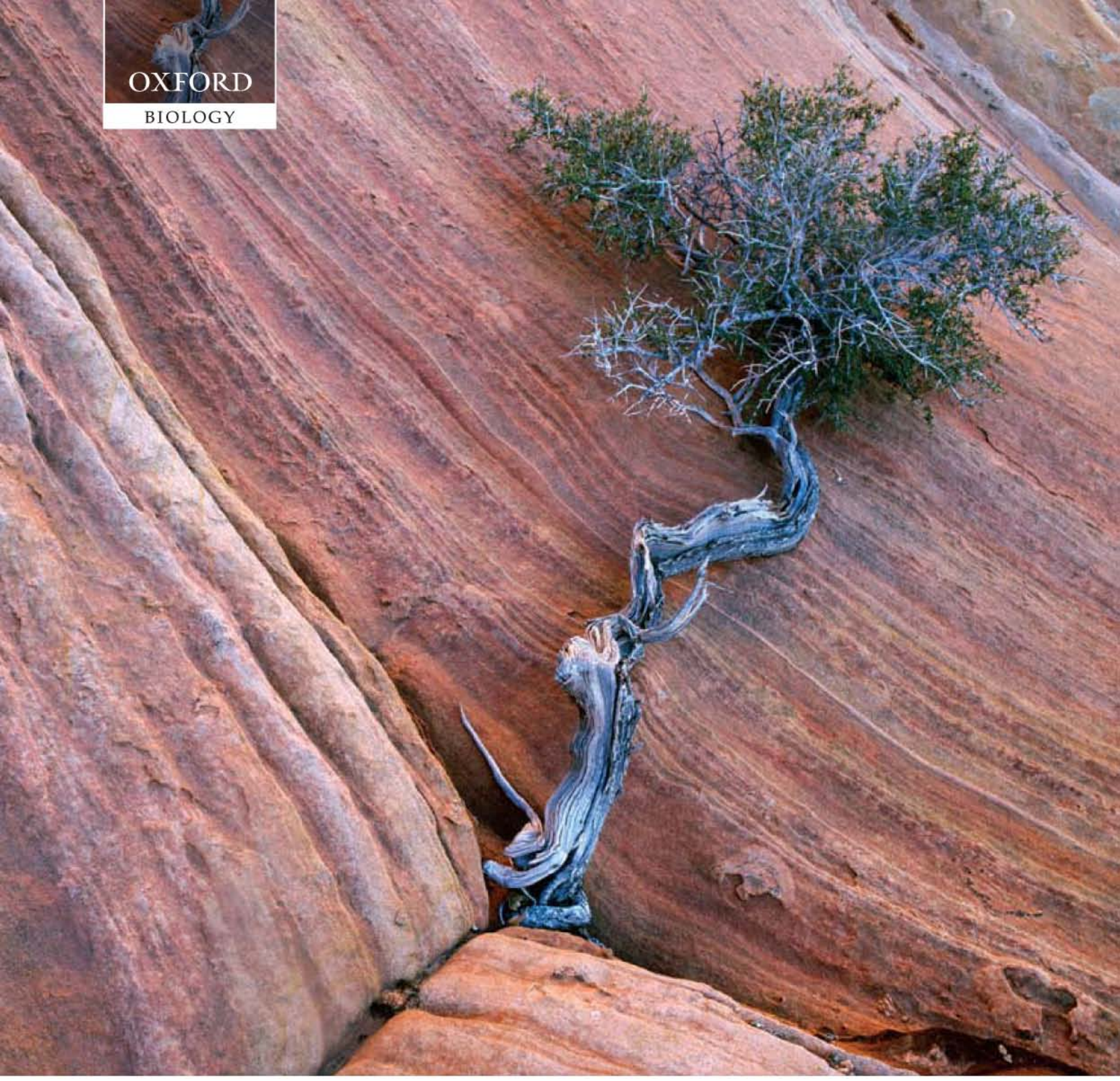

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# Monocots

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## Abstract

**Grasses, lilies, orchids, and many other plants from all biogeographical and climatic regions of the world constitute the monocotyledonous plants (monocots). They form a natural group of about 59,300 species in 81 families supported by morphological and molecular evidence and include many important crops, such as rice and corn, and ornamental plants. Previous analyses and new analyses presented here suggest a rapid radiation of all major monocot lineages during the Early Cretaceous (146–100 million years ago, Ma). Most extant monocot families were present at the Mesozoic–Cenozoic boundary (66 Ma).**

The monocots are a strongly supported monophyletic group comprising about 25% of the angiosperm diversity. They number 59,300 species (*1*) and are classified in 81 families and 10 orders by the Angiosperm Phylogeny Group (APGII) (*2*). A number of morphological characters are shared by most monocots, although these may have been (secondarily) lost in some lineages. The single cotyledon, leaves with linear venation, a basal meristem, scattered vascular bundles in the shoots and a lack of secondary growth of xylem and phloem, and sieve cell plastids are among the most obvious shared-derived morphological characters. Monocots usually possess trimerous flowers and uniaperturate pollen, which is most commonly monosulcate. Monocot characters also appear in other angiosperm groups. For example, sieve cell plastids occur in some Aristolochiaceae, scattered vascular bundles in Nymphaeaceae and some Piperaceae, and trimerous flowers with two perianth whorls are present in Nymphaeaceae and some magnoliids. Several monocots from different orders and families do have reticulate venation. This is, however, a derived condition thought to represent an adaptation to shaded habitats such as the forest understorey.

