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Kåre Bremer
Uppsala University

Thomas Janssen
Muséum National d'Histoire Naturelle

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GONDWANAN ORIGIN OF MAJOR MONOCOT GROUPS INFERRED FROM DISPERSAL-VICARIANCE ANALYSIS

KÅRE BREMER^{1,3} AND THOMAS JANSSEN²

¹*Department of Systematic Botany, Evolutionary Biology Centre, Norbyvägen 18D, SE-752 36 Uppsala, Sweden;*

²*Muséum National d'Histoire Naturelle, Département de Systématique et Evolution, USM 0602:*

Taxonomie et collections, 16 rue Buffon, 75005 Paris, France

³*Corresponding author (kare.bremer@adm.su.se)*

ABSTRACT

Historical biogeography of major monocot groups was investigated by biogeographical analysis of a dated phylogeny including 79 of the 81 monocot families using the Angiosperm Phylogeny Group II (APG II) classification. Five major areas were used to describe the family distributions: Eurasia, North America, South America, Africa including Madagascar, and Australasia including New Guinea, New Caledonia, and New Zealand. In order to investigate the possible correspondence with continental breakup, the tree with its terminal distributions was fitted to the geological area cladogram ((Eurasia, North America), (Africa, (South America, Australasia))) and to alternative area cladograms using the TreeFitter program. The results indicated that monocot evolution is related to the comparatively late (Eocene) connection (via Antarctica) and break up of South America and Australasia, but not to the much older connections and separations of the other areas. The family phylogeny and distributions were also subjected to dispersal-vicariance analysis using the DIVA program. A prevalence of Australasia and South America among the DIVA optimizations inside core monocots (i.e., monocots excluding *Acorus* and Alismatales), and especially so in Liliales, Asparagales, and at deep nodes in the core monocot and commelinid phylogeny, points to a South Gondwanan origin for those major groups; South Gondwana comprises South America (at least southern South America), Antarctica, and Australasia. Africa and the Northern Hemisphere were presumably not parts of the ancestral area for core monocots and commelinids.

Key words: biogeography, commelinids, dispersal, Gondwana, monocots, origin, vicariance.

INTRODUCTION

Monocots are worldwide in distribution and important or even dominating representatives of many plant communities. The Angiosperm Phylogeny Group (APG II 2003) classified monocots in 81 families in ten orders (with two families unplaced to order). The largest families are predominantly tropical in distribution, such as Araceae, Arecaceae, Eriocaulaceae, Orchidaceae, and Zingiberaceae, or worldwide with large subgroups concentrated either in the Northern or Southern Hemisphere, for example in Alliaceae, Asparagaceae, Cyperaceae, Iridaceae, and Poaceae. Many of the small families are, however, restricted to the Southern Hemisphere. This raises the question of whether monocots originally came from the Southern Hemisphere continents (cf. Raven and Axelrod 1974).

Reconstruction of the major outline of monocot phylogeny has made considerable progress during the last few years. Chase et al. (2000) proposed a first phylogeny including all orders, based on a large data set including three DNA regions (*rbcL*, *atpB*, and 18S rDNA [ribosomal DNA]), however with a comparatively limited taxon sampling. More detailed treatments are available for several orders (papers in Rudall et al. 1995 and in Wilson et al. 2000; Givnish et al. 1999; Kress et al. 2001; Vinnersten and Bremer 2001; Bremer 2002; Caddick et al. 2002). With the results of the available studies taken together we have at present a rather well-supported phylogeny resolved down to the family level. This provides us with a solid basis for research on biogeography and evolution of this group.

Recently, we presented a dated phylogeny of monocots (Janssen and Bremer 2004), with a representation of more than 800 genera from all but two of the 81 families. In that analysis we used nonparametric rate smoothing (Sanderson 1997) with *rbcL* sequences to infer divergence times of major lineages and crown node ages for most monocot families. It is obvious that considerable monocot diversification took place during the Early Cretaceous with most families already present at the Cretaceous-Tertiary boundary. Hence, evolution of major monocot groups is likely to be related to plate tectonics and continental breakup, at least in the Southern Hemisphere.

