicuous to insects and convey the message that pollination is over and the insects are not welcome anymore.

Colors of flowers and pigments responsible for the colors[2]

Color	Pigments (in glycosidic form)	Examples
Ivory and Cream	Flavones (apigenin) and flavonols (quercetin)	*Antirrhinum*, Sweet pea (white)
Yellow	(a) Carotenoid alone (b) Flavonol alone (e.g. quercetagetin) (c) Aurone alone (d) Carotenoid + flavonol/ chalcone	yellow rose primrose Yellow *Antirrhinum* Birds food trefoil, gorse
Orange	(a) Carotenoid alone (b) Pelargonidin + aurone	*Lilium regale* Orange *Antirrhinum*
Scarlet	(a) Pelargonidin (b) Cyanidin + carotenoid	Geranium, *Salvia* Tulip
Brown	Cyanidin + carotenoid	*Primula polyanthus*
Magenta or Crimson	Cyanidin	*Camellia hortense*
Pink	Peonidin	Peony, *Rosa rugosa*
Mauve/Violet	Delphinidin	*Verbena*
Blue	(a) Cyanidin as metal complexes (b) Delphinidin as metal complexes (c) Malvidin as co-pigment	*Centaurea cyanus* *Delphinium ajacis* *Primula obconica*
Black (Purple black)	Delphinidin at high concentration	Tulip ("Queen of the night").

1. *Anthocyanins*

The three anthocyanin pigments, pelargonidin, cyanidin and delphinidin, either singly or as mixtures, provide the whole range of flower colour from pink and orange to violet and blue. Broadly speaking, all pink, scarlet and orange red flowers have pelargonidin; all crimson and magenta flowers have cyanidin and mauve and blue flowers have delphinidin. The loss of 3-hydroxyl group results in yellowier colors responsible for the orange-red or orange-yellow colors in the corollas of *Gesnerium, Columnea* and *Kohleria* species. Substituting an-OH group at 6/8-position cause tangerine colored flowers of *Impatiens aurantiaca*. Methylation (causes a slight reddening effect), co-pigmentation (with flavonoids) and metal complexing with magnesium, iron and aluminium, pH of the cell sap and adsorption of anthocyanins on polysaccharides of the wall and even the concentration are the other factors affecting the color of a flower.

2. *Chalcones and aurones*

These are bright yellow compounds seen frequently in Asteraceae wherein they occur alongwith carotenoids. The yellow flowers of *Ulex europaeus* (Gorse) contain 2, 4, 4'-trihydroxychalcone, α- & β - carotenes, violaxanthin and taraxanthin. *Helychrysum* (the everlasting flower) contains the aurone bracteatin as the coloring matter. In yellow *Antirrhinum* and yellow *Dahlia,* aurones aureusidin and bracteatin are responsible for the flower color and in orange varieties they combine with pelargonidin.

3. *Flavones and Flavonols*

White, ivory or cream color of flowers as well as the "albino" color of flowers of colored-flowered plants are due to common flavones and flavonols. Kaempferol is the most common flavonol in such flowers, followed by quercetin. Luteolin and apigenin (the flavones) also occur commonly in white petals. These compounds add "body" to the color of petals which would otherwise appear translucent. Since flavones and flavonols absorb strongly in the ultra-violet, the flowers containing them can be "seen" by UV-sensitive bees and other insects and thus attraction is possible even in night.

4. Carotenoids

Carotenoids, including xanthophylls, are the yellow/ red pigments seen in many Asteraceae members like marigolds, chrysanthemums, gerberas and hawkweeds. They are also responsible for the bright colors of certain fruits like tomato and mango.

2. Fragrant principles and odours

One of the greatest intelligent moves the plant planned to attract pollinating insects is the manufacture of pheromones, the sex hormones of insects, as the components of many volatile oils in flowers. Most of the pheromones are usually simple molecules like long-chained aliphatic, lipophilic acetates, aldehydes or alcohols, often with one or two double bonds. In Diptera, Coleoptera and other groups, sex pheromones usually have more complex structures like cyclic or chiral compounds. A sex pheromone of an insect usually consists of a blend of different components, although there are exceptions to this. Benzyl acetate, eugenol and methyl cinnamate, the pheromones of euglossine bees are produced by some orchids of Central and South America which use these bees as pollinators. Apart from the mono/sesquiterpene compounds which emit agreeable fragrance, certain flowers produce some volatiles of disagreeable odour for inviting a specific pollinator to flowers. For example the aliphatic volatiles such as heptadecane, methyl oleate etc in some Orchidaceae (*Ophrys*) flowers are important attractants to male *Andrena* and *Eucena* spp. bees which pollinate the bee-shaped flowers during pseudo-copulation[3]. The various species of *Magnolia* have different profiles of compounds like pentadecane, acetophenone etc to attract specific beetles for pollination[4]. The unpleasant offensive aminoid odours due to indolic compounds in certain flowers of *Hellebore* and *Iris* form a chemical mimicry by which the plants produce a smell of decaying faeces to deceive carrion and dung flies.

3. Shape and appearance of petals

Since petal is the main organ mimicking and thus attracting pollinator insects, the shape and modifications of petals/corolla played very important roles in this process. Papilionaceous flowers are the best examples of mimicking an insect. (The word "Papillon" means insect and papilionaceous definitely means insect like). In Dicots evolved early in time, the flowers had a radial symmetry (actinomorphic). Since the flower had to act and appear like an insect to attract them, an actinomorphic flower definitely was at a disadvantage in that the insect visitor would easily understand that a colored flower was not of its kind and might fly away. Therefore the idea of asymmetry, more precisely bilateral symmetry, was conceived by earlier plants like the Violaceae and the Polygalaceae and slightly later in the Tropaeolaceae and Balsaminaceae. But in all these cases the petals were more or less similar in size and shape. Only in Fabaceae, petals in a single flower were made highly dissimilar. Here one petal became very large to resemble the spread wings of an insect and two petals on opposite sides fused by the side to produce a boat shaped structure (keel petals), which from a distance would look like the body of an insect. The remaining two petals remained close to the "body" on either side giving the appearance of closed wings on either side. Another clever adaptation here was that the anterior petal which resembled open wings was turned on the upper side by a clever resupinate movement of the pedicel[5].