Acorales is a small wetland order, consisting of only one genus, *Acorus* (sweet flag). The small flowers are densely placed on a thick axis forming a spadix. This inflorescence produces a strong odor attracting pollinators. The plants possess ethereal oils in specialized cells.

The Order Alismatales contains 14 families, which all have a preference for aquatic or wetland habitats. They possess stems with small scales or glandular hairs within the sheathing leaves at the nodes, extrorse anthers, and a large embryo. Araceae, or the arum family (Fig. 1), includes the calla lily and taro. The inflorescence of these plants is a spadix, which is surrounded by a leaf-like bract. The small floating duckweeds, *Lemna* and other genera, have previously been segregated into the Family Lemnaceae, but are recognized as part of Araceae by APGII (*2*). Alismataceae, or the water plantains, have comparatively large flowers and usually two- to polyporate pollen. The embryo is strongly curved, and

**Fig. 1** Monocot representatives. Top row, from left to right: *Cypripedium calceolus* L., Orchidaceae; *Convallaria majalis* L., Asparagaceae, with a straw of *Carex digitata* L., Cyperaceae. Bottom row, from left to right: *Dracunculus muscivorus* Parl., Araceae; *Tillandsia usneoides* L., Bromeliaceae; *Cynosurus cristatus* L., Poaceae. Credits: Ola Lundström (*Dracunculus*) and C. L. Anderson (all other images).

C. L. Anderson and T. Janßen. Monocots. Pp. 203–212 in *The Timetree of Life*, S. B. Hedges and S. Kumar, Eds. (Oxford University Press, 2009).

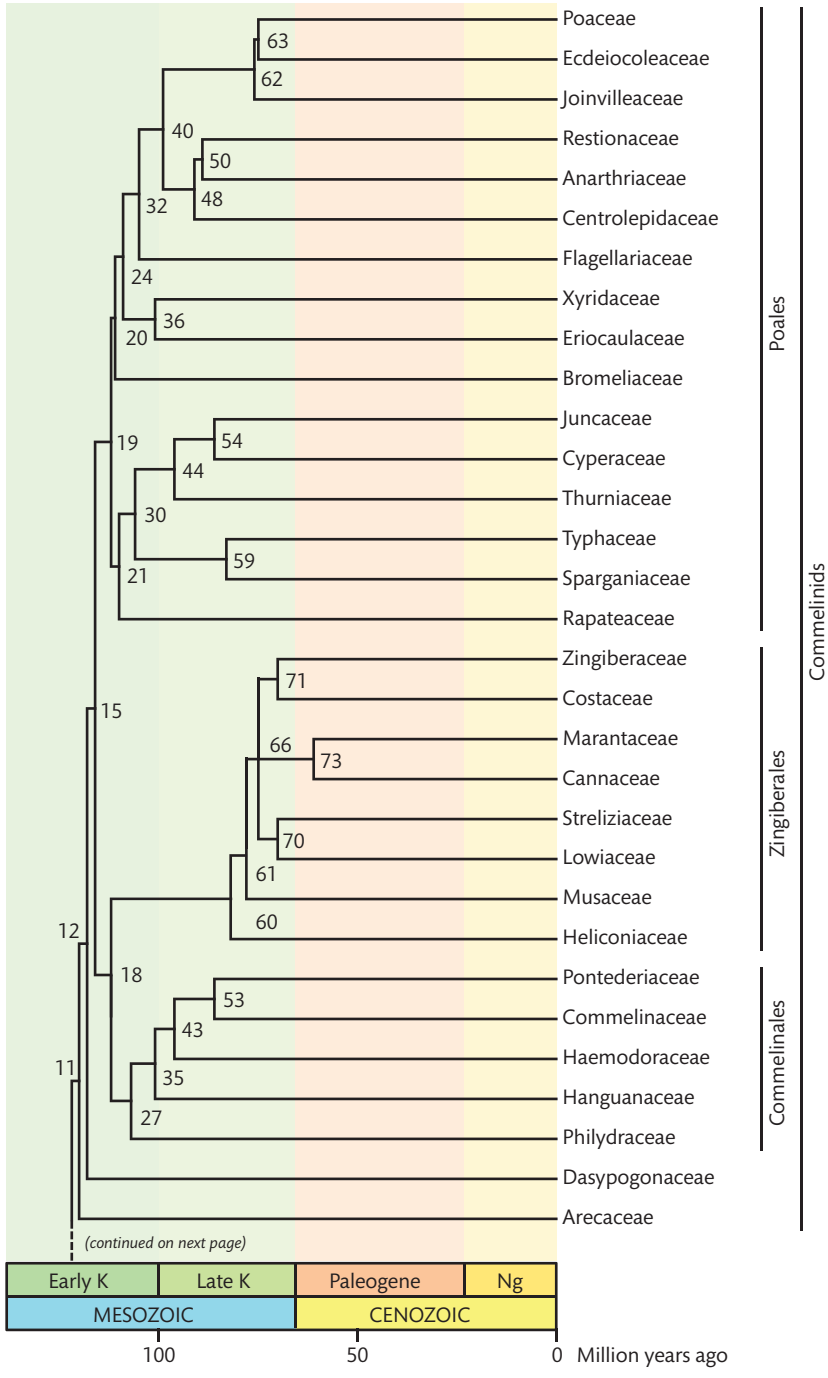


**Fig. 2** *Continues*

the plants possess white latex. Hydrocharitaceae, tape grasses, occur in both freshwater and marine habitats. The genera display several different pollination mechanisms: showy flowers above water pollinated by nectar-gathering insects, detached male flowers floating on the water surface until they meet a female flower, exploding anthers spreading pollen on the water surface, and underwater pollination are just some examples. In Alismatales we also find Potamogetonaceae, perennial herbs with either floating or submerged leaves and often jointed stems, Zosteraceae (seagrasses) consisting of a dozen species with ribbonlike leaves and creeping rhizomes,

