Systematics of *Dasyllirion*: Taxonomy and molecular phylogeny

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Abstract. The results of a systematic study in which *Dasyllirion* was fully monographed are reported. Sixteen species, including four new ones, were recognized. Data from chloroplast DNA restriction site analysis suggest that the species of *Dasyllirion* in southern Mexico are basal in the genus, that *Nolina parviflora* is particularly close to both *Dasyllirion* and *Beaucarnea*, and that *Calibanus* is closest to *Beaucarnea*. The phylogeny of *Dasyllirion* and the Agavaceae *sensu lato* was studied by comparison of cpDNA restriction sites and ITS rDNA sequences. The results strongly indicate that *Dasyllirion*, *Nolina*, *Beaucarnea*, and *Calibanus* are a monophyletic group that is closer to *Maianthemum*, *Polygonatum*, *Liriope*, *Dracaena* and *Sansevieria* than to *Yucca* and *Agave*. *Hosta* and *Camassia* are at the base of the branch leading to *Yucca* and *Agave*. The molecular data indicate that *Yucca whipplei* is more closely related to *Hesperaloe* than to other species of *Yucca*, and that *Agave dasyllirioides* and *A. striata* in the «Group Striatae» are basal to the rest of *Agave*. The resemblance of *Aloë* and *Xanthorrhoea* to the Agavaceae appears to be due to convergent evolution.

Key words : *Dasyllirion*, molecular phylogeny, Mexico, Nolinaceae, Taxonomy.

Resumen. Se realizó el estudio monográfico del género *Dasyllirion*. En esta revisión se reconocen 16 especies, incluyendo cuatro especies nuevas. El análisis de sitios de restricción del DNA de los cloroplastos (cpDNA) indica que las especies de *Dasyllirion* del sur de México son basales dentro del género, que *Nolina parviflora* está muy cercana a *Dasyllirion* y *Beaucarnea*, y que *Calibanus* está próximo a *Beaucarnea*. Se estudiaron las filogenias de *Dasyllirion* y de las Agaváceas mediante comparaciones del cpDNA y secuencias de la región ITS del rDNA. Los resultados indican claramente que *Dasyllirion*, *Nolina*, *Beaucarnea* y *Calibanus* se encuentran en un grupo que está más cercano a *Maianthemum*, *Polygonatum*, *Liriope*, *Dracaena* y *Sansevieria* que a *Yucca* y *Agave*. De la misma forma, *Hosta* y *Camassia* son basales a *Yucca* y *Agave*. Los datos moleculares indican que *Yucca whipplei* está más cercana a *Hesperaloe* que al resto de las especies de *Yucca*, y que *Agave dasyllirioides* y *A. striata* del «Grupo Striatae» son basales a las otras especies de *Agave*. La semejanza entre *Aloë* y *Xanthorrhoea* y las Agaváceas parecen deberse a la convergencia evolutiva.

Palabras clave : *Dasyllirion*, filogenia molecular, México, Nolinaceae, Taxonomía.

INTRODUCTION

Dasyllirion is a genus of 16 species found in rocky, arid regions of the southwestern U.S.A. and Mexico. It is dioecious and easily recognized by its dense rosettes of prickly leaves and long, narrow inflorescence stalks. It is commonly known as «sotol» and has been used for food, fiber, and the distillation of an alcoholic beverage also known as sotol. There have been few detailed studies of the taxonomy of *Dasyllirion* and consequently the identification of collections is often difficult. Although it is generally recognized that *Dasyllirion* is closely related to *Nolina*, *Beaucarnea* and *Calibanus*, it is not clear how these are related to *Yucca*, *Agave* and other members of the Agavaceae. Our research has focused on the taxonomy of species of *Dasyllirion* and the phylogenetic relationships of the species and the genus. In this paper we present a simplified overview of our results, the details will be published elsewhere. The first part is a general discussion of the genus with the results of a chloroplast DNA (cpDNA) restriction site study of the species of *Dasyllirion*. The second part presents the highlights of a cpDNA and ITS sequencing

study of the phylogenetic relationships of *Dasyllirion* and the Agavaceae *sensu lato*.