Even the spurs of Violaceae, Tropaeolaceae and Balsaminaceae (though they are meant for producing and storing nectar) looked like a protruding hind part of an insect Similarly in gamopetalous families also asymmetry was achieved by modifying the size and shape of petal lobes in corolla as in Scrophulariales and Lamiales and also in Asteraceae (in part).

3. Insect feeds

The need for a feeding material arose when the plant realized that the insects once cheated due the appearance of flowers may not visit the same flowers again. Moreover the insect visitor used to eat away to stamens and carpels (both the organs are rich in protoplasm containing abundant proteins and other stored food) of flowers. The plants knew that earlier in Cycads, insects visited the male cones to feed on pollen, used to return for further feeding and thus effected pollination. The reactions of the plant to the insects munching away of reproductive structures (stamens, pollens and carpels) were of two types. The first one was the production of alternative food and the second one was the reduction of the long thalamus (seen in Magnoliaceae) to a small rounded thalamus (this was later followed by the formation of disc to partially cover the ovary, and then cup-shaped thalamus within which the ovary was sunk and the final step of fusing the cup-shaped thalamus with ovary wall thus completely enclosing the ovary. But this mechanism saved only the ovules and not the stamen!). The food that was produced was nectar. To produce and secrete nectar, the plant had to develop special structures called nectaries which were located at the base of the sepals (as in Malvales), in special spurs (as in Violaceae, Balsaminaceae or Tropaeolaceae) or in ring-shaped discs at the base of the anthers or carpels. (The idea of fusion of corolla to form a cup to contain nectar did not strike the plants then and this concept, which was adopted by a large number of plants, came much later).

Whatever the case may be, nectar was produced as a sweet aqueous liquid within flowers. But here also the plants manufactured nectar having different tastes to suit different "customers". Some nectars were very sweet, some moderately sweet and some faintly sweet (in the same way some people prefer tea with a lot of sugar, some need moderately sweet tea and some with very little sugar). This was accomplished by carefully mixing the three common sugars glucose, fructose and sucrose in various proportions. A higher concentration of fructose made the nectar very sweet, more of sucrose moderately sweet and more of glucose less sweet. In addition, some plants used oligosaccharides like raffinose, maltose and melibiose to alter the taste. In addition, some nectars are found to contain flavonoids and even bitter principles (as in neem), which altered the taste of nectar to attract certain visitors or at times to repel certain unwanted visitors.

When we try to comprehend the great strategies adopted and the strides taken by the flowering plants which helped them to become the largest and dominant taxa in the plant world, it is explicit that the flower played a great role. The plants evolved many trends to achieve effective cross pollination along with maintaining the economy of resources. The petals, I feel, are the most distinguished part of the flower, crucial in achieving pollination mediated by insects. The processes incurred in developing a petal, its various shapes, multitude of colors using biosynthetically widely different compounds like anthocyanins, betacyanins, flavonoids and carotenoids, fragrant oils containing insect pheromones and processes leading to many types of nectar etc are absolutely perfect in conception and execution. It is therefore imperative that the stages in development of flower are indicative of different stages of evolution.

The need and logic of the proposed system of classification

With these facts in mind I would like to propose a phylogenetic, convenient and easy to comprehend classification. This scheme is greatly influenced by our researches on chemotaxonomy for the last thirty five years wherein my team had analysed about 2,000 plants belonging to about eighty Angiosperm families and the problems I had to face while teaching taxonomy of higher plants to both undergraduate and post-graduate students for the last thirty years. I still fail to convince students (even I am not convinced!) that the Euphorbiaceae is derived from Malvales or the Piperales from Magnoliales. I have great doubts on the evolutionary strategies of apetalous plants. All the characters of a petal which paved way for the success of flowering plants in general are lacking in them. The importance of a petal was understood by some of the advanced apetalous plants which developed colored bracts or sepals. Though the classification of Cronquist[6], Takhtajan[7] or Kubitzki[8] are widely accepted, they are of little use for a student to identify the plants in laboratory or in field. On the contrary, I was fascinated by the simplicity and logics of the classificatory scheme proposed by Bentham and Hooker[9] which was one of the earliest endeavours in classifying plants. In India we still follow Bentham & Hooker's classification for all practical purposes and in my class lectures I used to give a logical as well as evolutionary approach to this system and to my surprise, the classification of different plant groups unfolded as a well-knit story. This approach was liked immensely by our students and they started liking this subject. The same approach I introduced to teachers in refresher courses and conferences in various parts of this country and every one of my listeners appreciated this attempt and asked me to pen down the same so that they too can simplify the "difficult" subject of "Tax-on- me". Thus I started revising Bentham and Hooker's classification, but I accepted only the good points of that system, made a number of modifications to give the system a phylogenetic touch. My beliefs and convictions are explained as and where I tried to create a taxon. This system, on a broader perspective, is similar to that of Cronquist.

Major divisions of Magnoliophyta(Angiosperms)

Though pentamerous flowers appeared early in evolution, trimerous flowers appeared in the scene almost immediately. The adaptations to aquatic habit like fibrous root system, discarding secondary thickening, endosperm as the storage tissue in seeds making two cotyledons unnecessary etc. mark the deviation of the plants of **Liliopsida** from the terrestrial **Magnoliopsida** and these two groups are considered very natural groups by one and all.

Class Magnoliopsida

In both the classes Magnoliopsida and Liliopsida, the plants with primitive flowers indicate that they are early in evolution. I can visualize two groups of plants in **Magnoliopsida** with not too "successful" flowers. They are the Magnolids and the Apetalous plants. By all yardsticks the Magnolids are the most primitive flowering plants. The homoxylous wood, petals poorly differentiated from sepals, large number of members in every floral whorl and their arrangement in spirals, laminar stamens and often unsealed carpels are the features which indicate the primitiveness of the Magnolids. All these plants are included in the first subclass **Magnoliidae.** But I would prefer to keep only petaliferous (dichlamydous) plants here for the reasons described below. I have removed the Papaverales and Nymphaeales with syncarpous gynoecium which do not fit in here and are kept elsewhere.