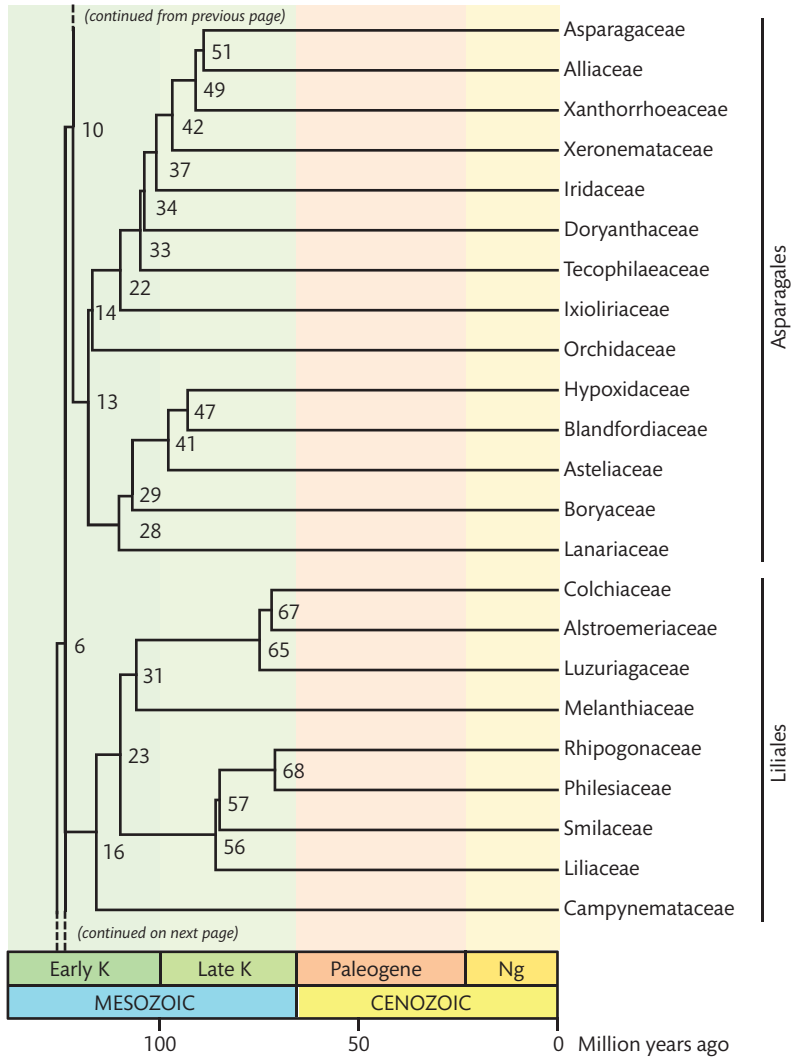


**Fig. 2** *Continues*

and a number of smaller families, often with only one genus, or even one species.

The core monocots include the orders Dioscoreales, Pandanales, Liliales, Asparagales and the commelinid orders Zingiberales, Commelinales, and Poales. The Families Petrosaviaceae (closest to the remainder of the core monocots) and Dasypogonaceae (closest to the Commelinales + Poales + Zingiberales) are not placed in any of the orders. Dioscoreales include the predominantly tropical Family Dioscoreaceae, twining vines with net-veined leaves, and with several members cultivated for their edible starchy tubers, called yams. Two other families belong to this order, Burmanniaceae and Nartheciaceae. Pandanales include the screw-pines, which are woody plants, branching trees, or shrubs, where the increase of trunk diameter is the result of primary thickening growth.

Liliales consists of 10 families, often with showy flowers, possessing tepals with basal nectaries. Liliaceae (tulips, lilies, and others) are herbaceous with bulbs or corms. They have actinomorphic, hypogynous flowers, often with various color patterns. Colchicaceae (autumn crocus and naked ladies) are a family of mainly seasonal perennials occurring in dry habitats in Africa and Eurasia, with a few exceptions confined to Australian rainforests and wet sclerophyllous forests. The presence of the highly poisonous alkaloid colchicine is a synapomorphy of the family. Within the Liliales we also find eight other families, examples being Alstroemeriaceae, with a distribution from Central America to southern South America,