TAXONOMIC HISTORY OF *DASYLLIRION*

The original description of *Dasyllirion* (Zuccarini, 1838) was based on an assortment of leaf collections, garden specimens and species now placed in other genera. The status of *Dasyllirion* was clarified as more collections became available for study (Zuccarini, 1840). Although there was at one time some confusion about the status of *Nolina* and *Beaucarnea* (Hemsley, 1884), the distinctive marginal leaf prickles of *Dasyllirion* have made it easy to distinguish. Early efforts to monograph *Dasyllirion* were made by Baker (1872, 1881) and Watson (1879). Most of the early descriptions were based on only a few specimens and some of the characters are now known to be more variable than previously supposed. The most recent monograph of *Dasyllirion* was made by Trelease (1911), who recognized 15 species, including the six species which Trelease described. The genus has recently been monographed and the 16 species of *Dasyllirion*, including four new ones, recognized by Bogler (1994) are presented in Table 1.

TABLE 1. Species of *Dasyllirion* and new combinations recognized by Bogler (1994).

<i>D. serratifolium</i> (Karwinski ex Schultes) Zuccarini
<i>D. lucidum</i> Rose
<i>D. acrotriche</i> (Schiede ex Schultes) Otto
var. <i>parryanum</i> (Trelease) Bogler
var. <i>occidentalis</i> Bogler
<i>D. glaucophyllum</i> Hooker
<i>D. berlandieri</i> Watson
var. <i>palaciosii</i> (Rzedowski) Bogler
var. <i>longistylum</i> (MacBride) Bogler
<i>D. miquihuanensis</i> Bogler sp. nov.
<i>D. treleasei</i> Bogler sp. nov.
<i>D. quadrangulatum</i> Watson [= <i>D. longissimum</i>]
<i>D. simplex</i> Trellease
<i>D. gentryi</i> Bogler sp. nov.
<i>D. durangense</i> Trellease
<i>D. sereke</i> Bogler sp. nov.
<i>D. wheeleri</i> Watson ex Rothrock
<i>D. cedrosanum</i> Trellease
<i>D. leiophyllum</i> Engelman ex Trellease
var. <i>glaucum</i> (I.M. Johnston) Bogler
<i>D. texanum</i> Scheele

MORPHOLOGY OF *DASYLIRION*

Habit. All species of *Dasyllirion* are polycarpic perennials with rosettes of fibrous leaves from a short or elongate caudex. Flowering is terminal, with the apical meristem developing into the inflorescence. Growth continues sympodially from axillary buds near the apex. Branching of the rosette occurs if more than one axillary bud becomes active.

Trunks. Most species of *Dasyllirion* have a woody caudex that increases in length and width. In a few species the caudex does not seem to grow much above ground level, while in some species it may grow into an upright trunk 2 m in height with a corky periderm. In most species, however, the trunk is not very wide or strong, and in older plants the trunk tends to recline on the ground. The trunks are often supported and protected by a skirt of stiff, dead leaves.

Roots. The root system is fibrous and spreading. The roots have a very tough, sclerified endodermis surrounded by a thick cortex of parenchyma cells. Young plants have 2-3 large, fusiform roots that are apparently contractile. Older plants have a densely spreading root system.

Leaves. Leaf characters are very important in the classification of *Dasyllirion*. The leaves are very fibrous and drought resistant. They are usually dilated at the base into a wide «spoon,» which in some species is thickened and functions in storage. The blade is held in varying degrees of erectness. The surface of the leaf ranges from smooth to

strongly papillate-roughened. The leaves of some species have a coat of wax, which gives the leaf a blue-green or white aspect. The margins are lined with a row of sharp, usually forward-pointing prickles. The prickles are occasionally recurved or distinctively colored in some species. In a few species the prickles are greatly reduced in size or absent. The tip of the leaf occasionally dies back and splits into a mass of fibers.

Inflorescence. The inflorescence is a very distinctive feature of *Dasyllirion*. It is a narrow, compound, spike-like panicle with an elongate, bracteate peduncle that ranges from 1-6 m in length from base to tip. Flowers are borne in contracted fascicles of finger-like racemes arranged along the axis. There is a gradual transition from the leaves to the bracts of the inflorescence and a gradual reduction in the size of the bracts up the stalk. In most species the bracts are well separated and stramineous, but are occasionally densely overlapping and green or reddish colored. The fascicles of flowers are borne in the axils of the large inflorescence bracts. There is generally a more or less elongated central axis with a number of side branches. The number of branches varies with the position on the fascicle on the inflorescence. In some species it is much branched while in others there is a reduction to 3 or fewer branches.