The importance of petals in the success of flowering plants keeps one wondering on the evolutionary strategies developed by apetalous plants. The concept of petaliferous flowers never dawned on them. The flowers here are clusters of stamens and carpels protected by a whorl of green leafy perianth. The usefulness of insect pollination was accepted and adopted by some of these plants which used the petalloid sepals or colored bracts to attract the pollinators. Though the classification proposed by Bentham and Hooker was not phylogenetic, these authors grouped all the apetalous plants in their Monochlamydeae, which was a clever way of stressing the importance of petals. Incidentally a number of primitive plants included here have problems in the development of perianth as well. Thus the families Eupteliaceae, Trochodendraceae, Cercidiphyllaceae and Eupomatiaceae have flowers with out perianth. Tetracentraceae, Austrobaileyaceae, Lactoridaceac and Ceratophyllaceae are the plants of Laurales, which were grouped in Magnoliidae by Cronquist, Takhtajan and others, which do not elaborate petals. Many groups here have a primitive type of stamen and open carpels. The Hamamelidae of Cronquist includes many of these plants and all of them are considered primitive. Incidentally in the latest APG classification (2007), almost all monochlamydous plants such as Santalales and Buxales (containing Euphorbiaceae), which were previously kept in Rosidae by other workers, are kept outside core Eudicots which contain only poly- and gamopetalous plants. Only the orders Garryales (in Asterids) and Fagales (in Rosids) are the monochlamydous taxa grouped in Core Eudicots. Therefore looking into the great significance of petals in the success and further evolution of plants, I would prefer to group all the monochlamydous plants (including those monochlamydous taxa grouped in Magnoliidae by Cronquist and others), except for the Centrospermae of Engler, in **Hamamelidae** *sensu lato* and make this subclass a taxon of wider circumscription. This group arose parallel to the Magnoliidae from Proangiosperms. Of course, within my **Hamamelidae** there are primitive (plants having monocolpate pollen) and advanced plants (having tricolpate pollen). Both Magnoliidae and Hamamelidae evolved parallel to each other from Proangiosperms

The third subclass **Caryophyllidae** forms a unique taxon evolved from the basal members of the Hamamelidae. Though most of the families included here are apetalous, this group is unique in producing betalains (except for the Molluginaceae and Caryophyllaceae), p-type plastids of great variety, pantoporate type of pollen resembling a golf ball in appearance, anomalous secondary thickening, CAM pathway and a peculiar syndrome of embryological features. At least two families here, Caryophyllaceae and Portulacaceae developed petals. Looking to these very special characters of this subclass I prefer to keep Polygonales and Plumbaginales elsewhere. The exclusion of these orders makes the Caryophyllidae a very homogeneous taxon. The Polygonales find a better place in subclass Hamamelidae and the Plumbaginales, in Ebeniidae.

All the remaining flowering plants evolved from the subclass Magnoliidae. Since the fusion of petals to make a gamopetalous corolla happened later in evolution, some comparatively advanced groups developed two successful evolutionary landmarks to store nectar, the disc and the thalamus cup. The primitive plants which could not elaborate these special adaptations are grouped here in a in a new (slightly primitive) subclass **Malvidae.** The plants included here possessed a large number of floral whorls and a superior ovary. This subclass is broadly similar to the Thalamiflorae of B & H (without Ranales) and Dilleniidae (without gamopetalous orders) of Cronquist. The Dilleniales are found to share more characters with Magnoliidae than the plants of this subclass and thus are kept there. The exclusion of Dilleniales necessitated a new name for this subclass and I prefer to keep the name Malvidae to this subclass. Nymphaeales and Papaverales find a better position here. This subclass evolved directly from the Magnoliidae.

Cronquist, Takhtajan and Kubitzki grouped plants elaborating a nectariferous disc together with those with a thalamus cup in their Rosidae. But I feel that such a grouping is not very logical because the disc cannot be equated with a cup-shaped thalamus. Both these structures may be analogous, but definitely are not homologous and represent a case of parallel evolution. Disc is a mere outgrowth (without vasculature) from thalamus, withering away after fertilization and does not contribute to the fruit formation. On the contrary, the thalamus cup protects the flower especially the carpels and in many cases contribute to the formation of the fruit. This is particularly true of the flowers with inferior ovary. Therefore the plants producing a disc are at a lower level of evolution and are grouped here in a separate subclass **Rutidae.** In this subclass the evolutionary trends seen are towards the reduction of stamens. The Rutidae evolved from the Malvidae from Thealian ancestors.

The plants with a thalamus cup or an inferior ovary are conveniently grouped in **Rosidae** *sensu lato*. Here, the trends in evolution are in making the flower inferior while the stamens remain mostly five or ten. Since the most primitive order here, the Rosales, are closer to the Magnoliidae; I would prefer to derive the Rosidae from the Magnoliidae. The taxa included in all the three polypetalous subclasses Malvidae, Rutidae and Rosidae are grouped together in the group Rosids of APG classification of 2007.

The gamopetalous plants grouped in "Asterids" in APG classification, is a very natural group. A gamopetalous corolla with adnate stamens is definitely a very advanced step in evolution and therefore all the plants possessing them are advanced. The inclusion of primitive gamopetalous flowers containing many members of perianth, androecium and gynoecium (Bentham and Hooker grouped them in their Heteromerae) with primitive polypetalous plants, as practiced earlier by almost all phylogenetic taxonomists, does not appear logical. But they are distinct from the other gamopetalous plants in having more than two carpels and more ovules. Therefore they are grouped here separately in a subclass **Ebenidae** and kept as the first such taxon in gamopetalous plants. The grouping of Ericales as a separate taxon closer to the Euasterids (corresponding to the old Bicarpellatae of B. & H. by Angiosperm Phylogeny Group supports this contention. The Ebeniidae can be derived from Thealian ancestors.

