

= Lilioid monocots =

Lilioid monocots (lilioids , liliid monocots , petaloid monocots , petaloid lilioid monocots) is an informal name used for a grade (grouping of taxa with common characteristics) of five monocot orders (Petrosaviales , Dioscoreales , Pandanales , Liliales and Asparagales) in which the majority of species have flowers with relatively large , coloured tepals . This characteristic is similar to that found in lilies (" lily @-@ like ") . Petaloid monocots refers to the flowers having tepals which all resemble petals (petaloid) . The taxonomic terms Liliaceae or Liliiflorae have also been applied to this assemblage at various times . From the early nineteenth century many of the species in this group of plants were put into a very broadly defined family , Liliaceae sensu lato or s.l. (lily family) . These classification systems are still found in many books and other sources . Within the monocots the Liliaceae s.l. were distinguished from the Glumaceae .

The development of molecular phylogenetics , cladistic theory and phylogenetic methods in the 1990s resulted in a dismemberment of the Liliaceae and its subsequent redistribution across three lilioid orders (Liliales , Asparagales and Dioscoreales) . Subsequent work has shown that two other more recently recognized orders , Petrosaviales and Pandanales also segregate with this group , resulting in the modern concept of five constituent orders within the lilioid monocot assemblage . This has resulted in treating monocots as three informal groups , alismatid , lilioid and commelinid monocots . The lilioids are paraphyletic in the sense that commelinids form a sister group to Asparagales .

= = Description = =

= = = True lilioids = = =

The descriptive term " petaloid lilioid monocot " relates to the conspicuous petal @-@ like (petaloid) tepals which superficially resemble true lilies (*Lilium*) . Morphologically , the petaloid or lilioid monocots can be considered to possess five groups (pentacyclic) of three @-@ fold (trimerous) whorls . Lilioid monocots all have flowers which can be considered to have been derived from a lily @-@ like flower with six relatively similar tepals , and six stamens . The typical lilioid gynoeceum has three carpels fused into a superior trilocular (three @-@ chambered) superior ovary , axile placentation , a single hollow style , and several ovules with anatropous orientation in one or two rows per locule and nectaries at the base .

However , floral synapomorphy (shared characteristics) is rare since most conform to the general monocot pattern . This pattern is ancestral (plesiomorphic) for the lilioid monocots . Structural monosymmetry is rare , except for Orchidaceae .

Various trends are apparent among the lilioids , notably a change to an inferior ovary and a reduction of the number of stamens to three . In some groups (such as the genus *Trillium* in the Liliaceae) , the tepals have become clearly differentiated , so that the flower has three coloured petals and three smaller green sepals . Almost all lilioid monocots retain at least three petal @-@ like tepals . Since some commelinids (e.g. *Tradescantia*) have petaloid flowers , the term ' lilioid ' is a more accurate one for the group which excludes them , since the term petaloid monocot is still occasionally used in describing commelinids . The morphological concept of petaloid monocots has been equated with " animal @-@ attracting " (that is , for pollination) as opposed to wind @-@ pollinating plants (such as grasses) that have evolved very different floral structures . Pollen structure shows that of the two main tapetum types , secretory and plasmodial , the lilioid monocots are nearly all secretory .

= = = Comparison with other monocot orders = = =

In the orders that branched off before the lilioid monocots , the Acorales and Alismatales , flowers differ in several ways . In some cases , like *Acorus* (Acorales) , they have become insignificant . In

others , like Butomus (Alismatales) , they have six coloured tepals , and so could be called ' petaloid ' , but stamens and carpels are more numerous than in the lilioid monocots .

The later evolved commelinids have various kinds of flower , few of which are ' lily @-@ like ' . In the order Poales , comprising grasses , rushes and sedges , flowers are either petal @-@ less or have small , unshowy petals . Many Zingiberales species have brightly coloured and showy flowers . However , their apparent structure is misleading . For example , the six tepals of cannas are small and hidden under expanded and brightly coloured stamens or staminodes which resemble petals and may be mistaken for them .

= = History = =

= = = Morphological definitions = = =

In one of the earliest monocot taxonomies , that of John Lindley (1830) , the grouping corresponding to the lilioid monocots was the " tribe " Petaloideae . In Lindley 's system the monocots consisted of two tribes , the Petaloideae , and the Glumaceae (the grasses and sedges) . Lindley divided the Petaloideae into 32 " orders " (roughly corresponding to families) and the Glumaceae into two further orders . Various successive taxonomies of the monocots also emphasized the grouping of species with petaloid (undifferentiated) perianths , such as Bentham and Hooker 's Coronarieæ and Hutchinson 's Corolliferae (" Corolla bearing ") (1936) . Hence the concept that there was a natural grouping of monocots whose flowers were predominantly petaloid , gave notion to the term " petaloid monocots " . The core group of petaloids were the Liliaceae , hence " lilioid monocots " .