Flowers. The individual flowers are borne in congested spirals along the branches of the fascicles. Each flower is borne in the axil of a small, membranous laciniate bract. Within this bract there may be one or two smaller bracts. The pistillate flowers are borne on a distinctly jointed pedicel. The receptacle is generally very small. There are six separate, elliptical or obovate tepals with weakly laciniate tips. The tepals are usually green or purple in color. There are six reduced, nonfunctional stamens opposite the tepals. The ovary is sharply 3-angled and has only one locule at maturity. Although there are initially six ovules, only one or rarely two ovules mature into seeds. There is a very short style with three weakly united stigma lobes. These stigma lobes form an open tube which closes shut after pollination takes place. Variation in the pistillate flowers involves primarily size differences in the tepals, style and stigma lobes.

The staminate flowers are borne on short, non-jointed pedicels and have a very short receptacle. There are six separate obovate tepals with weakly laciniate tips. The six stamens have glabrous filaments with exerted, dorsifixed and introrsely dehiscent anthers. There appears to be little variation in the staminate flowers of *Dasyllirion*.

Fruits. The mature fruit of *Dasyllirion* is hard to categorize. It is often described as an indehiscent capsule, but because it has only one seed it has also been called a nutlet (Dahlgren *et al.*, 1985). Since it also has three wings it has been called a samara. There is substantial variation in overall size, not only between species but sometimes within them as well. The length and shape of the wing lobes and the style notch have been frequently used to distinguish species of *Dasyllirion*. The seeds are trigonous, turbinate and golden brown. There is little variation in the seeds except with one species that has distinct lobed seeds.

Insect Visitors. There are many insect visitors to *Dasyllirion* (Bogler, 1994). The most common and abundant insects, and the ones that are probably responsible for most of the pollination, are small, short-tongued bees in the families Halictidae, Andrenidae and Colletidae. Most of these bees are generalists and have been associated with a variety of other plants. Larger bees, such as *Apis* and *Bombus* are also commonly found on *Dasyllirion*, as well as a variety of Syrphidae flies, Cleridae beetles, and Wasps. There is wood-boring beetle in the family Buprestidae which is often found on *Dasyllirion*, and its larvae develop inside of the inflorescence stalk.

CHLOROPLAST DNA RESTRICTION SITE VARIATION IN *DASYLIRION*

Evolutionary relationships between the species of *Dasyllirion* are not well known. About the only reference to this problem was made by Trelease (1911), who recognized two sections in his key. The larger section consists of all the species with flat leaves that have marginal prickles. The other section contains only one unusual species, *D. longissimum*, which has an enlarged upright trunk, quadrangulately thickened leaves and greatly reduced prickles. We have examined species relationships using molecular techniques and the results of our chloroplast DNA (cpDNA) restriction site analysis provide some evidence for subgeneric relationships. Although it was not possible to resolve all the species using cpDNA because of the low amount of variation present, the results correlate with some morphological characters and provide a foundation for future studies.

Methods. A cpDNA restriction site analysis of 37 populations of *Dasyllirion* and two species of *Nolina* was undertaken to try to resolve subgeneric relationships. The methods used in this study have been reported in Bogler and Simpson (1995). Populations for this study were selected from throughout the range of the genus and included all the known species. Total DNA extracts were prepared from frozen, powdered leaf material using 2X CTAB buffer. The DNA was digested with 12 restriction enzymes, run on agarose gels to separate the fragments and transferred to nylon membranes. The cpDNA fragments were visualized by hybridization with 25 labeled tobacco cpDNA probes followed by autoradiography (Bogler, 1994).

Results. In general the level of restriction site variation within *Dasyllirion* was low, which is not uncommon in woody, long-lived plants. However, 24 variable sites were found, 19 of which were synapomorphic. These data were used to analyze phylogenetic relationships in *Dasyllirion* using Hennig86 (Farris, 1988). Three trees were found with a length of 29 steps, a Consistency Index of 0.82 and a Retention Index of 0.92. One of these trees is presented in Figure 1.