The gamopetalous plants remaining in Magnoliopsida fall into two well defined groups, the first with a bicarpellary superior ovary, grouped in the subclass **Lamiidae** and the second with a bicarpellary inferior ovary, the subclass **Asteridae**. In Lamiidae, the trends of evolution operative are in the reduction of stamens and their dimorphy. In Asteridae, cohesion of stamens is the trend in evolution. Between these two subclasses, the Asteridae are more advanced because of the inferior ovary and reduction of ovules to one. Both these subclasses evolved independently from Ebeniidae. The inter-relationships of these subclasses and their phylogeny are represented in **Fig.1**

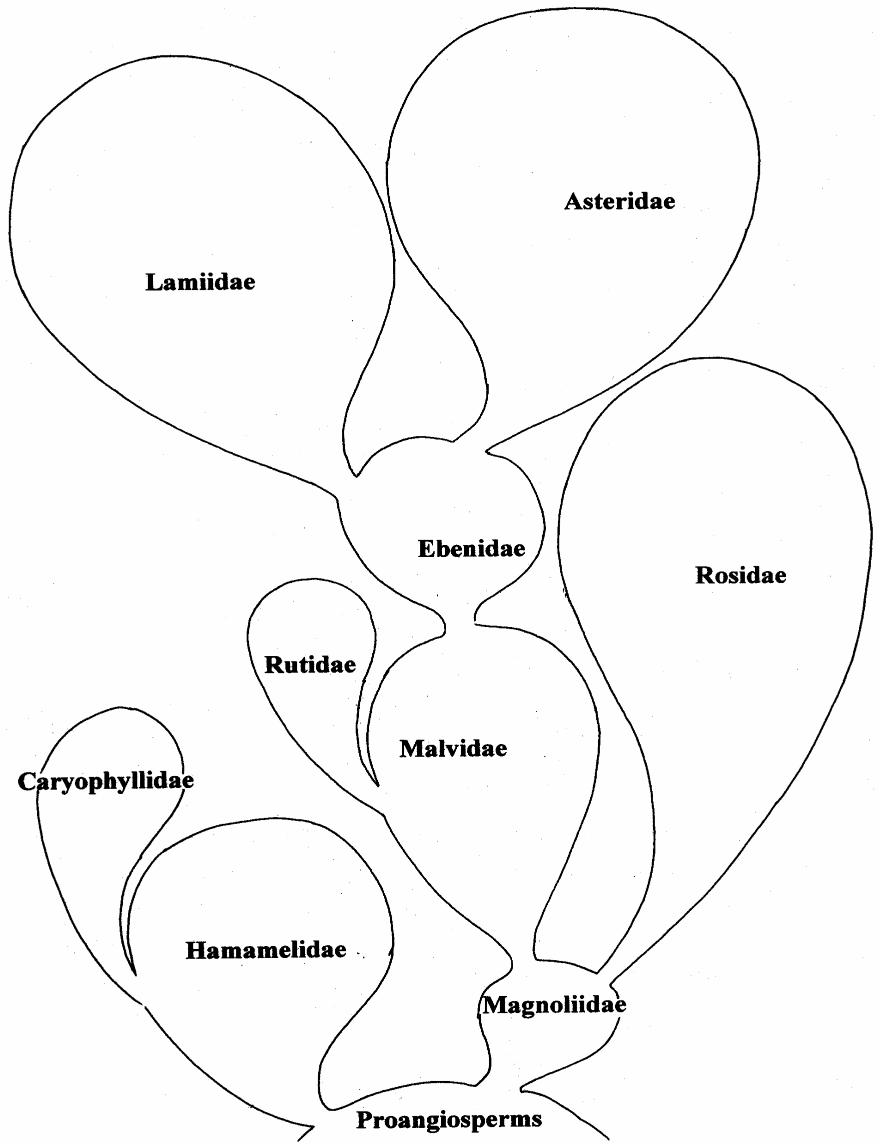

Fig - 1

Putative phylogenetic relationships among the subclasses of Magnoliopsida. The sizes of the balloons are approximately proportional to the number of species in each subclass

Synoptical arrangement of the subclasses of Magnoliosida

1. Flowers without petals. Sepals may be petalloid.
   2. Plants elaborating exclusively anthocyanins.
      Sieve tube plastids with starch .... **Hamamelidae**
   2. Plants with mainly betacyanins
      Sieve tube plastids with proteins ....**Caryophyllidae**
1. Flowers with petals
   3. Petals free from each other, stamens free from corolla

4. Flowers hypogynous, disc or Calyx cup absent **Malvidae**
4. Flowers generally perigynous, disc or Calyx cup present
    5. Disc present, calyx cup absent **Geraniidae**
    5. Calyx cup free or fused with Thalamus to make ovary inferior **Rosidae**
3. Petals fused to form a corolla, stamens epipetalous
    6. Ovary superior
        7. Carpels more than two **Ebenidae**
        7. Carpels two **Lamiidae**
    6. Ovary inferior **Asteridae**

Liliopsida

This class contains plants which migrated into aquatic habitats in land. The first few taxa are clearly fully aquatic, but it is seen that many of them survived well in marshes and from there they migrated back to land and survived there. The single cotyledon here may be due to the reduction of one cotyledon necessitated by the employment of endosperm as the nutritive tissue in seeds. The tendency of a single cotyledon seen in aquatic Nymphaeales where the cotyledons arise from a common primordium, more or less connate below into a ring indicate that the ancestors of Liliopsida would be some aquatic plants closer to this order.

The near absence or reduction in variety of insects in aquatic environments necessitated the rejection of insect pollination and acceptance of wind pollination as practised by sedges and grasses. These plants reduced perianth (no need of attracting insects!) and modified pollen, stamens, style and stigma so as to shed the pollen easily in wind and to trap the pollen coming through wind. Another group of plants opted for pollination by lesser common insects like carrion flies, moths and ants by producing foul smelling volatiles such as ammonia, indole, skatole, trimethylamine etc and they are the aroids. The plants returned back to land opted for insect pollination in a big way with special adaptations to mimic the insects, not by color, but by patterns and varying shapes. They migrated to forests and adapted epiphytic habit with the help of endophytic mycorrhiza and they are the orchids. Some other plants developed an arborescent habit, reduced the perianth to a single whorl of sepals but got pollinated by both bees and wind. They are the palms.