A number of biogeographical analyses of particular monocot groups have already been published (Linder 1987; Seberg 1988; Simpson 1990; Conran 1995; Givnish et al. 1999; Vinnersten and Bremer 2001; Bremer 2002). Several of these studies indicate that commelinid groups, Commelinales and Poales in particular, evolved in the Southern Hemisphere, corroborating earlier hypotheses by Raven and Axelrod (1974). In order to illuminate the geographical origin of major monocot groups we here present a biogeographical analysis of the dated monocot phylogeny with ages and interrelationships of monocot families.

MATERIALS AND METHODS

The dated phylogeny is taken from our earlier study on the age of major monocot groups (Janssen and Bremer 2004). We downloaded all monocot *rbcL* sequences available from GenBank with the goal to sample as many genera

as possible. Each genus is represented by a single sequence. The data set consists of the *rbcL* sequences of 878 genera from 79 families representing all ten orders of monocots. A topological backbone constraint tree was constructed combining well-supported clades from earlier studies focused on phylogenetic reconstruction of various monocot groups and based on data sets including two or more genes. All orders and families were constrained to be monophyletic. No constraints were applied within families. Ordinal interrelationships were adopted from APG II (2003) and interrelationships of families within orders were constrained using sufficiently supported nodes, that is, with bootstrap or jackknife frequencies of 85% or higher, from Les et al. (1997), Fay et al. (2000, Asparagales), Kress et al. (2001, Zingiberales), Vinnersten and Bremer (2001, Liliales), Bremer (2002, Poales), and Caddick et al. (2002, Dioscoreales). A completely resolved tree was obtained by a heuristic PAUP* vers. 4.0b6 search (Swofford 2001) with topological constraints enforced as specified above. Branch lengths were obtained using PAUP* vers. 4.0b6 with maximum likelihood and the GTR + Γ model of sequence evolution; substitution rates were assumed to follow a gamma distribution with a shape parameter of 0.5. The tree with its corrected branch lengths was subjected to nonparametric rate smoothing as implemented in the r8s program (Sanderson 1997, 1999). Calibration was done setting the crown group age of monocots to 134 Mya (million years ago) following Bremer (2000). For further details of tree construction and dating, see Janssen and Bremer (2004).

The major branches of the tree with all lineages leading to families are shown in Fig. 1. Resolution within families is not shown. The branch lengths correspond to estimated time durations. In our earlier paper we discussed possible error sources in the dating (Janssen and Bremer 2004). The uncertainty in dating particular nodes is probably in the order of ± 10 –20 Mya. This needs to be taken into consideration in the biogeographical analysis, when comparison with continental separation is made.

For the biogeographical analysis, we used families as terminal taxa. Although our phylogenetic tree involved more than 800 genera, the sampling and the supported resolution within families are insufficient for biogeographical analysis of all monocots at the genus level. For the families, we have defined five major areas to describe their distribution: Eurasia, North America, South America, Africa including Madagascar, and Australasia including New Guinea, New Caledonia, and New Zealand. For a more detailed biogeographical analysis (e.g., at the genus level) it would be appropriate to distinguish two or more areas within South America, Africa, and Australasia. In South America groups distributed either in southern South America with the Andes, or northern South America made up of the Amazon basin and the Guayana and Brazil shields, respectively, often display different biogeographical relationships (Crisci et al. 1991; Sanmartin and Ronquist 2004). Similarly, sometimes it is appropriate to distinguish tropical Africa from southern Africa. In Australasia, the islands of New Guinea, New Caledonia, and New Zealand should, of course, be distinguished in a more detailed study. The present analysis is focused on continental distributions, and hence we considered the more widely circumscribed areas to be sufficient. More resolved

areas would lead to numerous distributions for each family and corresponding difficulties in analysis and interpretation of the results.

The present distribution of each family, that is, its presence or absence in any of the five areas Eurasia, North America, South America, Africa, and Australasia, was recorded from information mainly taken from Kubitzki (1998a, b) and is given after the family names in Fig. 1. No a priori hypotheses regarding ancestral areas for families were attempted. In a few cases, rare occurrences in other continents were interpreted as comparatively recent dispersals; that is, the family was assumed not to be originally present in these outlying areas (Givnish et al. 2000; Bremer 2002). Hence, Rapateaceae were treated as being exclusively South American (one West African genus), Bromeliaceae as North and South American (one West African genus), Restionaceae as African and Australasian (one species in Chile), and Stemonaceae as Eurasian and Australasian (one species in southeastern North America).