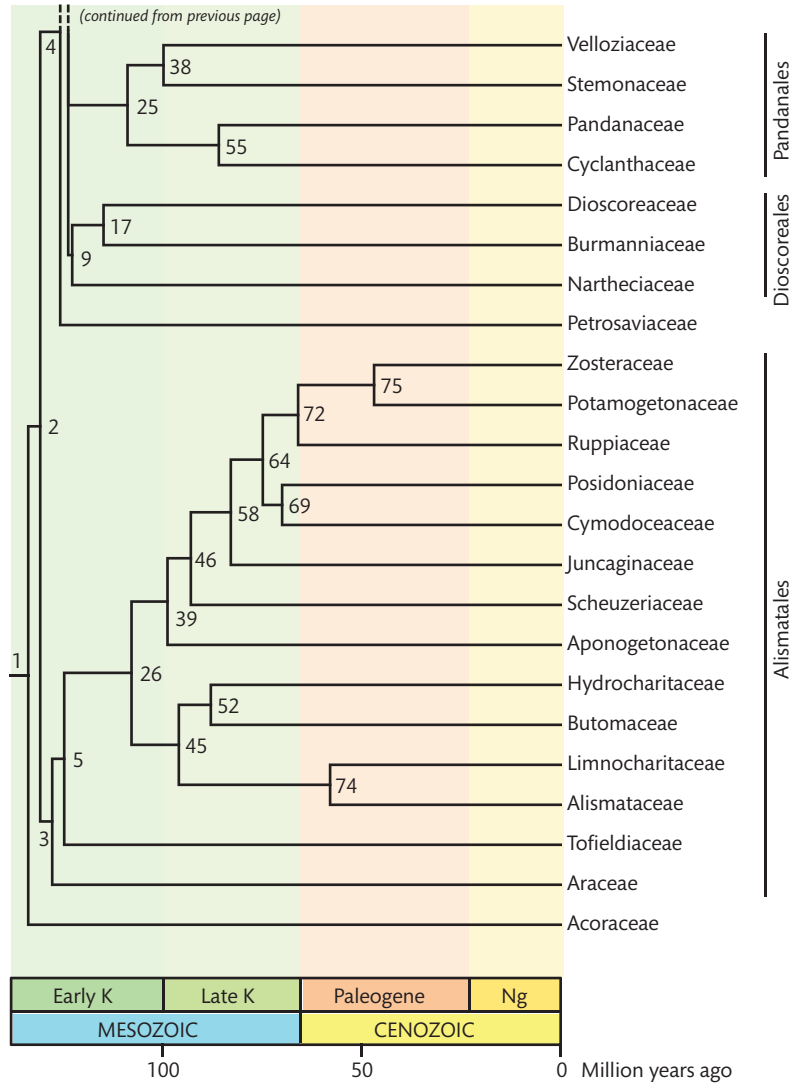


**Fig. 2** A timetree of monocots. Divergence times are shown in Table 1. *Abbreviations*: K (Cretaceous) and Ng (Neogene).

Campynemataceae, comprising a few species of perennial herbs in New Caledonia and Tasmania, Corsiaceae, which is a family of nonphotosynthesizing herbs and Smilacaceae, with representatives that typically have woody roots and a climbing or vining growth form.

Asparagales, according to APGII, include a large number of families. Their actual number varies according to the delimitation of individual families that is adopted. Orchidaceae, the orchids (Fig. 1), is the second largest of all plant families with about 20,000 known species, the majority being epiphytes in tropical rainforests. Floral organization is relatively constant with two whorls of tepals, and most often a column consisting of a single stamen adnate to the style and stigma. The flower forms and colors, however, display a great variety. Other examples of families within the Asparagales are Iridaceae (e.g., iris and saffron), Xanthorrhoeaceae (grass-tress, aloe, and asphodels), Alliaceae (onion, leek, and garlic), and Asparagaceae (asparagus, Lily-of-the-Valley (Fig. 1), agaves), the last two families now circumscribed to include a number of previously recognized families (Fig. 1).

The commelinids comprise about half of the species of monocots, and include the orders Arecales, Zingiberales, Commelinales, and Poales. The Arecales (palms) is a large order of woody tree-like or rarely climbing plants with pinnately or palmately veined leaves and trunks with primary thickening growth. Zingiberales comprise large, rhizomatous herbs with showy flowers. Well-known representatives are the banana in the Musaceae family, bird-of-paradise flower in Strelitziaceae, the canna-lilies in