There is a general agreement that the Alismatales and related taxa are the most primitive group in Liliopsida due to their apocarpous gynoecium, absence of endosperm (like Magnoliopsida) and aquatic habit. This group is the subclass **Alismatidae.** From this subclass evolution took place in two lines, one specializing in insect pollination and other opting for wind pollination. Subclass **Liliidae** of Cronquist is a very natural taxon evolved from Alismatidae in the insect pollinated category. Here the perianth is almost undifferentiated to calyx and corolla and all perianth lobes are petalloid. The differentiation of sepals and petals as well as developing nectar and nectaries as seen in the Commelinales marks a deviation which culminated in Zingiberales. Therefore I would group the Commelinales and Zingiberales as also Bromeliales together in the subclass **Zingiberidae.** It is to be remembered that Cronquist grouped Commelinales with Cyperales in his subclass Commelinidae. But I fail to understand the logic of grouping the insect pollinated Commelinaceae and allied families with wind-pollinated Cyperales and Eriocaulales in the subclass Commelinidae as practised by Cronquist, Takhtajan and Kubitzki. The second line of evolution lead to the formation of all the wind-pollinated orders (included in the Commelinidae of Cronquist; virtually all orders other than Commelinales) which are treated here into a new subclass **Cyperidae.** This origin of this group can be traced to the basal stock of the Alismatidae. The fifth subclass **Arecidae** contains all the plants which lost the petals or perianth altogether but still pollinated by bees (Arecales) or insects like carrion flies, moths and ants (Arales) The phylogeny of these subclasses is represented in **Fig.2**

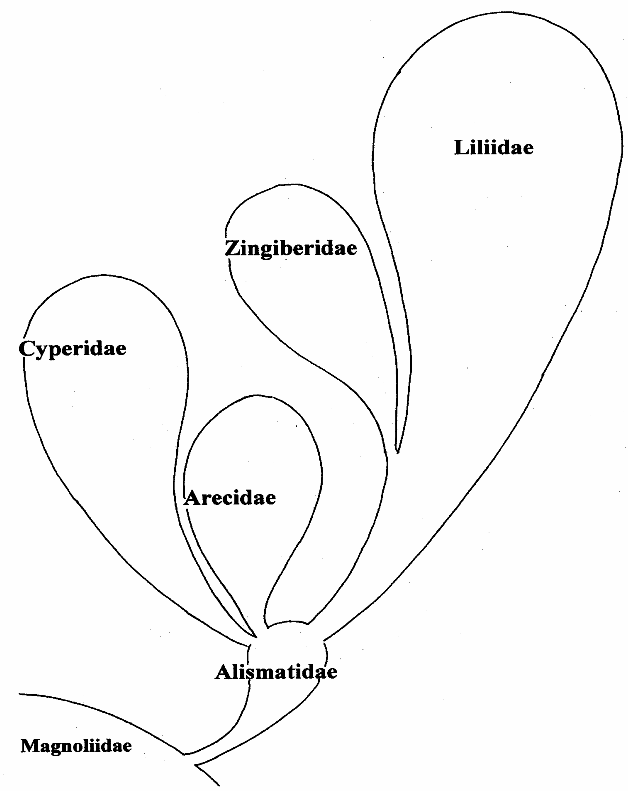

Fig - 2

Putative phylogenetic relationships among the subclasses of Liliopsida. The sizes of the balloons are approximately proportional to the number of species in each subclass

The detailed classification of the Class Magnoliopsida

1. Subclass Magnoliidae

By all yardsticks this is one of the most primitive groups of Magnoliophyta. This group evolved alongwith the Hamamelidae from the “Proangipsperms”. The relative poor specialization in almost all the characters is a clear proof for this contention. The relatively unspecialized vascular tissues (homoxylous condition in quite a few taxa), monocolpate type of pollen, spiral arrangement as well as large number of floral whorls, perianth undifferentiated to sepals and petals in many plants, laminar stamens, open or unsealed carpel, laminar parietal type of placentation, many stamens, carpel, ovules, seeds and seeds with more than one cotyledon (seen in a few plants) are the archaic features seen in this subclass. The defensive compounds here are the volatile oils and the benzyl isoquinoline alkaloids. Ranunculales with their herbaceous habit and benzyl isoquinoline alkaloids are relatively advanced. But it is the Annonaceae, with their cyclic perianth and acetogenins, the most advanced group here and that is the reason why I prefer to keep both Annonaceae and Eupomatiaceae in a separate order Annonales. Almost all the groups, except for the apetalous taxa, evolved from this taxon.

My **Magnoliidae** is definitely much smaller than that of Cronquist and Takhtajan because I removed the apetalous orders such as Laurales, Piperales and Aristolochiales from this subclass. All the plants with apocarpous pistil and primitive stamens and carpels and a large number of non-essential whorls are included here. I would prefer to keep Dilleniales with apocarpous pistil here. Illiciales of other authors are included within Magnoliales. Annonaceae and Eupomatiaceae with trimerous flowers (a trend similar to the monocots) and acetogenins in the former family definitely show another line of evolution than the Ranunculales and thus kept separate in Annonales. Nelumbonales form the aquatic order in this group. The Nymphaeales and Papaverales with fused carpels are removed from this taxon and are placed comfortably in Malvidae.

This subclass contains five orders, 20 families, 306 genera and 6444 species.

The orders included here are Magnoliales, Dilleniales, Ranunculales, Nelumbonales and Annonales

Synoptical arrangement of the orders of Magnoliidae

1. Plants with volatile oils, mostly trees – *1. Magnoliales*.
1. Plants without volatile oils, trees, shrubs and herbs
    2. Seeds arillate – *2. Dilleniales*.
    2. Seeds non-arillate
        3. Herbs, plants with pentamerous flowers and isoquinoline alkaloids
            4. Terrestrial plants – *3. Ranunculales.*
            4. Aquatic plants – *4. Nelumbonales*
        3. Flowers trimerous, plants elaborating acetogenins – *5. Annonales*

Subclass 2. Hamamelidae

The concept of a very specialized colorful flower is not adapted and accepted here. The flowers in these plants are mere modified shoots (similar to cones!) bearing stamens and carpels protected by one whorl of leafy perianth. The large number of wind-pollinated plants in this group is the reason for the absence of petals. Many of the plants included here are of temperate regions where the insect diversity is less. Though some of the members of Euphorbiales developed colored leaves or nectaries, by and large these flowers are colorless or green. One may consider this subclass as an offshoot parallel to the Magnoliidae.