Discussion. Although the levels of cpDNA variation in *Dasyllirion* were low, there was enough to resolve several

well defined groups. There seems to be strong geographic component to the distribution of restriction site mutations. The most interesting result of this study is a restriction site that is shared by *Nolina* and a group of species of *Dasyllirion* from southern Mexico, *D. serratifolium*, *D. lucidum* and *D. acrotriche*. The cpDNA data indicate that this group is separate from and perhaps basal to the other species found in northern Mexico and the U.S.A. These species typically have no wax on their leaves and have a distinctive «brushy» leaf tip.

Several restriction site mutations support a clade containing populations of *D. wheeleri* from Texas, New Mexico, Arizona and two populations from Sonora. One of these populations we recognize as *Dasyllirion gentryi*, which occurs in the Rio Mayo region and is recognized by its very large, rose colored fruits and glabrous leaves. Although *D. durangense* and *D. cedrosanum* have waxy leaves like *D. wheeleri*, they appear on separate clades. *Dasyllirion durangense* shares a restriction site mutation with *D. simplex*, a dwarfish species with a clump-like habit and reduced flower fascicles. *Dasyllirion cedrosanum* is the name given to a complex of waxy-leaved populations from Coahuila and Zacatecas. Both the cpDNA and morphological evidence indicates that hybridization of *D. cedrosanum* with surrounding species has occurred.

Another clade contains a complex of species from southwestern Texas and Coahuila. This group includes *D. leiophyllum*, *D. stewartii* and *D. stewartii* var. *glaucum* which have recurved leaf prickles, and three populations of *Dasyllirion* with mixed prickle curvature and waxy leaves. After careful examination of the herbarium material, it was concluded that there was very little reason to separate *D. stewartii* and *D. heteracanthum* from *D. leiophyllum*, and that the waxy leaves of *D. stewartii* var. *glaucum* are probably the result of introgressive hybridization with nearby populations of *D. cedrosanum* to the south. There is some evidence that *D. leiophyllum* and *D. texanum* are closely related and hybridize in west Texas. The population of *D. texanum* from near Austin, Texas, appears to be isolated in terms of cpDNA restriction sites.

Several species from northeastern Mexico and the Sierra Madre Oriental, *D. berlandieri* and *D. longissimum* appear to be related to some extent, but the cpDNA evidence is rather weak. *Dasyllirion longissimum* is a peculiar species with large upright trunks, quadrangulately thickened leaves lacking prickles and massive inflorescences. Two populations of *D. longissimum* were included in this study, one from Tamaulipas and the other from Hidalgo. However, these two populations are not united by any cpDNA synapomorphies, and the one from Hidalgo has a unique mutation. It turns out that there are actually two species represented here which differ in morphological characters and bloom at different times of the year. The new species, *D. treleasei* which occurs in San Luis Potosi and Hidalgo also has flatter, more prickly leaves and an inflorescence that is more like other species of *Dasyllirion*. In our monograph we use the more clearly

FIG. 1. One of three most parsimonious trees obtained from analysis of 24 cpDNA restriction sites in *Dasyliiron*. Length 29 steps, Consistency Index 0.82, Retention Index 0.92. Black boxes indicate non-homoplasious restriction site mutations, white boxes are homoplasious. Voucher numbers and collection localities follow taxon names.

defined name *D. quadrangulatum* for the populations of *D. longissimum* in Tamaulipas and Nuevo Leon.

Although *D. longissimum* looks very different at first sight, its flowers and fruits are similar to the rest of the genus. The presence of rudimentary prickles at the base of its leaves suggest it evolved out of a flat-leaved ancestor that had prickles. The cpDNA indicates a connection between *D. berlandieri* and *D. longissimum*, possibly through an intermediate taxon from near Miquihuana, Tamaulipas. This taxon, which we are calling *D. miquihuanensis*, is large and has very erect, prickly leaves that are somewhat quadrately thickened as in *D. longissimum*. Possible hybrids between this taxon and *D. berlandieri* have been seen. Although *D. berlandieri* is distinct from other species in many respects, with its droopy leaves, club-shaped inflorescences, green bracts and very large fruits, the populations are not well resolved by the cpDNA data. There is at least some support for a relationship between *D. berlandieri* and *D. palaciosii*, which are very similar and considered a single species.