**Table 1.** Divergence times (Ma) among monocots.

| Timetree | | Estimates | | | Timetree | | Estimates | | |
|---|---|---|---|---|---|---|---|---|---|
| Node | Time | Ref. (*24*)(a) Time | Ref. (*24*)(b) Time | Ref. (*24*)(c) Time | Node | Time | Ref. (*24*)(a) Time | Ref. (*24*)(b) Time | Ref. (*24*)(c) Time |
| 1 | 134 | 134 | 134 | 134 | 39 | 99 | 99 | 108 | 98 |
| 2 | 131 | 131 | 124 | 131 | 40 | 99 | 99 | 97 | - |
| 3 | 128 | 128 | 123 | 128 | 41 | 98 | 98 | 39 | 104 |
| 4 | 126 | 126 | 107 | 126 | 42 | 97 | 97 | 53 | 100 |
| 5 | 125 | 125 | 123 | 124 | 43 | 96 | 96 | 97 | 98 |
| 6 | 124 | 124 | 104 | 124 | 44 | 96 | 96 | 97 | 98 |
| 7 | 124 | 124 | 104 | 124 | 45 | 96 | 96 | 92 | - |
| 8 | 124 | 124 | 102 | 124 | 46 | 93 | 93 | 106 | 92 |
| 9 | 123 | 123 | 101 | 123 | 47 | 93 | 93 | 39 | 100 |
| 10 | 122 | 122 | 102 | 122 | 48 | 91 | 91 | 92 | 97 |
| 11 | 120 | 120 | 100 | 120 | 49 | 91 | 91 | 45 | 93 |
| 12 | 118 | 118 | 98 | 119 | 50 | 89 | 89 | 90 | 96 |
| 13 | 118 | 118 | 70 | - | 51 | 89 | 89 | 40 | 91 |
| 14 | 117 | 117 | 70 | 119 | 52 | 88 | 88 | 78 | 88 |
| 15 | 116 | 116 | 98 | 117 | 53 | 86 | 86 | 97 | 89 |
| 16 | 116 | 116 | 98 | 112 | 54 | 86 | 86 | 97 | 88 |
| 17 | 115 | 115 | 75 | 117 | 55 | 86 | 86 | 41 | 98 |
| 18 | 114 | 114 | 101 | 116 | 56 | 86 | 86 | 40 | 91 |
| 19 | 112 | 112 | 97 | 114 | 57 | 85 | 85 | 40 | 90 |
| 20 | 111 | 111 | 98 | 113 | 58 | 83 | 83 | 98 | 82 |
| 21 | 110 | 110 | 97 | 112 | 59 | 83 | 83 | 70 | 89 |
| 22 | 110 | 110 | 66 | 112 | 60 | 78 | 78 | 36 | 88 |
| 23 | 110 | 110 | 71 | - | 61 | 78 | 78 | 35 | 87 |
| 24 | 109 | 109 | 98 | - | 62 | 76 | 76 | 97 | 90 |
| 25 | 109 | 109 | 90 | - | 63 | 75 | 75 | 97 | 89 |
| 26 | 108 | 108 | 114 | - | 64 | 75 | 75 | 92 | - |
| 27 | 107 | 107 | 97 | 110 | 65 | 75 | 75 | 59 | 79 |
| 28 | 107 | 107 | 40 | 113 | 66 | 75 | 75 | 35 | - |
| 29 | 107 | 107 | 40 | 109 | 67 | 72 | 72 | 59 | 76 |
| 30 | 106 | 106 | 97 | - | 68 | 71 | 71 | 30 | 76 |
| 31 | 106 | 106 | 71 | 109 | 69 | 70 | 70 | 70 | 67 |
| 32 | 105 | 105 | 98 | 108 | 70 | 70 | 70 | 35 | 78 |
| 33 | 105 | 105 | 60 | 108 | 71 | 70 | 70 | 35 | 79 |
| 34 | 104 | 104 | 59 | 107 | 72 | 66 | 66 | 85 | 65 |
| 35 | 101 | 101 | 97 | 104 | 73 | 61 | 61 | 26 | 68 |
| 36 | 101 | 101 | 97 | 105 | 74 | 58 | 58 | 46 | 57 |
| 37 | 101 | 101 | 55 | 103 | 75 | 47 | 47 | 77 | 47 |
| 38 | 100 | 100 | 90 | 108 | | | | | |

*Note*: Node times in the timetree are obtained from a penalized likelihood (a) reanalysis of the data set in ref. (*24*). Estimates from (b) PATHd8 and (c) nonparameteric rate smoothing are also shown (*24*).

Cannaceae, and ginger and cardamom in Zingiberaceae. The largest family within the Commelinales is the Commelinaceae (spiderworts). The latter are more or less succulent herbs with colorful flowers often having fringed filaments. The Poales contain some families highly specialized for wind pollination, for example Poaceae (grasses, Fig. 1), Cyperaceae (sedges, Fig. 1), Juncaceae (rushes), and Restionaceae. Within Poales we find important crop plants like barley and rice (Poaceae) or pineapple in the Family Bromeliaceae, which contains genera with showy flowers pollinated by insects, birds, or bats. The Spanish moss (Fig. 1) and many other tropical epiphytes belong here.

Despite the monocots being recognized as a group since the seventeenth century (*3*), relationships of and within the group were poorly understood before molecular phylogenetic studies starting in the mid-1990s. Since then several larger studies using extensive samplings and molecular data from plastid, nuclear, and mitochondrial regions have been conducted (e.g., *3–8*). Today, there is a broad consensus about a stable backbone of the monocot phylogeny, even though some nodes are still not convincingly resolved. Mitochondrial phylogenies are in conflict with the generally accepted monocot phylogeny. However, the results from mitochondrial analyses have been suggested to suffer from error sources like paralog sampling and highly divergent evolutionary rates (*4, 8*).

Chase *et al.* (*9*) recognized six major monophyletic groups: Alismatales, Dioscoreales, Pandanales, Liliales, Asparagales, and commelinids (including Poales, Commelinales, Zingiberales, Dasypogonaceae, and Arecales). *Acorus* was concluded to be the closest relative of the rest of the monocots, but internal relationships between the larger clades were less well supported. Relationships between the orders have been extensively analyzed since Chase *et al.* and most studies propose similar topologies (e.g., *1, 3–8*). Current consenus has Acorales as closest to all other monocots. Alismatales attaches to the next higher node and is closest to the remainder of monocots, that is the so-called core monocots. Petrosaviaceae is branching off after Alismatales, and is hence the closest relative of all other core monocots. The remaining problematic area in the monocot topology concerns the relative position of Pandanales, Dioscoreales, and Liliales. The position of Liliales with respect to the other orders remains ambiguous. Recent multigene analyses (*5, 7*) suggest Pandanales and Dioscoreales to be closest relatives, although with moderate support. The same studies conclude that Asparagales and the commelinids are closest relatives, one study (*7*) obtaining high support and the other (*5*) obtaining moderate support for this group. To this date, the majority of phylogenetic analyses tend to support Liliales as the closest relative to the Asparagales-commelinids-clade (*2, 5–7*). Following molecular phylogenetic studies, the traditional distinction between Liliales and Asparagales based mostly on characters of the seed and nectaries has been revised and major taxonomical rearrangements have been made. Most notably, two large families earlier classified within Liliales, the Iridaceae and Orchidaceae, are now transferred to Asparagales (*2*). Within the Liliales, the main Family Liliaceae is currently more narrowly circumscribed than in earlier taxonomical treatments (*10*). Within the commelinid clade Arecales are closest to the remainder, most likely followed by Dasypogonaceae. Poales and Zingiberales form a clade, which is closest to Commelinales (*11*). Detailed studies of phylogenetic relationships within monocot orders are available for Asparagales (*12*), Dioscoreales (*13*), Liliales (*13, 14*), Poales (*11*), and Zingiberales (*15*).