The Hamamelidae visualized here contain all monochlamydous and apetalous families. Both Cronquist and Takhtajan distributed these families far and wide in all the subclasses. But that treatment resulted in many dissimilar groups coming together adding to the difficulty to a young student initiated in taxonomy. I do not see any group included here has a distinct evolutionary feature. Some may have advanced vasculature indicating their advanced position within the subclass. The presence of vasculature to the 'lost petals" which is considered a proof for the derivation of apetalous groups from petaliferous groups would in fact be the initial processes in producing a petal and then abandoned due to the resorting to wind pollination.

The Hamamelidae as treated here include 23 orders containing 66 families. The total plants are 628 genera incorporating 20191 species. I will consider Rafflesiales (due to parasitic habit), Aristolochiales, Polygonales, and Euphorbiales (due to colored petals or other adaptations facilitating entomophily) as the advanced groups here.

Synoptical arrangement of the orders of the Hamamelidae

1. Plants total or semi parasites.
    2. Ovules many in deeply intruded parietal placenta – 4. *Rafflesiales*
    2. Ovules few in free – central or basal placenta, seeds solitary or few–17. *Santalales*
1. Plants autotrophic
    3. Plants Aquatic
        4. Sepals petalloid - 19. *Podostemales*
        4. Perianth reduced or absent – 23. *Callitrichales*
    3. Plants terrestrial
        5. Wood homoxylous – 1. *Trochodendrales.*
        5. Vessels present in wood.
            6. Ovules many per carpel
                7. Ovary superior, perianth small – 3. *Hamamelidales*
                7. Ovary inferior, perianth united, corolloid – 8. *Aristolochiales*
            6. Ovules 2 or 1 per carpel
                8. Embryo minute – 6. *Daphniphyllales*
                8. Embryo well developed
                    9. Flowers in aments
                        10. Pistil of one carpel – 8. *Leitneriales*
                        10. Pistil of more than one carpel
                            11. Inflorescence a spadix. Stem anatomy like monocots- 5. *Piperales*
                            11. Inflorescence catkin or otherwise, not spadix, stem anatomy usual to dicots
                                12. Leaves opposite or alternate
                                    13. Ovule solitary
                                        14. Leaves pinnate -9. *Juglandales*
                                        14. Leaves simple.
                                            15. Leaves succulent. 22. *Batales*
                                            15. Leaves not succulent -10. *Myricales*
                                    13. Ovules 2 or more
                                        16. Parietal placentation- 21. *Salicales*
                                        16. basal or axile placentation-11. *Fagales*
                                12. Leaves reduced, whorled – 12. *Casurinales*
                            11. Flowers not in aments.
                                17. Flowers tetramerous – 18. *Proteales*
                                17. Flowers pentamerous.
                                    18. Staminate flowers with two connate stamens – 13. *Didymelales*
                                    18. Stamens distinct
                                        19. Ovules 2 in a single locule – 14. *Eucommiales*
                                        19. Ovules 1 in a locule, if two, only one

maturing
20. Anthers many, dehiscing by valves – 2*. Laurales.*
20. Anthers few dehiscing longitudinally
21. Ovary bicarpellary – 15*. Urticales*
21. Ovary tricarpellary
22. Leaves ochreate – 20*. Polygonales*
22. Leaves not ochreate – 16*. Euphorbiales*

Subclass 3. Caryophyllidae

I have kept only the members possessing the characteristic features of the subclass here and thus contain only one order the Caryophyllales. This subclass is characterized by free central or basal placentation and anomalous secondary growth. These are the plants opted for marshy/desert habitats where water is scarce. The CAM pathway is a clear proof for this. The adaptive values of betacyanins and abnormal secondary thickening are still obscure. But they may have some bearing in the marshy/halophytic/desert conditions where these plants thrive well. Two smaller orders Polygonales and Plumbaginales which are customarily associated with the Caryophyllales are presently removed from this subclass. The Polygonales with their quinones are definitely not related to the Caryophyllales and the due to the absence of petals they can be conveniently placed as an advanced taxon of the Hamamelidae. The gamopetalous Plumbaginales with their quinones and lack of p-proteins, pantoporate type of pollen etc finds a better place in the Ebeniidae. This order contains a single order Caryophyllales, 12 families and about 10,000 species.

Subclass 4. Malvidae

This is Cronquist's Dilleniidae sans Dilleniaceae. This subclass contains the early plants with perfect flowers and completely specialized floral whorls. It is slightly advanced over the Magnoliidae in introducing syncarpy and evolving flowers with less number of floral whorls. The carpels are fused in different ways i.e. in Papaverales, Capparales and Violales there is the fusion of open carpels and this is one line of evolution in this subclass. The Papaverales, Violales and Capparales would have evolved as parallel lines from the Magnoliales. The rest of the plants wherein closed carpels fused by their ventral sutures formed another line of evolution and this line is continued further. The Theales, the most primitive group in this subclass, is closest to the Magnoliales, but differ in possessing syncarpy and tannins. Nymphaeales would have evolved from the Nelumbonales. The Malvales and Polygalales are the groups evolved from the Theales. The toxic bisbenzyl isoquinolines have been replaced by other less toxic, but more efficient sulphur-containing glucosinolates (Capparales), tannins (Theales), mucilages (Malvales) and saponins (Polygalales). The orders Nymphaeales and Papaverales are the two controversial taxa I have included here. These orders were customarily placed in Magnoliidae and there these syncarpous taxa created heterogeneity among the apocarpous pistil bearing plants. The reported presence of alkaloids especially bisbenzyl isoquinolines in *Nymphaea* is yet to be proved conclusively. But this genus is found to contain sesquiterpene alkaloids, tannins, diterpenes etc. The spiral arrangement of the perianth whorls is the only discordant note for keeping Nymphaeales in Malvidae. But then this can be considered as the retention of some primitive characters by this group. Similarly the Papaverales, placed in this group, is highly dissimilar to other members of Magnoliidae where it was customarily placed, in not having large number of perianth whorls and apocarpous pistils, the two typical characters of the Magnoliidae. They do have only a single character common with the some of the Magnoliidae that is the presence of benzyl isoquinolines. Therefore I prefer to keep Papaverales in Malvidae itself. This subclass contains seven orders, 62 families, 1137 genera and 18710 species