The term " lilioid monocot " or lilioid " has had widely varying interpretations . One of the narrower applications is " lily @-@ like " monocots , meaning the two orders Asparagales and Liliales , but the term has also been applied to Takhtajan 's superorder Lilianae , the whole of Liliales , or restricted to Cronquist 's broadly defined Liliaceae . Although " petaloid " and " lilioid " have often been used interchangeably , as Heywood points out , some usages of " petaloid monocot " , particularly in horticulture , are so broad as to be almost meaningless in that it had been used to refer to all species with conspicuous petals or perianth segments (tepals) , which would cover a broad swathe of families (he estimated three dozen across many orders) . Other authors have defined it equally broadly as " having two whorls of tepals (sepals and petals) that are petal @-@ like " .

As Kron and Chase stated in 1995 , this taxonomic unit had been in a considerable state of flux , with significant variation between the systems of Cronquist (1981) , Thorne (1983 , 1992) , and Dahlgren (1985) . When classification systems were based on morphological characters alone , lilioid species which clearly departed from the " lily " pattern were easily placed into separate families . For example , the Amaryllidaceae contained species whose flowers had six stamens and an inferior ovary . The Iridaceae contained those with three stamens and an inferior ovary . The remaining taxa were put together in a very broadly defined Liliaceae , usually refereed to as Liliaceae sensu lato (s.l.) . The Cronquist system 's definition , for example , is the broadest of all . Rolf Dahlgren and colleagues were responsible for one of the most radical reorganisation of families , and in their 1985 monocot monograph defined the two orders (Asparagales and Liliales) which contain the bulk of monocot geophytes , as constituting the lilioid monocots .

The development of DNA sequencing and the use of genetic data in determining relationships between species of monocots confirmed what many taxonomists had long suspected : Liliaceae s.l. was highly polyphyletic . The family was demonstrated to include a significant number of unrelated groups , which belonged to quite separate families and even orders . For instance some genera such as Hyacinthus , previously placed in Liliaceae s.l. , were reclassified in families within Asparagales (in this case Asparagaceae) . In 1995 Chase et al. reviewed the understanding of the lilioids and equated them to Dahlgren 's Liliiflorae , which they designated as superorder Lilianae . They pointed out that the understanding of the phylogenetics of this group was critical for the establishment of a monocot classification . They also noted that while many authors treated this

group as monophyletic (having a common ancestor) , a closer reading of their texts revealed evidence of paraphyly (excluding some descendants of a common ancestor) . For instance , Dahlgren had based monophyly on a single synapomorphy , that of a petaloid perianth , yet in discussing his Liliiflorae admitted it was undoubtedly paraphyletic . Dahlgren treated the monocots as split between ten superorders and placed five orders (Dioscoreales , Asparagales , Liliales , Melanthiales , Burmanniales and Orchidales) in his Liliiflorae .

= = = Phylogenetic era = = =

In the 1995 study by Chase et al. referred to above , which was the largest yet to use purely molecular data , the results demonstrated paraphyly of the lilioids . However , because their data contradicted purely morphological phylogenies they were reluctant to draw definite conclusions as to the monophyly of this group . They identified four major clades of monocots . They named these alismatids , aroids , stemonoids and dioscoreoids , in addition to Acorus , and a core group of Asparagales , Liliales and commelinoids . They based the names of these groups on the closest corresponding superorders and orders of Dahlgren , with the exception of stemonoids (based on Stemonaceae for which there was no obvious equivalent) .

There was no clear clade corresponding to Dahlgren 's Liliiflorae , whose families were distributed amongst the aroids and dioscoreoids . Of Dahlgren 's Liliiflorae , the Dioscoreales largely grouped into dioscoreoids , with the exception of Stemonaceae . The Asparagales formed two major groupings , which they labelled " higher " and " lower asparagoids " , and included both the Iridaceae and Orchidaceae from Dahlgren 's Liliales . On the other hand , a number of families from three other orders (Asparagales , Dioscoreales , Melanthiales) segregated together with the remaining Liliales families . Genera from Dahlgren 's Melanthiales were found in both dioscoreoids and the redefined Liliales . Finally Dahlgren 's Burmanniales were found to belong with the dioscoreoids . Some Asparagales taxa were also found amongst the commelinoids . The stemonoids were formed from Stemonaceae and other families from a variety of orders , including Pandanaceae (which alone formed Dahlgren 's Pandaniflorae) .

In an attempt to resolve the apparent differences between morphological and molecularly defined trees , a combined analysis was undertaken which confirmed superorder Liliiflorae as monophyletic , provided that a few modifications were undertaken . These included the removal of two tribes of Melanthiaceae (Melanthiales) and the inclusion of three additional families (Cyclanthaceae , Pandanaceae and Velloziaceae) from other superorders . This newly and more narrowly redefined Liliaceae / Liliiflorae contained three orders , Asparagales , Liliales and Dioscoreales (which now included the stemonoids) . This analysis also allowed for the establishment of a single synapomorphy , although this time by the presence of an inferior ovary . Significantly , the authors noted that it was no wonder the authors of angiosperm classifications had been exasperated by the Liliaceae .