A major surprise arising from molecular phylogenetic reconstructions is the position of the Family Hydatellaceae (formerly classified in the Poales), which is now suggested not to be a monocot, but most closely related to the Nymphaeales (*16*). The closest relative of the monocots has yet to be determined. A number of studies suggest eumagnoliids (with slightly different definitions of the latter) (*8*, *17, 18*), other studies *Ceratophyllum* (*19–21*), and others Piperales (*22*) or Laurales (*23*).

The largest data set employed for monocot dating so far has been compiled by Janssen and Bremer (*24*). There are some differences in the tree topology derived from the Janssen and Bremer data set (878 taxa, or "800+ data set") as compared to the more recent phylogenetic studies. However, it has been shown (*25*) that the influence of minor changes in topology on divergence time estimation is small compared to the influence of alternative fossil calibrations, methods, and taxon sampling. The differences between the topology derived from the 800+ data set and recent phylogenetic studies are all within orders, not in the monocot backbone. Within the Alismatales, Aponogetonaceae branches off before Scheuchzeriaceae, instead of the opposite, and Ruppiaceae is the closest relative of the Potamogetonaceae–Zosteraceae clade instead of being closest to Posidoniaceae. The orders Dioscoreales and Pandanales are not closest relatives, but are collapsed into a trichotomy with the rest of the core monocots. The Orchidaceae is not the closest relative of the rest of the Asparagales in the 800+ data set. Instead, there is a basal split between the Orchidaceae

and the clade consisting of Boryaceae, Blandfordiaceae, Lanariaceae, Asteliaceae, and Hypoxidaceae. Internal nodes of the latter clade generally receive low support, and the branching order differs substantially between studies. Within the Commelinales, Commelinaceae is closest to Pontederiaceae, and this clade constitutes the closest relative of Haemodoraceae. Within the Poales, Restionaceae and Anarthriacae form a clade, with Centrolepidaceae as its closest relative, as opposed to the more recently suggested Restionaceae–Centrolepidaceae relationship, with Anarthriacae branching off before (*7*). Flagellariaceae are the the closest relative of a larger clade consisting of Restionaceae–Anarthriacae–Centrolepidaceae and Joinvilleaceae–Ecdeiocoleaceae–Poaceae, instead of being closest to the latter clade only.

The divergence time of the living lineages of monocots has been estimated in a number of studies: Savard *et al.* (*26*) proposed 200 Ma, Goremykin *et al.* (*27*) 160 Ma, and Leebens-Mack *et al.* (*28*) 135–131 Ma. Bremer (*29*) estimated the split between Acorales and the rest of the monocots to 134 Ma, with a possible age span of 147–121 Ma. The age 134 Ma coincides with the earliest recorded fossil angiosperm pollen (*30*), and could therefore be regarded as plausible. This age was later used as a fixed age constraint for the monocot root node by Janssen and Bremer (*24*). The Janssen and Bremer study is the dating study with the most extensive sampling (800+ data set) of monocot taxa. The authors use evidence from eight reference fossils to calibrate a nonparametric rate smoothing (*31*) analysis. The study revealed that all major lineages diverged in the Early Cretaceous (146–100 Ma), with most families being present at the Mesozoic–Cenozoic (M-C) boundary. Uncertainties associated with each node (divergence age estimate) were suggested to be in the order of ±10–20 million years.

Developments following Janssen and Bremer's study include new molecular dating methods and extended possibilities of incorporating fossil constraints in dating analyses, plus new fossil discoveries that may be used for constraining and calibrating divergence time estimations of monocots. We have compared the author's original results from NPRS dating by reanalyzing the same molecular dataset using the penalized likelihood (PL) (*32*) as well as the PATHd8 (*33*) methods, and included additional age constraints from five new fossils. We have utilized the earliest occurrence of extinct lineages of Araceae (*34*) to provide a minimum age (120 Ma) for the split between Alismatales and the core monocots. A fossil assigned to the Family Triuridaceae (*35*) gives a minimum age of 90 Ma for the living lineages of Pandanales. The placement of this fossil has, however, been disputed (*36*). Fossil grasses belonging to different lineages within Poaceae (*37*) assign a minimum age of 65 Ma to the living lineages of Poaceae. A fossil belonging to the palm subtribe Mauritiinae (*38*) attributes a minimum age of 65 Ma to the living lineages of Arecaceae. Finally, pollen belonging to the African Restionaceae clade (*39*) was used as a minimum age constraint for the living lineages of Restionaceae.