Synoptical arrangement of the orders of the Malvidae

1. Plants aquatic - 1. *Nymphaeales*
1. Plants terrestrial
    2. Placentation parietal
        3. Ovary bicarpellary
            4. Laticiferous plants with isoquinoline alkaloids – 2. *Papaverales*
            4. Plants without laticifers, glucosinolates present- 5. *Capparales*
        3. Ovary tricarpellary – 3. Violales
    2. Placentation axile
        5. Flowers zygomorphic or stamens poricidal – 7. *Polygalales*
        5. Flowers regular
            6. Mucilage, stellate hairs and bast fibres present – 6. *Malvales*
            6. Mucilage, stellate hairs and bast fibres absent- 4. *Theales*

Subclass 5. Rutidae

The elaboration of a disc, which is entirely a different process from calyx cup and gamopetaly, for producing and storing nectar and also for providing partial protection to the ovary, justifies my creation of this subclass away from the Rosidae of Cronquist and other workers. In some of the Rhamnaceae members the disc, completely enveloping the ovary, fuses with it so that the ovary gets embedded in the disc. The disc may be extrastaminal, a primitive feature or intrastaminal (close to gynoecium), an advanced feature.

All the plants of “Disciflorae” of Bentham and Hooker are included here. But the woody, limonoid/quassinoid containing plants of the Geraniales (B&H) are taken out and circumscribed as a new order Rutales. The Rutales being the largest order, the name of the subclass is derived from this taxon. Thus the Rutidae include six orders containing 44 families. Almost all orders possess their peculiar assortment of advanced characters. Celastrales and Rhamnales with five stamens are the highly advanced orders, though Sapindales (unisexual flowers, reduction of stamens and carpels) and Rutales (Limonoids and quassinoids) also are advanced. Zygomorphy in Balsaminaceae and Tropaeolaceae keeps the Geraniales also advanced. This subclass contains 6 orders, 42 families, 761 genera and 12859 species

Synoptical arrangement of the orders of the Rutidae

1. Stamens 10, obdiplostemonous
    2. Herbs without bitter principles – *1. Geraniales*
    2. Trees or shrubs with limonoids/quassinoids – *2. Rutales*
1. Stamens five or less.
    3. Petals clawed – 4*. Linales*
    3. Petals not clawed,
        4. Stamens five, flowers bisexual
            5. Stamens alternating with petals – 5*. Celastrales*
            5. Stamens opposite to petals – 6*. Rhamnales*
        4. Stamens generally less than five, plants polygamous, resinous or gum-producing plants- 3*. Sapindales*

Subclass 6. Rosidae

This subclass is characterized by either a cup - shaped thalamus within which the gynoecium is well - protected or thalamus fusing with the gynoecium. The ovary is half inferior in the former case and inferior in the latter. The Rosales evidently are at the bottom in an evolutionary hierarchy in this subclass. Many of the primitive Taxa here possess a large number of stamens. Fabales with very high sophistication in petal morphology, reduction of carpels to one, elaboration of isoflavonoids, lupinane alkaloids and large number of non- protein aminoacids, evidently is the most successful group here. Apiales with umbels, bicarpellary inferior ovary and cremocarp also is at par with the Fabales in evolution. The gamopetalous nature of the corolla as seen in the Mimosaceae, Cucurbitaceae, Caricaceae, Fouquieriaceae and Loasaceae can be seen as attempts of evolving a gamopetalous corolla here. The Rosidae consists of 8 orders containing 48 families wherein the genera are 2216 and species, 42162.

Synoptical arrangement of the orders of the Rosidae

1. Aquatic plants – *5. Haloragales*
1. Terrestrial plants
    2. Carpels apocarpous
        3. Carpels many – *1. Rosales*
        3. Carpel one – *2. Fabales*
    2. Carpels Syncarpous
        4. Stamens monadelphous - *6. Lecythidales*
        4. Stamens free
            5. Ovary tricarpellary – *8. Cucurbitales*
            5. Ovary bi-or pentacarpellary
                6. Ovary bicarpellary
                    7. Fruit a cremocarp, flowers in umbels – *9. Apiales*
                    7. Fruit a berry or drupe, flowers not in umbels- *7. Cornales*
                6. Ovary pentacarpellary -
                    8. Stem with internal phloem, stamens and ovules many - *4. Myrtales*
                    8. Stem without internal phloem, ovules 2 per locule Plants often mangroves - *3. Rhizophorales*

Subclass 7. Ebenidae

The Ebenidae are the most primitive subclass among the gamopetalous groups. It arose directly from Thealian ancestors of Malvidae. The primitive members possessed large number of floral whorls though in the advanced members the number of members in each of whorl is reduced to five. From this subclass the Asteridae evolved in one direction and Lamiidae in another direction. This subclass consists of six orders and 23 families. There are 416 genera containing 10046 species

Synoptical arrangement of the orders of the Ebenidae

1. Ovary unilocular or if multilocular, partitions are only at the base
    2. Ovules pendulous- *3. Olacales*
    2. Ovules erect
        3. Ovules many in free central classification- *5. Primulales*

3. Ovule one in basal placentation – *6. Plumbaginales*
1. Ovary multilocular
4. Petals basally connate only, stamens obdiplostemonous- *1. Ericales*
4. Petals gamopetalous, stamens in two whorls,
5. Gynoecium tricarpellary – *4. Diapensiales*
5. Gynoecium bi or pentacarpellary- *2. Ebenales*

Subclass 8. Lamiidae

This subclass is one of the most advanced groups of Dicots, almost reaching the level of the Asteridae. The reduction in carpels to two and didynamous stamens in half of the members are the highly advanced characters here. Apocynales with a near perfect pollination mechanism with pollinia represent another line of evolution. The chemical adoptions here are the iridoids and cardiac glycosides. The regular flowers and similar stamens of primitive members gave rise to zygomorphy and didynamous stamens in advanced members. The maximum reduction in ovules achieved is only four (as compared to one per flower in advanced Asteridae). The Gentianales are the most primitive group and Lamiales, the most advanced. The Lamiidae contain 6 orders comprising of 32 families. The genera here are 1980 and species 35844.