The family phylogeny in Fig. 1 with the present distributions of the families is the input data for the biogeographical analysis. In order to investigate the possible correspondence with continental breakup, the tree with its terminal distributions was fitted to the geological area cladogram using TreeFitter (Ronquist 2002a, b; Sanmartin and Ronquist 2002, 2004). The geological area cladogram for the five areas is ((Eurasia, North America), (Africa, (South America, Australasia))) (Hallam 1994; McLoughlin 2001). The monocot tree was also fitted to all 104 alternative area cladograms (for five terminals there are 105 possible cladograms).

TreeFitter estimates the total cost in fitting the organism tree to the area cladogram. The total cost is calculated as the sum of the costs for all necessary vicariance, duplication (= speciation within an area), extinction, and dispersal events postulated in fitting the organism tree to the area cladogram. The costs for individual events were set to the default values in TreeFitter, that is, 0.01 for vicariance and duplication events, 1.0 for extinction, and 2.0 for dispersal events (see Ronquist 2002a and Sanmartin and Ronquist 2004 for an explanation of these cost assignments). Alternatively, the costs were set according to the maximum vicariance (= maximum codivergence) approach (Page 1995; Ronquist 1998), that is, -1 for vicariance and 0 for duplication, extinction, and dispersal events.

Widespread terminals are treated by TreeFitter according to different options, depending on the age of the terminals in relation to area separation. Several families are older than the breakup of the trans-Antarctic connection between South America and Australasia, but since most families are younger than the breakup of all other connections between the five continental areas (see Fig. 1 and Discussion), widespread family distributions were treated under the Recent option, which assumes these distributions to be the result of dispersal. Furthermore, the Recent option forces vicariance events onto ancestral nodes in the phylogeny and is, therefore, more powerful in separating phylogenetically-constrained distribution patterns from random data in the randomization test used here (Sanmartin and Ronquist 2004).

A randomization test implemented in TreeFitter was used to assess the statistical significance of the fit between each of the 105 possible area cladograms and the monocot tree.