Monocots are an assemblage of many lineages rather heterogeneous with respect to life forms, ecological preferences, and hence most likely also with respect to their evolutionary history. Divergence time analysis of the entire monocots will hence face the problem of rate heterogeneity in different parts of the tree. For example, phylograms reveal that palms have very short internal branches, whereas grasses have long branches, suggesting a slowdown in evolutionary rate in the former group, and a speedup in the latter (*40*). In such heterogeneous trees, the dating algorithm and the number of fossil constraints used may have considerable influence on age estimates (*33*). Furthermore, closest relatives with many vs. few representatives, with highly different branch lengths, with different habits (e.g., woody vs. herbaceous), and with long vs. short generation times frequently occur in the monocot tree and may account for further analytical problems. Age estimates of such lineages should be regarded as a rough approximation and should be interpreted with caution. Herein, we compare divergence time estimates from three different methods highlighting where major discrepancies occur and briefly discussing possible causes.

Our reanalysis using PL yields highly similar age estimates to the NPRS study (see Table 1). Within Poales, the PL age estimates are slightly older, with deviations up to 15 million years and therefore within the suggested error range for the NPRS analysis (*24*). Age estimates obtained with PATHd8 sometimes differ substantially from those obtained with PL and NPRS. Except for the divergences of the families within the Alismatales from their closest relatives (see Fig. 2), PATHd8 generally obtains younger ages than PL or NPRS (see Table 1). Divergences of families within Pandanales and Dioscoreales differ in the magnitude of 20 Ma. Within Liliales, the estimates differ in the magnitude of 40 Ma. Divergences of families within the Asparagales deviate as much as 50–70 Ma from results obtained with PL and NPRS. PATHd8 also often suggests more rapid divergences.

The divergence of Alismatales from its closest relative was dated to 131 Ma, and the divergence of all living

lineages of Alismatales to 128 Ma by Janssen and Bremer. In the PL analysis presented here, both divergence events receive the same ages, while the PATHd8 analysis yields somewhat younger ages, 124 and 123 Ma, respectively. The oldest fossil that can be assigned to the Alismatales (*34*) is from the Early Cretaceous, about 120–110 Ma old, which means that all of the three methods yield results in agreement with the fossil record. Janssen and Bremer estimated the divergence of Petrosaviaceae from its closest relative to 126 Ma, and the divergence of its living lineages to 123 Ma. The former age estimate is also obtained using PL, whilst the latter is then 121 Ma. PATHd8 estimates both divergence events at 107 and 41 Ma, respectively, which is substantially younger.

The split of Dioscoreales from their closest relatives was dated to 124 Ma, and the divergence of living lineages to 123 Ma in Janssen and Bremer (*24*). We obtain the same results using PL, whereas PATHd8 estimates these divergences at 104 and 101 Ma, respectively. The NPRS derived age for the split of Pandanales from its closest relative is 124 Ma, that for the divergence of living lineages of Pandanales is 114 Ma. Using PL, the former age is identical and the latter age is 109 Ma. PATHd8 yields slightly younger ages 104 and 90 Ma, respectively. The age for the divergence of Liliales from its closest relative is estimated to 124 Ma by both NPRS and PL. The divergence of living lineages of Liliales is estimated to 117 Ma by NPRS and 115 Ma by PL. PATHd8 suggests ages that are substantially younger, 102 and 75 Ma, respectively.

The divergence of Asparagales from their closest relative is dated to 122 Ma by both NPRS and PL, while PATHd8 estimates this age to 102 Ma. Both NPRS and PL suggest a gradual divergence within the living lineages of that order, starting at 119 and 118 Ma, respectively. PATHd8 suggests a much younger divergence time for the living lineages, 70 Ma, and rapid divergence at the internal nodes of the Asparagales at 40 Ma.

The split of Arecaceae from their closest relative is dated to 120 Ma by both NPRS and PL, the divergence of living lineages of that family is estimated to 110 Ma by NPRS and 97 Ma by PL. PATHd8 gives the ages 100 and 65 Ma, respectively. Dasypogonaceae diverged at 120 Ma (NPRS and PL) or 100 Ma (PATHd8) from its closest relative, and the living lineages diverged at 100 Ma (NPRS), 88 Ma (PL), or 39 Ma (PATHd8), respectively.

The most recent common ancestor to the most closely related Commelinales and Zingiberales receives the age 114 Ma according to NPRS, 112 Ma according to PL, and 97 Ma according to PATHd8. The living lineages of Commelinales diverged at 110 Ma (NPRS) or at 107 Ma (PL), followed by a gradual divergence. PATHd8 estimates the divergence of Commelinales from Zingiberales to 97 Ma, with a rapid divergence of all families within Commelinales. Living lineages of Zingiberales are estimated to be younger than the living lineages of Commelinales by all methods: 88 Ma (NPRS), 78 Ma (PL), and 36 Ma (PATHd8). The young age obtained with PATHd8 suggests a very rapid divergence of the living lineages of Zingiberales, while these start to diverge in the mid-Upper Cretaceous, at about 78 Ma, according to the PL analyses.

The divergence of Poales from their closest relative is estimated to 117 Ma (NPRS), 116 Ma (PL), or 98 Ma (PATHd8). The living lineages diverged at 113 Ma (NPRS), 111 Ma (PL), or 98 Ma (PATHd8). PATHd8 thereby suggests an almost "explosive" radiation of the numerous poalean families at the boundary between the Lower and Upper Cretaceous (~100 Ma), while the other methods suggest a slower radiation, starting about 15–20 Ma earlier, in the mid-Lower Cretaceous, with most family stem groups appearing in the Upper Cretaceous, 40 Ma later.