Synoptical arrangement of the orders of the Lamiidae

1. Flowers tetramerous – 1. *Plantaginales*
1. Flowers pentamerous.
2. Flowers regular, stamens 5
3. Leaves opposite
4. Laticiferous herbs, styles free uniting at the apex, stigma single -3. *Apocynales*
4. Latex absent. Style one/2, stigma two – 2. *Gentianales*
3. Leaves alternate- 4.*Solanales*
2. Flowers zygomorphic, stamens 4, didynamous
5. Ovules many – 5. Scrophulariales
5. Ovules four – 6. Lamiales.

Subclass 9. Asteridae

This subclass is the most advanced one in Magnoliopsida. The inferior ovary, zygomorphy, reduction of carpels to two and special androecial conditions are the advanced characters shared by all families. Rubiales, with their regular flowers, is the least advanced and Asterales, the highly advanced taxon. All the other orders fall in between these two. The characters of Asterales which made them the most evolved are the herbaceous habit, head inflorescence, zygomorphic unisexual flowers, pappus hairs, syngenesious anthers, protandry and protogyny in bisexual flowers and a single seed. The chemical arsenal of this order includes polyacetylenes and sesquiterpene lactones which are excellent allelochemics and good antimicrobials. This subclass contains 16 families included in 5 orders. The total number of genera are 2327 and species 36611.

Synoptical arrangement of the orders of the Asteridae

. Ovary unilocular
2. Ovule pendulous- 2. *Calycerales*

2. Ovule basal – 5. *Asterales*
1. Ovary bilocular
3. Leaves stipulate, stipules interpetiolar bearing colleters- 3. *Rubiaceae*
3. Leaves estipulate
4. Leaves opposite – 1. *Dipsacales*
4. Leaves alternate – 4. *Campanulales*

Subclasses of Liliopsida

Subclass 1. Alismatidae

This subclass includes the most archaic group of monocotyledonous plants. The plants are aquatic herbs with poorly lignified vascular system and the vessels are confined to roots. Gynoecium is apocarpous and the endosperm, mostly absent. The origin of this group can be traced to the Magnoliidae through Nelumbonales. This subclass contains 4 orders containing 16 families. The genera included are 58 and species, 467. The Triuridales with their terrestrial achlorophyllous plants strike a discordant note here in this otherwise homogenous group.

Synoptical arrangement of the orders of the Alismatidae

1 . Plants aquatic or semi aquatic
2. Perianth differentiated to sepals and petals
Flowers bracteate
3. Carpels distinct – 1. *Alismatales*
3. Carpels syncarpous 2. *Hydrocharitales*
2. Perianth undifferentiated to sepals and petals- 3. *Najadales*
1. Plants terrestrial, without chlorophyll- 4. *Triuridales.*

Subclass 2. Arecidae

The plants included here are characterised by many small flowers, a spadix inflorescence subtended by a spathe, and pollination is by honeybees, bats or even wind. The Arecaceae with their arborescent habit is the largest taxon here, closely followed by the Araceae. This is another line of evolution parallel with the Cyperidae wherein the tendency is to the secondary reduction of perianth whorls due to resorting to wind pollination . The four orders included here consist of 5 families, 325 genera and 6300 species.

Synoptical arrangement of the orders of the Arecidae

1. Plants arborescent, stem unbranched with a crown of leaves – 1. *Arecales*
1. Plants herbs or shrubs. Stem branched
2. Plants palm like herbs- 2. *Cyclanthales*
2. Plants rhizomatous herbs or branched shrubs
3. Plants shrubs with prop roots, fruit syncarp- **3.** *Pandanales*
3. Plants rhizomatous/tuberous herbs
Fruit a berry- 4. *Arales*

Subclass 3. Cyperidae

Plants included here possess chaffy or much reduced perianth or perianth wanting. Pollination mostly by wind, water or self. About 75% species belong to the single family Poaceae and Cyperaceae together account for 90% of the species. Evidently, Poaceae is the most advanced taxon here, highly successful due to the adaptations for wind- pollination. This subclass consists of 6 orders containing 12 families. The total species here are 15881 included in 834 genera.

Synoptical arrangement of the orders of the Cyperidae

1. Ovules axile if ovary multilocular or basal if unilocular
    2. Ovary multilocular, ovules three- many- 3. *Juncales*
    2. Ovary unilocular, ovule one – 4. *Cyperales*
1. Ovules pendulous.
    3. Perianth differentiated to sepals and petals- 1. *Eriocaulales*
    3. Perianth undifferentiated
        4. Flowers hydrophilous- 5. *Hydatellales*
        4. Flowers anemophilous.
            5. Seed solitary- 6. *Typhales*
            5. Seeds many- 2. *Restionales*

Subclass 4. Zingiberidae

All the plants included here are insect or bee-pollinated and thus have perianth differentiated to well defined sepals and petals. Nectar and nectaries often present. The Zingiberales are the largest and most successful order with very effective trends in reduction in essential whorls. The three orders included here consists of 13 families containing 209 genera and 5240 species

Synoptical arrangement of the orders of the Zingiberidae

1. Leaves parallel-veined and not pinnate parallel, stamens 6 or 3
    2. Leaves with a green basal sheath and smooth margins- 1. *Commelinales*
    2. Leaves with a colored base with minute peltate scales, margins spiny- 2. *Bromeliales*
1. Leaves pinnate parallel, stamens five or one- 3. *Zingiberales*

Subclass 5. Liliidae

The members here possess showy flowers with the sepals being petalloid and an ovary with many ovules. These plants exploited insects to a maximum extent for pollination. The largest and most successful family is the Orchidaceae which circumscribe about two-thirds of the total species, followed by the Liliaceae. Included here are two orders which contain 17 families. The total genera present are 1327 and species, 28777.

Synoptical arrangement of the orders of the Liliidae

1. Plants not mycotrophic, seeds of normal size, flower actinomorphic- 1. *Liliales*
1. Plants mycotrophic, seeds many, minute, flower zygomorphic- 2. *Orchidales*

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