= = = Angiosperm Phylogeny Group = = =

These findings , presented at the first Monocot Conference in 1993 , with the addition of several studies that had become available in the interim , formed the basis of the 1998 consensus Angiosperm Phylogeny Group (APG) ordinal scheme . Among other things , the Alismatales were expanded and new orders such as Acorales (a placement for Acorus) and Pandanales (which now represented the stemonoids as well as new families) added . While not formally assigning any supraordinal ranks , the classification did recognize an informal grouping of monocot orders as the commelinoids . Otherwise the APG recognized only six monocot orders (Acorales , Alismatales , Asparagales , Dioscoreales , Liliales and Pandanales) . The last four were however grouped together in the resulting cladogram and most closely represent the concept of lilioids , although this left some unplaced monocot families , including Corsiaceae and Petrosaviaceae .

Simultaneous with the release of the 1998 APG classification were two events : the publication of Kubitzki 's major monograph on the monocots and the Second Monocot Conference . Kubitzki

defined superorder Lillanae as all monocots except superorders Commelininae , Alismatanae and the Acoraceae , that is the four orders Asparagales , Liliales , Dioscoreales and Pandanales . The Monocot Conference devoted an entire section to Systematics of the Lilioids and included an update of their previous research by Chase and colleagues . On this occasion the latter felt that there was now enough data to put forward a definitive classification , defining the Lilioids as comprising the four orders placed in Lillanae by Kubitzki . Rudall and colleagues (2002) followed Chase (2000) , in using the term " lilioid monocots " and again noting unresolved polytomy between these four orders and the remaining monocot clades (commelinids and Petrosaviaceae) , although at that time the Petrosaviaceae were still unplaced .

There was now enough new data to justify revising the APG system , and a new classification was issued in 2003 . Although this resulted in changes within the orders , it did not affect the relationship between them . Lilioid monocots were discussed but not formally recognized (commelinids , renamed from commelinoids , being the only supraordinal grouping in the monocots to be named) and Petrosaviaceae remained unplaced . The second version of the APG coincided with the third Monocot Conference (2003) , the findings from which , using additional molecular markers , helped to resolve some of the remaining questions regarding relationships within this assemblage . Petrosaviaceae was shown to be included in what Chase refers to as " liliids " and placed in order Petrosaviales , while Dioscoreales and Pandanales were demonstrated to be sister clades . Rapid advances in understanding monocot relationships necessitated the release of another revision of the APG classification (2009) , which incorporated these advances . Further definition of the relationships between lineages using multiple markers is continuing .

Textbooks and other sources produced in the last century are inevitably based on older classifications . Publications using versions of the APG system are now appearing and the World Checklist of Selected Plant Families from the Royal Botanic Gardens , Kew now uses the APG III system , as does the Angiosperm Phylogeny Website and hence the classification of the lilioid monocots shown in the cladogram below . The Kew botanists treat the monocots as falling into three major groupings : alismatid monocots (Acorales , Alismatales) , lilioid monocots (the five other non @-@ commelinid monocots) and commelinid monocots . They also organize their monocot research into two teams I : Alismatids and Lilioids and II : Commelinids . A similar approach is taken by Judd in his Plant systematics .

= = Phylogeny and evolution = =

The cladogram shown below displays the orders of Lillanae sensu Chase & Reveal (monocots) based on molecular phylogenetic evidence . Lilioid monocot orders are bracketed , namely Petrosaviales , Dioscoreales , Pandanales , Liliales and Asparagales . These constitute a paraphyletic assemblage , that is groups with a common ancestor that do not include all direct descendants (in this case commelinids which are a sister group to Asparagales) ; to form a clade , all the groups joined by thick lines would need to be included . While Acorales and Alismatales have been collectively referred to as " alismatid monocots " , the remaining clades (lilioid and commelinid monocots) have been referred to as the " core monocots " . The relationship between the orders (with the exception of the two sister orders) is pectinate , that is diverging in succession from the line that leads to the commelinids . Numbers indicate crown group (most recent common ancestor of the sampled species of the clade of interest) divergence times in mya (million years ago) .

While this is the most commonly understood relationship , Davis et al . (2013) using a combination of plastid genomes have suggested that if Asparagales is treated sensu stricto by excluding its largest and most atypical family , Orchidaceae then Asparagales sensu APG may not be monophyletic and that Orchidaceae and Liliales may be sister groups , and in turn are the sister of Asparagales . However , their data produced conflicting models . Zeng et al . (2014) using nuclear genes also found evidence for a sister relationship between Asparagales and Liliales . Although divergence time estimates within the lilioids have varied considerably , they were also able to obtain molecular clock estimates for the origin of the lilioids at approximately 125 mya (Cretaceous period) . On the other hand , a large data set using a combined analysis of nuclear , mitochondrial and

plastid genes together with nuclear phytochrome C was in agreement with the earlier APG relationships .

= = Subdivision = =

Five orders make up the lilioid monocots .

Petrosaviales Takht . (1997)

Dioscoreales R.Br. (1835)

Pandanales R.Br. ex Bercht . & J.Presl (1820)

Liliales Perleb (1826)

Asparagales Link 1829