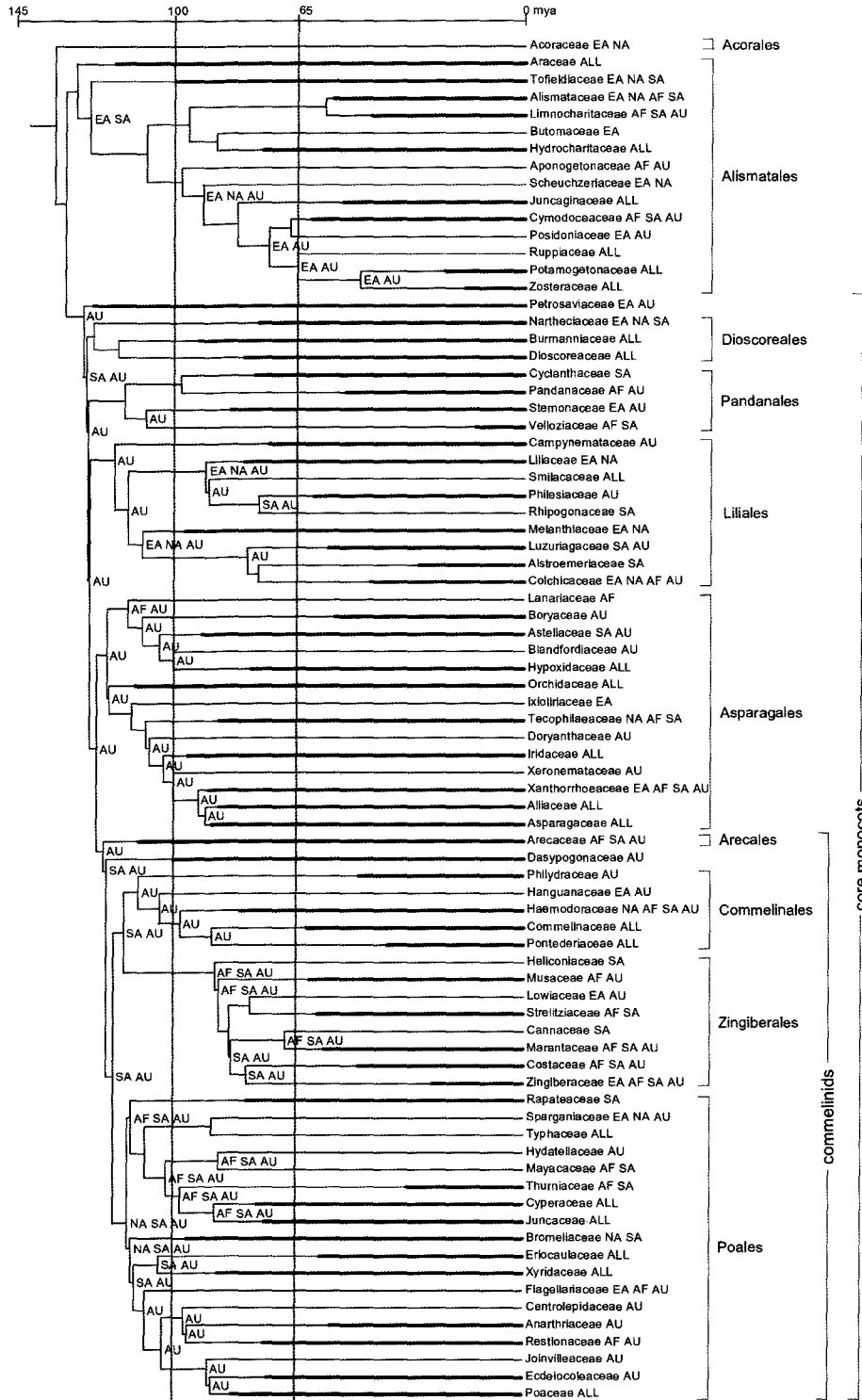


Fig. 1.—Dated phylogeny of monocot flowering plant families from Janssen and Bremer (2004) with area optimizations from dispersal-vicariance analysis. Branch lengths are proportional to time duration. Thick bars show inferred crown node ages (absent in families represented by a single terminal). The two vertical lines show the Mid-Cretaceous 100 Mya and the Cretaceous–Tertiary boundary 65 Mya. Present distributions for the families are given after each family name. Areas found by the dispersal-vicariance analysis are given for nodes with less than four areas. Only areas are shown, not the various combinations of the areas found in different optimizations; EA = Eurasia, NA = North America, AF = Africa, SA = South America, AU = Australasia, ALL = all five areas.

TreeFitter generated 1000 random data sets for which the terminal distributions in the monocot tree and the areas in the area cladogram were randomly permuted. The cost of fitting each area cladogram onto the nonpermuted monocot tree could then be compared to the cost over each of the 1000 random data sets. The significance (P) value was calculated as the percentage of random data sets that fit the area cladogram better than the nonpermuted monocot tree.

The family phylogeny and distributions were also subjected to dispersal-vicariance analysis using DIVA (Ronquist 1997a, b). DIVA optimizes distributions over the whole tree, allowing for vicariance and duplications, but penalizing dispersals and extinctions. DIVA finds all most-parsimonious distributions for all nodes of the tree. Hence, with DIVA it is possible to hypothesize ancestral distributions for major groups, that is, for the nodes throughout the tree.

RESULTS

The cost for fitting the monocot tree to the 105 alternative area cladograms varied between 21.77 and 40.58 using TreeFitter's default cost settings. The cost for fitting the tree to the geological area cladogram was 25.69 and there were nine alternative area cladograms with lower fit costs. Similar results were obtained with maximum vicariance cost settings. The randomization test gave a nonsignificant P -value of 0.079 for the geological area cladogram and significant P -values between 0.007 and 0.046 for the nine alternative area cladograms with lower fit costs. Since there are nine less costly alternatives than the geological area cladogram in fitting the monocot tree, and since the fit costs for these nine alternative area cladograms are significantly better than random, whereas this is not the case for the geological area cladogram, it cannot be concluded that the evolution of monocots is related to the entire sequential breakup of the five areas Eurasia, North America, Africa, South America, and Australasia. However, if the nine area cladograms with low fit costs are examined, it is seen that they all have South America and Australasia as sister areas, as in the geological area cladogram, but varying interrelationships of the other three areas. The TreeFitter analysis, therefore, clearly indicates that monocot evolution is related to the comparatively late (Eocene, see below) connection and breakup of South America and Australasia, but not to the much older connections and separations of the other areas.