GENERIC RELATIONSHIPS OF *DASYLIRION*

Several viewpoints concerning the phylogeny and family classification of *Dasyllirion* have been advanced. Hutchinson (1934) and Cronquist (1981) favored a close relationship between *Dasyllirion*, *Nolina*, *Beaucarnea* and *Calibanus* with *Agave* and *Yucca*, and included all these taxa in the Agavaceae (*Agavaceae sensu lato*). Other systematic treatments (Dahlgren *et al.*, 1985) place *Dasyllirion* and its allies in a separate family, the Nolinaceae, and restrict the Agavaceae to just *Yucca* and *Agave* and their closest allies (*Agavaceae sensu stricto*). The situation is somewhat confusing because both systems are in use at the present time.

The morphological evidence suggests that the closest relatives of *Dasyllirion* are *Beaucarnea*, *Nolina* and *Calibanus*. These genera all have similar xeromorphic features, relatively small flowers and dry, often winged fruits with 1-3 light brown seeds. They are nearly all dioecious and most have a chromosome number of $n=19$. They are pollinated mainly by a number of small bees. The Nolinaceae are usually placed near *Dracaena*, which differs in having baccate fruits. Although *Yucca* and *Agave* might be considered to resemble the Nolinaceae in having fibrous leaves and often woody habit, they differ in most other respects. *Yucca*, *Agave*, and their allies generally have large, fleshy, perfect flowers adapted for pollination by a variety of large bees, moths, hummingbirds and bats. The fruits are mostly dehiscent, many seeded capsules. The seeds of *Yucca* and *Agave* are black and strongly flattened. The chromosome of these taxa is $n=30$, or multiples of 30 in some *Agave*. The karyotype of these genera is very distinctive, with 5 large chromosomes and 25 small ones (Granick, 1944).

A number of other taxa in the Liliaceae *sensu lato* have at various times been placed near *Dasyllirion* or *Yucca* and *Agave*. *Dasyllirion* and other Nolinaceae are considered

close to the baccate-fruited *Dracaena*, which has often been associated with *Sansevieria*. Other baccate taxa in the Liliaceae *sensu lato* include *Maianthemum*, *Polygonatum*, *Liriope* and *Asparagus*. Based on the similarity of their karyotypes, *Hosta* has sometimes been considered near *Yucca* and *Agave* (Tahkajan, 1980). Other woody lilioid taxa such as *Aloë* and *Xanthorrhoea* have sometimes been considered close to the *Dasyllirion* or the Agavaceae, but whether the woody habit has arisen once in these taxa or several times is not at all clear. Recently, some progress has been made by the analysis of *rbcL* sequences in the Agavaceae and Asparagales (Eguiarte *et al.*, 1994). Their results indicate that there are several major lineages in this group of taxa and provide support for a narrow interpretation of the Agavaceae. We have found additional support and resolution using cpDNA restriction site analysis (Bogler and Simpson, 1995) and ITS rDNA sequencing (Bogler *et al.*, in press).

CHLOROPLAST DNA RESTRICTION SITE VARIATION IN THE AGAVACEAE

Methods. An analysis was made of chloroplast DNA (cpDNA) restriction site variation in 40 taxa in the Agavaceae *sensu lato*. Detailed procedures are presented in Bogler and Simpson (1995). Total DNA was extracted from frozen tissues using 2X CTAB buffer. The DNAs were digested with 12 restriction enzymes. The fragments were separated on agarose gels, transferred to nylon membranes and hybridized with 25 radioactively labeled probes made from known tobacco cpDNA templates. Partial restriction site maps were constructed from the autoradiograms and 110 informative restriction sites were selected for phylogenetic analysis with PAUP (Swofford, 1993) and Hennig86 (Farris, 1988).

Results. Heuristic analysis with the characters treated as unordered resulted in 44 equally parsimonious trees of 170 steps, a Consistency Index of 0.64 and a Retention Index of 0.91. A consensus of these trees is presented in Figure 2.

Discussion. The result of this study provide strong additional evidence that there are two major clades in the Agavaceae *sensu lato*. However, the cpDNA data also indicate that the lineage containing *Dasyllirion* and *Dracaena* is much closer to the Convallariaceae than previously thought. In addition, the cpDNA data support the association of *Hosta* to *Yucca* and *Agave*, as the similarity of their karyotypes suggests. This observation has implications for the family classification of the Agavaceae *sensu lato*. Since *Dasyllirion* appears to be closer to genera such as *Liriope* and *Maianthemum*, then it really is not appropriate to view *Dasyllirion* as a member of the Agavaceae in the sense of Cronquist (1981). Instead, the cpDNA supports the view that *Dasyllirion*, *Nolina*, *Beaucarnea* and *Calibanus* should be considered in a family apart, the Nolinaceae *sensu* Dahlgren *et al.* (1985). The bootstrap values for these lineages are very high.