The differences between PL and NPRS on one hand, and PATHd8 on the other, might be due to systematic errors (*33*, *41*). The first two methods smoothen or minimize age differences between mother and daughter lineages, while PATHd8 minimizes age differences between closest relatives. Without enough calibration points, both approaches can result in a number of systematic errors, for example NPRS and PL overestimating ages for large groups with short branches, and PATHd8 underestimating the ages for the same group. In the monocot data set, some groups are likely to suffer from this phenomenon, and from further analytical problems (*41*), and their age estimates should therefore be used with caution, regardless of the method employed. These groups include Arecaceae, Orchidaceae compared to the rest of the Asparagales, age estimates within Zingiberales and Commelinales, and the family Poaceae. For further discussion of methodological issues, see (*41*).

Several studies focusing on divergence time estimation within monocot orders and families have been published and will briefly be compared to results obtained in the analysis by Janssen and Bremer (*24*) and during our reanalysis of their data set. Two large studies, one focusing on Poales (*11*) and one on monocots as a whole (*24*), use NPRS to estimate divergence times and present deviating age estimates for families within the Poales. This seems to be a methodological artifact related to the number of taxa sampled. A larger taxon sampling is susceptible to yield older ages (*24*). However, age estimates are

in general differing less than 20 Ma for the divergences of living lineages of the respective families, and less than 10 Ma for divergences among most closely related families. The largest differences are found in Poaceae, Cyperaceae, and Juncaceae, and also in Restionaceae. Our reanalysis of the 800+ data set gives age estimates comparable to other published results, except for the divergence times of Arecaceae and Bromeliaceae that are probably being underestimated by the PATHd8 method.

In a study of divergence times within Liliales (*14*), similar ages were obtained using NPRS and the mean-path length method (MPL) (*42*). Reanalysis of the 800+ data set using PATHd8 also yielded similar ages. Most differences among these three analyses are in the magnitude of 10 Ma. However, the NPRS and PL analyses of the 800+ data set suggest much older ages for the divergences from their respective closest relatives and for the divergences of living lineages for the order Liliales, as well as for the Families Liliaceae, Melanthiaceae, Campynemataceae, and Luzuriagaceae.

In a study of divergence dates within Zingiberales (*15*) a data set comprising three genes, 24 ingroup taxa (21 of them identical to the 800+ data set), and two calibration points were used and analyzed with three methods: NPRS, PL, and a local clock approach. Similar estimates were obtained for all three methods in this study. The age estimates show considerable differences compared to the 800+ data set. All analyses suggest a rapid radiation of Zingiberales, but at different times: 110–100 Ma according to Kress and Specht (*15*), 88 Ma according to Janssen and Bremer (*24*), and 78 Ma (PL) or 36 Ma (PATHd8) according to this reanalysis of (*24*).

Linder and Rudall (*43*) compiled a chronogram of Poales using Janssen and Bremer (*24*) and Bremer (*11*). Nodes lacking divergence time estimates in either of these studies were evenly spread between dated nodes, in an attempt to approximate ages within the graminid and xyrid clades. Datings have also been done for the Families Costaceae (*44*), Restionaceae (*39*), and Rapateaceae (*45*). Since these studies focus on nodes within monocot families, we will not review them here.

Few monocot fossils have been discovered in early and mid-Cretaceous strata (*36*). This scarcity does not reflect a true lack of monocots in this time period, but rather taphonomic filtering of herbaceous plants (i.e., they are less likely to be preserved). Furthermore, the frequent lack of distinctive features in monocot pollen likely accounts for early monocot fossil pollen records remaining unrecognized. The earliest indisputable monocot found so far, *Mayoa portugallica*, from the late Barremian–early Aptian (~125 Ma) of Portugal (*34*), is suggested to be part of the lineages of Arales that split off before the divergence of the living lineages. Accordingly the minimum age of monocots as evidenced by the fossil record is 120 Ma, which is relatively close to the calibration age of the root node used for the analysis of the 800+ data set (134 Ma). The fossil record of Alismatales also extends back to the early Cretaceous (*46*). The fossil angiosperm *Pennistemon/Pennipollis* might be related to Alismatales and the first *Pennipollis*-type pollen occurs around the Barremian–Aptian boundary (*47*). The earliest diverse monocot flora containing flowers, fruits, and stems from various monocot plants occurs in Maastrichtian (71–66 Ma) strata in India (*36*). From the middle of the Late Cretaceous (100–66 Ma), the monocot fossil record provides evidence that monocots were diverse and widespread (*48*). Still many monocot orders have sparse or no records in the Late Cretaceous.

Several biogeographical studies of groups within the monocots have been published (see e.g., *49–53*). A biogeographical analysis of the whole monocot group was conducted by Bremer and Janssen (*54*), who combined their earlier dating with the 800+ data set in a dispersal-vicariance analysis. They were focusing on the continental distribution of monocots, using widely circumscribed areas for the analysis. They concluded that a majority of the monocots have a South Gondwanan evolution, since the Australasian and South American optimizations dominate in the deeper nodes of the phylogeny. It is however not possible to specify an ancestral distribution for the most recent ancestor of all monocots, since the Alismatales have many widespread representatives, that obviously are easily spread due to their aquatic habit.

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