Area optimization results from biogeographical analysis using DIVA are shown in Fig. 1. The exact alternative area combinations found by DIVA at each node are omitted; the areas given at the nodes are those involved in the different optimizations. Alismatales are widespread and show a high number of possible area combinations at most nodes. A prevalence of Australasia and South America among the optimizations inside core monocots (i.e., monocots excluding *Acorus* L. and Alismatales), and especially so in Liliales, Asparagales, and at deep nodes in the core monocot and commelinid phylogeny, points to a South Gondwanan origin for those major groups. South Gondwana comprises South America (at least southern South America), Antarctica, and Australasia. Africa and the Northern Hemisphere were presumably not parts of the ancestral area for core monocots and commelinids.

DISCUSSION

The breakup of Pangaea commenced in the Mid-Jurassic 180–165 Mya with the separation of the northern and southern continents (Hallam 1994; McLoughlin 2001). North America and Eurasia were isolated by continental seaways in the Mid-Cretaceous 100–80 Mya (Sanmartin et al. 2001). Africa and South America also separated in the Mid-Cretaceous around 100 Mya (Scotese et al. 1988; McLoughlin 2001). South America and Australia remained connected via Antarctica well into the Tertiary and breakup of this connection took place in the Eocene around 50–35 Mya (Veevers et al. 1991; McLoughlin 2001). Glaciation of Antarctica did not begin until late Eocene and during the early Tertiary Antarctica enjoyed a habitable climate with widespread *Nothofagus* Blume forests (Anderson et al. 1999; Dingle and Lavelle 2000). The biogeographical timing of continental separations is somewhat uncertain because it is unclear when an effective dispersal barrier was established, and this also may differ for groups with different dispersal capabilities. Also, stepping-stone dispersal routes on oceanic islands between South America and Africa (Raven and Axelrod 1972) and across a habitable Antarctica between South America and Australia may have delayed biogeographical isolation into the late Cretaceous and the late Eocene, respectively. Nevertheless, it appears that the biogeographical separation of Africa and South America is about twice as old as the termination of the trans-Antarctic connection between South America and Australia (Hallam 1994; McLoughlin 2001).

The results from the TreeFitter analyses are in agreement with parts of the geological history. A strong correspondence is seen between the monocot tree and the comparatively late South America–Australasia sister area relationship, but not to the other area relationships displayed by the geological area cladogram. The trans-Antarctic connection apparently played an important role in monocot evolution. The results from the DIVA analysis reinforce this conclusion. DIVA optimization shows Australasia and/or South America at many deep nodes of the monocot tree, indicating that ancestors to major groups of monocots were restricted to either or both of these areas.

DIVA optimizations represent the most-parsimonious solutions for ancestral distributions, given the cost settings for vicariance, duplications, dispersals, and extinctions. There is no support method available to assess the strength of these optimizations compared to less-parsimonious alternatives, but the prevalence of Australasia and South America throughout most of the deeper nodes is in itself a strong indication for a South Gondwanan evolution of a majority of monocots. A possible error source is erroneous tree topology. Rearrangement of nodes lacking strong support (see Janssen and Bremer 2004) does not, however, change the general picture of a South Gondwanan evolution. One example is the stem node for Dioscoreales and their sister group of Pandanales + Liliales + Asparagales + commelinids. Rearranging this relationship such that Dioscoreales + Pandanales are sister to Liliales + Asparagales + commelinids (an equally parsimonious topology given the *rbcL* data) does not change DIVA optimizations in the monocot tree except inside Dioscoreales and Pandanales.

Given the DIVA optimizations and the age estimates for

the nodes of the monocot tree in Fig. 1, it is at least theoretically possible to identify possible vicariance events resulting from continental breakup. There is, however, no such obvious correspondence between a DIVA optimization specifying vicariance at any particular node, the age of which is roughly the same as a corresponding continental breakup, for example between Africa and South America around 100 Mya. The TreeFitter analysis indicates that there may have been several vicariance events involving the breakup of the trans-Antarctic connection between South America and Antarctica, but identification of these events requires analysis with more terminals (genera) resolving the basal phylogeny within the families. Such vicariance events have been hypothesized inside Liliales and Poales in previously published DIVA analyses of these orders (Vinnersten and Bremer 2001; Bremer 2002).