The cpDNA data also indicate a number of other interesting relationships. In the Nolinaceae, *Beaucarnea*

FIG. 2. Strict consensus of 44 trees obtained from analysis of 110 cpDNA restriction sites in the Agavaceae and related families. Length 170 steps, Consistency Index 0.64, Retention Index 0.91. Black boxes indicate non-homoplasious cpDNA restriction site mutations, white boxes are homoplasious. Bootstrap values from 100 replications are shown below the branches. Family names follow Dahlgren *et al.* (1985).

FIG. 3. Strict consensus of 4 trees obtained by analysis of combined ITS1 and ITS2 rDNA sequence data sets in the Agavaceae and related families. Length 979 steps, Consistency Index 0.659, Retention Index 0.815. The numbers above the branches are the number of shared base substitutions, those below the branches are bootstrap values obtained from 100 replications. Family names follow Dahlgren *et al.* (1985).

and *Calibanus* are evidently closely related to each other. Although *Nolina* is most likely basal to the other genera, it appears that *N. parviflora* is more closely related to both *Dasyllirion* and *Beaucarnea*. In the Agavaceae *sensu stricto* it appears that *Yucca whipplei* is more closely related to *Hesperaloë* than it is to other species of *Yucca*, a result which has implications for the interpretation of the pollination biology of *Yucca* (Bogler *et al.*, in press). Relatively low levels of cpDNA variation were found within *Agave* and genera such as *Manfreda*, *Polianthes* and *Prochnyanthes*, indicating that these genera are very closely related.

ITS RIBOSOMAL DNA SEQUENCE VARIATION IN THE AGAVACEAE

Methods. Relationships between these taxa were further studied using ITS rDNA sequences. For the sequencing study we included the same taxa as the cpDNA study plus a few additional outgroups. The internal transcribed spacers (ITS1 and ITS2) of the 26S-5.8S-18S nuclear ribosomal DNA region were amplified by PCR, sequenced using a direct, double stranded technique and optimally aligned using PILEUP in the GCG (1994) package (Bogler, 1994; Bogler *et al.*, in press). These sequences have been deposited in Gen Bank. The aligned sequences were analyzed using PAUP (Swofford, 1993).

Results. Sequence length in the Agavaceae *sensu stricto* was about 250 bp in ITS1 and 211-239 bp in ITS2. The ITS1 and ITS2 sequences were aligned and the matrices were analyzed with PAUP, both separately and combined together. In general, the phylogenetic analyses of ITS1 and ITS2 produced trees that were congruent in the major lineages found. Analysis of a combined data set results in 4 equally parsimonious, well resolved trees with 979 steps and a Consistency Index of 0.659. A strict consensus of these 4 trees is shown in Figure 3.

Discussion. The ITS sequence data strongly support the existence of two major lineages, one with *Dasyllirion* and its allies in the Nolinaceae, Dracaenaceae and Convallariaceae and the other with the Agavaceae *sensu* Dahlgren *et al.* (1985). *Nolina* is at the base of the clade leading to both *Dasyllirion* and *Beaucarnea*, which is closely related to *Calibanus*. One interesting result was that *Camassia* appears to be closely related to *Yucca* and the Agavaceae *sensu stricto*. The sequence data also indicates a close relationship between *Yucca whipplei* and *Hesperaloë*. It appears that *Agave dasyliroides* and *A. striata* in the Group Striatae, which was thought to be primitive in the genus by Gentry (1982), are indeed on a separate and basal lineage from the other species of *Agave* examined here. The ITS sequence data indicate that *Cordylina*, *Aloë* and *Xanthorrhoea* are not closely related to the Agavaceae.

From these phylogenetic studies we conclude that *Dasyllirion* and related genera in the Nolinaceae belong to a lineage that is distinct from *Yucca* and *Agave*. The lineage which contains the Nolinaceae also includes the Dracaenaceae

and Convallariaceae. Our results strongly support a narrow interpretation of the Agavaceae.

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