For monocots as a whole and for the phylogenetically basal Alismatales there are several alternative DIVA optimizations involving all five areas. This is due to the widespread distribution of several of the Alismatales members, many of which are water plants with apparently efficient dispersal capabilities. Hence, it is not possible to specify the ancestral distribution for monocots in general, or for Alismatales, from analysis of present distributions. Alternatively, we could interpret our results such that originally during the Early Cretaceous monocots, in general, and Alismatales, were widely distributed across the five continental areas, which at that time were connected in Laurasia and Gondwana.

Core monocots are, according to our results, an originally South Gondwanan group, first occurring in Australasia and/or in South America, and presumably also in Antarctica. The DIVA optimization has Australasia only at the crown node of core monocots (Fig. 1). There are alternative topologies for the interrelationships of the basal branches of core monocots, concerning the positions of Dioscoreales and Pandanales, but as noted above these alternatives do not affect the optimization for core monocots as a whole. Furthermore, there is such a dominance of Australasia and South America at the various deep nodes in the core monocot phylogeny that a South Gondwanan (that is, involving either or both of these areas) origin seems a plausible hypothesis. Alternatively, core monocots were originally widespread, as were monocots in general, and a subgroup comprising commelinids and their immediate sister groups Asparagales and Liliales were originally South Gondwanan in distribution.

Dioscoreales and Pandanales are mainly tropical groups, meaning that they are distributed in at least four of the five continental areas as circumscribed in the present analysis; not only Africa and South America comprise tropical regions, but also Eurasia with Southeast Asia and Malesia, and Australasia with New Guinea. Dioscoreales also have North American representatives, notably the mainly Northern Hemisphere Nartheciaceae. As for monocots in general, and for Alismatales, it becomes difficult to narrow down their ancestral distribution.

Liliales today have distinct groups with either a Northern Hemisphere or a Southern Hemisphere distribution, and in the analysis by Vinnersten and Bremer (2001) the ancestral area of Liliales could not be specified. African and South American subgroups do not attach at deep nodes of the Lil-

iales phylogeny, however, and with the Australasian ancestral distribution found for the related groups of Asparagales and commelinids, our DIVA optimization also indicates an Australasian ancestry for Liliales. Asparagales comprise many small families, with a Southern Hemisphere distribution, especially in Australasia, and this gives a DIVA optimization specifying an originally Australasian distribution for the order.

Commelinids are, according to our results, an originally South Gondwanan group. This ancestral area hypothesis is well supported due to the exclusive presence of South America and/or Australasia at all basal-most nodes of the commelinid phylogeny (Fig. 1). Givnish et al. (1999) came to a compatible conclusion with South America at the basal-most nodes of their commelinid phylogeny. Commelinales are, according to the DIVA results, originally Australasian. Zingiberales have all three southern continental areas at the crown node of the order in the DIVA optimization. The crown group of Zingiberales is much younger than the breakup of Africa from South America (but, see Kress et al. [2001], who suggest that Zingiberales may be older), so their presence in Africa must be interpreted as the result of dispersal from an earlier South Gondwanan distribution as is hypothesized for the common ancestor of Commelinales and Zingiberales (Fig. 1).

For Poales, the DIVA results also indicate North America as a possible ancestral area. This is apparently due to the deep attachment of Bromeliaceae, which have North American representatives, in the Poales phylogeny. The presence of North America at deep nodes of the Poales phylogeny, if real, must be due to dispersal from South America since Poales (and commelinids) are much younger than the Jurassic separation of North and South America. Excluding North America, our DIVA analysis indicates Poales originally to be distributed in South America or Australasia, or both. Bremer (2002), in a more detailed analysis of Poales, concluded that the order is South American in origin.

The above hypotheses on ancestral distributions for major groups of monocots should be possible to test by more extensively sampled analyses of all orders and of widely distributed families that attach at deep nodes of the tree, such as Araceae, Arecaceae, and Orchidaceae. With enlarged sampling and more precise knowledge about phylogeny and distribution of phylogenetically basal groups within the families, DIVA optimizations at the deep nodes of the monocot tree should be even more restricted to South America and Australasia, if major groups of monocots are South Gondwanan in origin, as is here proposed.

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